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SID 5 Research Project Final Report

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Project identification

1. Defra Project code: BD1624
2. Project title: Comparison of new and existing agri-environment scheme options for biodiversity enhancement on arable land
3. Contractor organisation(s): NERC Centre for Ecology and Hydrology
4. Total Defra project costs (agreed fixed price): £ 240,000
5. Project: start date .... 01 April 2003
   end date 31/03/2007

6. It is Defra's intention to publish this form.
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(b) If you have answered NO, please explain why the Final report should not be released into public domain

Executive Summary

7. The executive summary must not exceed 2 sides in total of A4 and should be understandable to the intelligent non-scientist. It should cover the main objectives, methods and findings of the research, together with any other significant events and options for new work.

1. A multi-site experiment was conducted on six arable farms in eastern England for 5 years to investigate the effectiveness of new agri-environment scheme options for conserving and enhancing a broad range of taxa and ecosystem functions;
2. The six treatments varied in the degree of management intervention from growing a cereal crop with restricted use of pesticide to complete removal of land from production and either allowing natural regeneration of vegetation or sowing seed mixtures which included: seed-bearing crops, tussocky grasses, pollen-and nectar-rich forbs, and fine-leaved-grasses and forbs. All treatments were compared with a conventional cereal crop control;
3. Residual soil fertility in the non-cropped field margins remained as high as the cropped land despite 5 years of cutting and removal of vegetation in the absence of fertiliser input. However, it was possible to establish and maintain a diverse mixture of wildflowers on this fertile soil and this resulted in a significant (25%) increase in soil carbon as measured by loss on ignition compared with the cropped treatments;
4. Diversity of plant species was highest in the sown wildflower margins and this was maintained throughout the study. However, annual cultivation of the field margin was the only treatment to promote the diversity of declining arable plants;
5. Bumblebee abundance was significantly higher (×14) in margins sown with pollen- and nectar-rich species compared with all other treatments for the first 3 years only. Diversity of rare bees was also higher in this treatment. After year 3 there was a marked decline in the abundance bee forage plants and a corresponding increase in grass cover. Bee abundance and species richness was significantly higher in the wildflower margins compared with the other treatments throughout the experiment;
6. Butterfly abundance and diversity was highest in the wildflower, and pollen and nectar margins compared with the other treatments throughout the experiment;
7. Abundance and diversity of soil macro invertebrates was significantly higher in the non-cropped margin treatments sown with perennial seed mixtures compared with the cultivated treatments. Abundance of earthworms was 50% higher in these undisturbed, perennial margins;
8. Abundance of soil surface active detritivores was significantly higher in the non-crop margins compared with the cropped treatments in both autumn and spring. Seed predators were more abundant in the natural regeneration margins in the autumn. Richness and abundance of all invertebrates was significantly lower in the tussocky grass margins compared with all other treatments in the spring, probably reflecting lower activity;
9. Diversity of canopy-active invertebrates caught by both suction and sweep net sampling was

significantly higher in the wildflower margins compared with all other treatments. Diversity was also higher in the other non-crop margins compared with the crop. Total abundance of invertebrates was higher in non-cropped margins compared with the crop treatments. This reflected a greater abundance and diversity of detritivores, herbivores and pollinating insects. In contrast, abundance of predatory (beneficial) invertebrates was significantly higher in the tussocky grass and wildflower margins;

10. Abundance of farmland bird indicator species in winter was significantly higher in the field centre patches sown with seed bearing crops compared with the adjacent crop. However, the magnitude of these differences declined considerably after the December visit each year as seed resources diminished. There was also evidence of a marked decline in the quality of this habitat after year 3;
11. Small mammal activity was significantly higher in the patches sown with wild bird seed mixture compared with the crop and field margin during the winter months. However, this pattern of utilisation was reversed in the summer;
12. *Synthesis and applications*: removal of land from arable production was a more practical and effective means of enhancing biodiversity and ecosystem functions than extensification of management practices. Creation of species-rich field margin vegetation resulted in significant beneficial effects for the widest range of taxa and functions both above- and below-ground. Management prescriptions specifically targeted to the requirements of declining taxa were generally more effective than those designed to deliver a broader range of environmental benefits. However, the benefits delivered by two of these 'targeted' prescriptions (pollen and nectar and wild bird seed mixtures) were short-lived and did not persist in after year 3. Such habitats will require frequent re-establishment in new locations.

Project Report to Defra

8. As a guide this report should be no longer than 20 sides of A4. This report is to provide Defra with details of the outputs of the research project for internal purposes; to meet the terms of the contract; and to allow Defra to publish details of the outputs to meet Environmental Information Regulation or Freedom of Information obligations. This short report to Defra does not preclude contractors from also seeking to publish a full, formal scientific report/paper in an appropriate scientific or other journal/publication. Indeed, Defra actively encourages such publications as part of the contract terms. The report to Defra should include:

- the scientific objectives as set out in the contract;
- the extent to which the objectives set out in the contract have been met;
- details of methods used and the results obtained, including statistical analysis (if appropriate);
- a discussion of the results and their reliability;
- the main implications of the findings;
- possible future work; and
- any action resulting from the research (e.g. IP, Knowledge Transfer).

Project aims and objectives

The aim of this project is to compare the effectiveness of new and existing agri-environment scheme prescriptions for the enhancement biodiversity on arable land.

1. Establish a multi-site, replicated experiment comparing the following AE scheme options with a conventionally managed crop: (i) conservation headland; (ii) natural regeneration margin; (iii) tussocky grass margin; (iv) grass and wildflower margin; (v) pollen and nectar seed mixture; (vi) seed-bearing crops for farmland birds.
2. Examine the effects of these options on the abundance and diversity of a wide range of plant and animal groups;
3. Transfer these findings to Natural England project officers and the farming community through organised training events held at the different sites.

All of the project aims and objectives have been met in full.

Introduction

Intensive agricultural practices have highly detrimental impacts on biodiversity (e.g. Tapper & Barnes 1986; Sutcliffe & Kay 2000; Donald 2001; Robinson & Sutherland 2002; Steffan-Dewenter *et al*. 2005). Indeed, within certain taxa, such as birds (Gregory, Noble & Custance 2004) and plants (Preston *et al*. 2002), the fastest declining species in the UK over the last few decades have been those associated with farmland. The two primary drivers for this are, firstly the trend for simplified cropping systems applied to increasingly consolidated land parcels leading to loss of non-crop habitat, such as hedgerows and ponds; and secondly, the intensification of management practices within the cropping systems themselves, including the increased use of pesticides and fertilisers, and shorter fallow periods (Stoate *et al*. 2001). The resultant loss of species and habitats, together with the associated pollution and eutrophication may also serve to perturb key ecosystem functions, including pollination, natural regulation of pest species, carbon sequestration and soil nutrient cycling (Hector & Bagchi 2007).

The UK Entry Level Stewardship (ELS) agri-environment scheme (Anon. 2005) recognises that the impacts of modern agriculture on biodiversity and ecosystem function can be mitigated through approaches which either decrease the intensity of agricultural management on farmed land ('extensification') or protect areas from intensive farming practices (Bignal 1998). There is now a large body of research on the effectiveness of these different management strategies for conserving different taxa (reviewed by Marshall & Moonen 2002; Vickery *et al*. 2004). However, considerably less is known about their effectiveness in promoting key ecosystem functions and services. On arable farmland in the UK the most popular means of enhancing biodiversity by extensification of management is through conservation headlands (Stevenson 2007) which are cereal field margins (usually about 6 m wide) which are selectively sprayed with pesticides (Sotherton 1991). This approach has proved to be beneficial to broad-leaved annual plants (Wilson 1990), butterflies (Dover 1997), bumblebees (Kells, Holland & Goulson 2001) and birds (Rands 1995). The most popular means of protecting biodiversity by removal of land from production is by creating tall grassy strips at the field margin (Stevenson 2007). This dense, sheltered vegetation is known to provide important habitat for hibernating carabid and staphylinid beetles, spiders, small mammals, nesting bumblebees and certain breeding birds (e.g. Smith *et al*. 1993; Thomas *et al*. 1992; Collins *et al.*, 2003a,b; Kells & Goulson 2003; Shore *et al*. 2005; Pywell *et al*. 2005a). Similarly, research has shown that sowing non-crop field margins with perennial wildflowers can significantly enhance their value for butterflies, bumblebees, honeybees, hoverflies and other invertebrates (e.g. Lagerlöf *et al.* 1992; Feber *et al.* 1996; Meek *et al.* 2002; Carvell *et al*. 2004; Pywell *et al*. 2005b).

More recent prescriptions have been specifically developed to address the requirements of declining farmland taxa. One of the most popular of these 'targeted' prescriptions involves sowing mixtures of seed-bearing crops to supplement the over-winter food supply for declining farmland birds to counter winter mortality (Stoate *et al*. 2004; Bradbury *et al*. 2004). Similarly, research has shown that sowing field margins with simple mixtures of pollen- and nectar-rich legume species is a cost-effective means of providing late-summer foraging habitat for bumblebees (Carvell *et al.* 2007; Pywell *et al*. 2006). Finally, uncropped, annually cultivated margins have proved an effective means of conserving populations of declining arable plant species (Walker *et al*. 2007).

To date there has been few detailed comparative study of these different approaches to the enhancement of biodiversity on arable land promoted under the agri-environment schemes (Kleijn & Sutherland 2003). In this study we present the results of a multi-site experiment which compares the effects of six widespread crop and field margin management strategies on a broad range of taxa and ecosystem functions over five years. This enabled us to test the following hypotheses:

H1: Extensification of arable land management results in greater biodiversity, and a more efficient delivery of a wider range of ecosystem services. However, complete removal from crop production (i.e. protected wildlife areas) is a more practical and effective means of enhancing biodiversity and delivering these key functions and services;

H2: Management prescriptions specifically targeted to the requirements of declining taxa are more effective than those designed to deliver a broader range of environmental benefits;

H3: The positive effects of management prescriptions on different taxa are reproducible over a wide variety of locations and soil types, and these patterns persist or strengthen over time;

H4: Soil biodiversity is positively correlated to increases in above-ground biodiversity, and has a potentially important impact on ecosystem function; and,

H5: Sowing seed mixtures to create species-rich vegetation on land removed from production will result in the greatest increases in trophic complexity in above- and below-ground food webs.

The results are discussed in the context of (i) the ecological role of the different habitats in the conservation of a range of taxa, and (ii) the implications for future agri-environment scheme policies aimed at the enhancement of biodiversity on farmland.

Methods

STUDY SITES AND EXPERIMENTAL TREATMENTS

The experiment was conducted at six sites across central and eastern England on a range of soils (Fig. 1): clay at Abbots Hall, Essex (51°48'N, 0°51'E), sandy loam (over chalk) at Whittlesford, Cambridgeshire (52°6'N, 0°07'E), calcareous clay at Colworth, Bedfordshire (52°15'N, 0°35'W), sandy loam at Little Wittenham, Oxfordshire (51°38'N, 1°12'W), clay with flints (over chalk) at Marlow, Buckinghamshire (51°36'N, 0°48'W), and variable loam at Westow, Yorkshire (54°5'N, 0°49'W). In September 2001 six contiguous plots, each measuring 50 m long and 6 m wide, were established along the east- and west-facing margins (replicates) of the same arable field at each site. Each margin was situated adjacent to a hedge typically 2 m high. Experimental treatments representing one of five ELS field margin management prescriptions (Anon. 2005; Appendix 1, Table 1) were assigned to plots at random, with the exception of the crop and conservation headland which were assigned randomly to either end of each replicate to enable farming operations. In addition, a rectangular, field centre patch of 0.3 ha was sown each spring with a mixture of four seed-bearing crop species to provide winter food resources of declining farmland bird species.

The control treatment was a winter-sown cereal (wheat, barley or oats) grown with conventional inputs of fertiliser and pesticide. Broad-leaved break crops of oilseed rape, peas or sugar beet were grown on just 6 occasions on four sites over the six years of the project (see Appendix 2 for full details). Data for the crop and conservation headland treatments were excluded from the analyses for specific sites in break crop years. The conservation headland treatment comprised growing a cereal crop without application of insecticides and only selective herbicides (Sotherton 1991). This was to allow populations of broad-leaved plants and their associated insects to develop which provided food for farmland birds and benefited declining arable plant species. The remaining treatments required the complete removal of land from arable production to create a range of protected wildlife habitats. The least interventionist of these was natural regeneration of vegetation from the seed bank and hedge bottom. This treatment was cut and lightly cultivated (to a depth of *c.* 15 cm) each autumn to maintain an open vegetation community dominated by annual species which provided habitat for invertebrates and food resources for seed-eating birds. In the remaining treatments seed mixtures were sown to direct succession to a desired end-point. The simplest of these involved sowing a low cost mixture of six fine- and broad-leaved grass species at 20 kg ha^{-1} (£60 ha^{-1}; €70 ha^{-1}) to created tall, dense tussocky grass strip (see Appendix 3 for seed mixture). This vegetation was cut in the establishment year to control volunteer crops and undesirable species, but subsequently unmanaged. This treatment had a number of aims, including protection of boundary features against pesticide and fertiliser drift, provision of overwintering habitat for invertebrates, nesting sites for bumblebees and habitat for small mammals, and supply of food resources for seed-feeding birds. The pollen and nectar seed mixture comprised sowing four agricultural varieties of legumes with three fine-leaved grass species at 20 kg ha^{-1} (£90 ha^{-1}; €111 ha^{-1}) specifically designed to provide mid- to late-season foraging resources for pollinating insects, particularly bumblebees and butterflies (Carvell *et al*. 2007; Pywell *et al*. 2006). The wildflower treatment required sowing 21 species of native forbs comprising a range of functional types with three fine-leaved grass species at 37.2 kg ha^{-1} (£891 ha^{-1}; €1098 ha^{-1}) to provide vegetation with both a diverse structure and composition for the widest range of invertebrate species. Finally, in the spring of each year a mixture of four annual seed-bearing crops was sown at 7.5 kg ha^{-1} (£50 ha^{-1}; €62 ha^{-1}) in the field centre wild bird seed (WBS) mixture plots to provide late winter food resources for seed-eating birds.

In the establishment year the sown habitats were managed by cutting and removal of herbage in May and September to reduce competition from crop volunteers and other undesirable species. In subsequent years the pollen and nectar and wildflower treatments were always cut and removed in September with an occasional cut in April if required. In addition, at two sites in the first year a graminicide (Fusilade Max: fluazifop-P-butyl) was applied at half rate (0.8 l in 200 l of water ha^{-1}) to the pollen and nectar and wildflower margins to reduce competition from the annual grass weeds, *Anisantha sterilis* and *Alopecurus myosuroides*. Mollusc herbivory in the sown treatments was reduced by two applications of baited pellets containing 4% w/w metaldyhyde at 7.5 kg ha^{-1} at four sites on heavy soil in the spring of year 1. Similar applications were made to the WBS mixture patches in the spring at three sites on heavy soil. Other invertebrate pests, particularly flea beetles (*Phyllotreta* spp.) (Coleoptera: Chrysomelidae) and pollen beetles (*Meligethes aeneus*) (Coleoptera: Nitidulidae), were controlled in the WBS patches by one or two applications of synthetic pyrethroid pesticide during the spring and summer (following recommendations from BD1623). This typically comprised the application of EC 100 g l^{-1} cypermethrin A.I. applied at 250 ml ha^{-1} or EC 240 g l^{-1} tau-fluvalinate A.I. applied at 200 ml ha^{-1} (BD1623).

MONITORING

Soil nutrients

In January 2006 four soil cores (150 mm deep × 70 mm wide × 140 mm long) were collected using a spade along a zig-zag transect through the centre of each plot, avoiding a 1 m buffer around the edge. The cores were bulked, thoroughly mixed for each plot and analysed for Olsen extractable phosphorous (P), exchangeable potassium (K), magnesium (Mg) and total nitrogen (N%) using standard methods (Allen *et al*. 1974; MAFF 1986). At the same time 10 soil cores were collected in the same zig-zag pattern from each plot to a depth of 100 mm using a 20 mm diameter gouge auger. Each core was divided into two depth fractions (0-5 cm and 6- 10 cm) and placed into separate polythene bags. Samples for each plot and depth fraction were bulked and thoroughly mixed. Total carbon content was estimated by loss on ignition (%LOI) in the muffle furnace at 375°C for 16 hours (Allen *et al*. 1974).

Vegetation composition and structure

Between late June and early July of each year vegetation composition of each treatment was recorded from five 1 × 1 m quadrats placed at random in each plot, avoiding a 1 m edge buffer. Percentage cover of all vascular plant species and bare soil was estimated as a vertical projection. Finally, cover abundance of all species present in the treatment plot was estimated each year using the DAFOR score (Kershaw & Looney 1985). Plant nomenclature followed Stace (1997).

Height and structure of the vegetation was recorded from ten drop disk measurements (diameter 300 mm, weight 200 g) (Stewart, Bourn & Thomas 2001). Both mean sward height and the variation in sward height as expressed by standard deviation of the mean were calculated. Finally, drop disk measurements were used to estimate vegetation production (g m^{-2}) in each treatment using a simple linear regression model developed from a grassland restoration experiment sown with similar species at Little Wittenham, Oxfordshire (51°38'N, 1°12'W) (Coulson *et al*. 2001). In this study a highly significant relationship was found between mean biomass (based on five 40 × 40 cm quadrats) and mean vegetation height (based on 20 drop disks 300 mm diameter, 200 g), namely biomass m^{-2} = 23.53 + 14.14 Sward ht (cm); $F_{1,19}$ = 16.56; P<0.001; R^2 = 48%; *R.F.Pywell unpublished data;* see Appendix 4 for details).

Flower resources

The forb flower resource was estimated for each treatment plot (excluding the WBS plots) following each bumblebee and butterfly transect count. All flowering forbs were first identified to species and the approximate abundance of single flowers and multi-flowered stems (racemes, corymbs, e.g. *Trifolium pratense*; capitulums, e.g. *Centaurea nigra*; umbels, e.g. *Daucus carota*) was scored using a simple floristic index (Carvell *et al*. 2004; Pywell *et al*. 2005b, 2006): 1. Rare (approx. 1 – 25 flowers per 300 m^2 plot); 2. Occasional (approx. 26 - 200 flowers); 3. Frequent (approx. 201 - 1000 flowers); 4. Abundant (approx. 1001 - 5000 flowers); 5. Super-abundant (more than 5001 flowers).

Pollinator transects

The abundance and diversity of bumblebees and butterflies were recorded from transect walks through the centre of each field margin plot (excluding WBS mixture plots) on between seven and nine occasions between May and September each year (Banaszak 1980; Pywell *et al*. 2005b). Walks were carried out between 10.00 am and 17.00 pm when weather conditions conformed to the Butterfly Monitoring Scheme (BMS) rules (temperature above 13°C with at least 60% clear sky, or 17°C in any sky conditions; no count at all if raining) (Pollard & Yates 1993). The shade (ambient) temperature, percentage sunshine and wind speed were recorded at the end of each transect walk. Butterflies and foraging bumblebees were recorded to species level across the entire plot width. In addition, bees were further sub-divided into caste where possible (following Prŷs-Jones & Corbet 1991). Voucher specimens of rare species were collected for verification. Workers of *Bombus terrestris* and *B. lucorum* were collectively recorded as these cannot be reliably distinguished in the field. The cuckoo bumblebees (subgenus *Psithyrus* sp.), which are brood parasites of true *Bombus* species, were counted together as a group for analysis, but honeybees and solitary species were not noted. The flowering plant each bee was first seen to visit was also recorded to species level.

Soil invertebrates

In January 2006 four soil cores (150 mm deep × 70 mm wide × 140 mm long) were collected using a spade along a zig-zag walk through the centre of each plot. Each core was stored in a sealed and labelled polythene bag at 3°C prior to sorting. Cores were placed in a warm room (18°C) for 12-18 hours prior to sorting to encourage invertebrate activity and therefore increase the probability of catching individuals by hand sorting. Each core was placed into large, deep tray and broken up by hand (Thomas *et al.* 1992). The fragments of soil and vegetation were thoroughly searched for invertebrates for a fixed period of ten minutes. All invertebrate species were counted and identified to phyla, order or sub-order level with the exception of Coleoptera which were identified to family level.

Soil surface active invertebrates

The activity and density of soil surface active invertebrates was recorded using pitfall traps (8 cm diameter × 11 cm deep plastic cups) sunk into the ground with the top level with the soil surface (Luff 1996). Each trap was one-third filled with a preservative solution of propylene glycol diluted 1:1 with water. Rain shelters (12 cm diameter) were placed over each trap to prevent flooring. Eight traps were set at 5 m spacing placed along the centre line of each plot. Traps were opened for 22 days between late April and May, and again between early and late October each year. All traps from each plot were combined and contents counted and identified to the appropriate taxonomic level under a microscope. Nomenclature followed Luff & Duff (2001) for Carabidae, Lott & Duff (2003) for Staphylinidae, and Roberts (1993) for Araneae.

Canopy active invertebrates

The abundance and diversity of canopy active invertebrates were sampled in each plot in early July of each year from 2003 onwards using two complementary approaches (Standen 2000). Sampling was undertaken between 10.00 am and 17.00 pm when the vegetation and soil were dry. Firstly, a sample was collected using a Vortis™ suction sampler (www.burkard.co.uk) (Arnold 1994). Each sample comprised nine 10-s 'sucks' collected in a zig-zag pattern through each plot (avoiding a 1 m edge buffer), giving a total sample area of 0.174 m^2. Secondly, a standard sweep net of 0.46 m diameter with a 0.7 m handle was vigorously swept through the vegetation canopy along the centre line of each plot. Sampling was undertaken by the same individual on all occasions. One sample unit comprised 35 strokes of approximately 1 m width at 1 m intervals giving a total area swept of *c.*16 m^2 per sample. The contents of each sample were transferred to separate, labelled plastic bag and immediately placed in a cool box. All samples were killed by freezing within 6 h of collection. The contents of each sample were counted and identified to the appropriate taxonomic level under a microscope. Nomenclature for Chrysomelidae followed Strejcek (1993), Morris (2003) for Curculionoidea, Heteroptera followed Southwood & Leston (1959), LeQuesne & Payne (1981) for Auchenorrhyncha, and Chandler (1998) for Diptera.

Winter bird abundance

Bird counts were made monthly between December and March of each year on the WBS mixture plots and an equivalent area of crop in the field centre. This was achieved by firstly observing bird utilisation of the two areas from a distant vantage point, avoiding disturbance of the birds, for a fixed 20 minute period and then walking a transect through the middle of both plots to flush out any remaining birds (modified after Perkins *et al*. 2000). Counts were not made in adverse weather conditions (heavy rain, strong winds or poor visibility).

Small mammal utilisation

Small mammal activity and utilisation of the WBS mixture patches, adjacent crop and field margins were recorded by live-trapping using Longworth traps over a one week period at five sites in November/December 2004 and again in late May/early June 2005. The Abbots Hall site was excluded from the sample due to poor establishment of the WBS treatment in that year. At each site trapping was carried out simultaneously on all three habitats Traps were baited with wheat or maize, casters (fly pupae) and apple or carrot (Shore *et al.* 2005). Traps were laid in a grid with 12 m spacing which typically comprised two lines of 13 traps each in the WBS patch, with an identical grid either side of the patch in the equivalent crop. In addition, a line of 18 traps was placed along one of the field margin replicates. Traps were set on pre-bait for three nights and then set to catch for three nights with trap rounds carried out each morning and evening. Captured animals were identified, sexed, weighed and individually marked for identification purposes with a unique microchip (www.avidcanada.com) before being released.

STATISTICAL ANALYSIS

Response variables

A total of 1776 response variables for soil, flora and fauna were calculated and analysed in order to test the research hypotheses. These included site by treatment means for selected species, and calculated groupings based on ecological function, taxonomy and conservation status. Mean values were calculated for both individual years and across all years (1186 variables). Logarithmic or arcsine transformations were undertaken on count and percentage cover data respectively to achieve normality of residuals as required. Species richness data were untransformed.

Mean percentage cover of plant species were calculated for each site and treatment in each year. In addition, summary variables of mean cover of sown and unsown forbs and grasses were calculated, together with total species number (richness) per m^{-2}, richness of annuals, perennials, grasses and forbs. Finally, the conservation status of arable plant species was determined from Wilson & King (2003). Mean diversity of declining arable plants was calculated both per m^{-2} and per plot based on DAFOR scores. The median of the flower abundance range class (1-5) was calculated for each species and averaged for each treatment plot per visit. From this total abundance and species richness of flowers per visit were calculated, together with abundance of flowers of key plant families, and the sub-groupings of sown and unsown species, and bee forage species.

Mean counts of individual bumblebee species were calculated per visit for each treatment at each site and year. In addition, total abundance and species richness of all bees, rare bees, reproductives (males and queens) and *Psithyrus* spp. were calculated. The functional classification of short-tongued (*B. terrestris/lucorum*, *B. pratorum* and *B. lapidarius*) and long-tongued species (*B. pascuorum, B. hortorum, B. muscorum, B. ruderatus*) (Goulson *et al*. 2004) were applied to these data. Similarly, counts of individual butterfly species were calculated per visit, together with total abundance and richness, and the functional classifications of mobile and immobile species (Warren 1992).

Spring and autumn counts of soil surface active invertebrates caught by pitfall trapping were analysed separately. Counts from all eight traps were summed for each treatment plot. Mean total abundance and species richness were calculated for each site, treatment and year. In addition, abundance and richness were calculated for individual families and the functional groupings of decomposer, herbivore, seed predator and predator (beneficial). Summer counts of canopy-active insects derived from vacuum and sweep net sampling were combined for analysis. Mean total abundance and species richness were calculated. In addition, abundance and richness were calculated for individual families, and the functional groupings of decomposer, herbivore, nectar feeder, pollen-feeder, pollinator, seed predator, predator and parasite.

Total abundance and species richness of birds were calculated for each WBS mixture patch and the equivalent area of crop, both for each month and for each year. In addition, the data were classified into the functional sub-groups of granivorous passerines (Bradbury *et al*. 2004) and species comprising the Farmland Bird Index (Gregory, Noble & Custance 2004). The abundance and species richness of small mammal was calculated for each site and habitat for each season (summer / winter). A factor was applied to correct for small differences in trapping effort between sites and the catches per 100 trap nights were calculated.

Data analysis

Three main approaches to data analysis were used to address the research hypotheses: 1) an oversites analysis of variance (ANOVA) with site and treatment in the model and Tukey's pairwise comparison tests to investigate the magnitude and generality of within-year treatment effects; 2) ANOVA with repeated measures to test for average treatment effects across all years, to determine how these changed over time, and to investigate treatment × time interactions. The Geisser-Greenhouse method (Maxwell & Delaney 1990) was used to calculated ε values for adjustment of degrees of freedom according to the amount by which the population covariance matrix departs from homogeneity; and 3) a meta analysis of significant and highest ranked treatment effects averaged across all years to provide a broad comparison between all treatments. In addition, linear regression was used to investigate the relationship between key factors, such as the log-transformed abundance of bees and dicot flowers. All analyses were undertaken using GenStat® 7.0 for Windows (Payne *et al*. 2002).

Results

OVERALL TREATMENT EFFECTS

Significant treatment differences were detected in 37% of the ANOVA tests carried out on the 1186 variables averaged across all years. Field margins sown with the wildflower seed mixture had the highest proportion (14.9%) of significant tests compared with the other treatments (Fig. 2a), followed by pollen & nectar (7.0%), tussocky grass (6.6%) and natural regeneration (6.2%) margins. The conservation headland (1.9%) and crop (1.0%) treatments had a considerably lower proportion of significant tests than expected by chance alone (5%). Vegetation variables accounted for a high proportion of significant tests in the wildflower and natural regeneration treatments. Soil invertebrate variables accounted for a high proportion of significant tests in the tussocky grass and wildflower treatments. Soil surface active invertebrates accounted for a high proportion of significant tests in the conservation headland, natural regeneration and wildflower treatments. Pollinators accounted for a high proportion of the significant tests in the pollen and nectar, and wildflower treatments. Finally, canopy active invertebrates accounted for a high proportion of the significant tests in the wildflower, tussocky and pollen and nectar treatments.

Wildflower margins had the highest proportion (24.7%) of top ranked variables regardless of significance (Fig. 2b), followed by natural regeneration (20.6%), pollen and nectar (18.6%), tussocky grass (15.8%) and conservation headland (14.1%). Once again the crop treatment had the lowest proportion of top ranked variables (6.3%). The proportion of top ranked variables accounted for by different taxa and functional groupings for each treatment was broadly the same as for the significant tests.

SOIL NUTRIENTS

After 5 years there were no significant differences in soil pH or the concentrations of macro nutrients (P. K, Mg, %N) between the different field margin treatments and the conventionally managed crop (Table 2). However, there were significant treatment differences in the accumulation of soil organic matter as estimated by percentage loss on ignition (Fig. 3). Sowing field margins with the wildflower and pollen and nectar seed mixtures resulted in significant (ANOVA $F_{5,20}$=8.91; P<0.001) increases (25% and 18% respectively) in %LOI values in the 0-5 cm depth fraction compared with the conventional crop and conservation headland. Similarly, %LOI was significantly higher in the wildflower margin compared with the annually cultivated Natural regeneration. In contrast, there were no significant differences in %LOI between treatments of the 6-10 cm depth fraction ($F_{5,20}$=1.22; P>0.05). Finally, when %LOI was averaged for the 0-10 cm depth fraction, values were significantly higher in the wildflower treatment (21%) compared with the crop, conservation headland and natural regeneration margins ($F_{5,20}$=3.72; P<0.05).

VEGETATION STRUCTURE AND COMPOSITION

Vegetation was significantly taller in the crop and conservation headland compared with the non-crop margin treatments both overall and in individual years except 2006 (Table 3). There were significant differences in vegetation height between years, particularly crop and conservation headlands. In addition, variation in vegetation height was significantly greater in the natural regeneration margin compared with the cropped treatments. Variability in vegetation structure diminished rapidly after year 1. Finally, there were large significant differences in estimated productivity between treatments (Fig. 4), with biomass significantly higher in the crop and conservation headland compared with the non-crop treatments.

Vegetation species richness was significantly higher in the wildflower followed by the natural regeneration margins compared with all other treatments (Table 4). Species richness of the other non-cropped margins was significantly higher than the crop. There was a small but significant decline in species richness with time, reflecting the loss of annual species after the first year (10.6 m^{-2} in 2002 to 9.4 m^{-2} in 2006). The significant time × treatment interaction reflected the greater magnitude of this effect in the margins sown with perennial seed mixtures compared with the annually cultivated treatments. Richness of annual species was significantly higher in the natural regeneration margins compared with all other treatments. Annuals were also more diverse in the conservation headland compared with the perennial margins (Fig. 5a). Richness of annual species declined more rapidly with time in the margins sown with perennial seed mixtures compared with a gradual increase in the natural regeneration treatment. Similarly, richness of perennial was significantly higher in the wildflower treatment compared with all others, followed by the pollen and nectar and tussocky margins (Fig. 5b). After 5 years the Natural regeneration treatment contained significantly more perennial species than the two cropped treatments. There was no significant time or time × treatment interactions for perennial species. Diversity of grasses was significantly higher in the non-crop margin treatments compared with the cropped treatments (Table 4). Diversity of grasses significantly declined with time in the tussocky margins, but increased in the pollen and nectar treatment. Finally, richness of forbs was significantly higher in the wildflower treatment compared with all others, followed by natural regeneration. Forb richness was lowest in the crop and tussocky margins. There was a significant decline in forb richness with time reflecting the loss of annual species after year 1. The decline of forb richness was significantly higher in the pollen and nectar margins, so that after 2004 there were no more forb species in this treatment compared with the crop. The richness of sown species remained relatively stable in the wildflower treatment and there was no significant change with time ($F_{4, 20}$=2.05; $P<0.05$; Fig. 6). Finally, there were no significant differences in species richness of declining arable plants per m^{-2} ($F_{5,25}$=1.16, $P>0.05$). However, richness of these species at the plot scale was significantly higher ($F_{5,25}$=3.86, $P<0.01$) in the annually cultivated natural regeneration margins compared with all other treatments except pollen and nectar (Fig. 7).

Cover of sown grasses was significantly higher in the tussocky grass margins, followed by the pollen and nectar and wildflower treatments compared with all others (Table 5). There was a significant increase in grass cover in the pollen and nectar margins and a decline in the wildflower margins with time compared to other treatments. Cover of sown forbs was significantly higher in the wildflower followed by the pollen and nectar treatments compared with all others. There was a significant decline in sown forb cover with time. This was most marked in the pollen and nectar treatment where cover declined rapidly after year 3 (Fig. 8). Cover of unsown grasses was significantly higher in the conservation headland compared with all other treatments except the crop. Cover was next highest in the natural regeneration treatment compared with all others. Cover of unsown grasses remained relatively stable with time and there was no significant year effect. Cover of unsown forbs was significantly higher in the natural regeneration compared with all other treatments. Finally, cover of bare ground was significantly higher in the crop and conservation headland, followed by natural regeneration compared with all other treatments.

FLOWER RESOURCES

There were highly significant differences in the abundance per m^{-2} of forb flowers between treatments in all years and overall (Table 6; Fig. 9). In year 1 flower abundance was significantly higher in the pollen and nectar margins compared with all others. Abundance was also higher in the wildflower margins compared with all treatments except natural regeneration. In years 2 and 3 abundance was significantly higher in the wildflower, and pollen and nectar margins compared with all others. However, from year 4 onwards flower abundance was significantly higher in the wildflower treatment compared with all others. There was no difference in abundance between the pollen and nectar margins and the other treatments. Flower abundance declined significantly with time from 9.2 per m^{-2} in 2002 to 4.4 m^{-2} in 2006. Much of this was due to the dramatic loss of flowers, particularly of sown species, in the pollen and nectar treatment (21.4 m^{-2} in 2002 to 3.0 m^{-2} in 2006). The abundance of flowers of sown species showed a virtually identical pattern of response. Abundance of flowers of unsown species was consistently and significantly higher in the natural regeneration compared with all other treatments. There was a significant decline in unsown flower abundance after year 1 which was more marked in the treatments sown with perennial seed mixtures. Finally, species richness of the flower resource was significantly higher in the wildflower treatment compared with all others in every year and overall. Richness was next highest in the natural regeneration and pollen and nectar treatments compared with all others.

The abundance of Asteraceae (Thistles and Daisies) flowers was significantly higher in the wildflower margins followed by natural regeneration compared with all other treatments (Table 7). Abundance of Fabaceae (Legumes) flowers was significantly higher in the pollen and nectar margins compared with all others followed by the wildflower treatment. Abundance of bee forage flowers was significantly higher in the wildflower margins, followed by the pollen and nectar margins compared with all other treatments.

POLLINATOR TRANSECTS

A total of 15,722 bumblebees were recorded on the field margin treatments during the experiment, representing nine species of *Bombus* and three species of *Psithyrus*. *B. lapidarius* was the most common bee (n=6815) closely followed by *B. pascuorum* (n=6066). Three rare bee species were recorded: *B. muscorum* (n=40); *B. ruderarius* (n=17); and *B. ruderatus* (n=148). Over the five years mean bumblebee counts per visit were significantly higher in the pollen and nectar treatment compared all other treatments (Table 8; Fig. 10a). Bee counts were also significantly higher in the wildflower margins compared with the remaining treatments except natural regeneration. In years 1 to 3 there were significantly more bees recorded per visit on the pollen and nectar margins compared with all other treatments. In year 4 bee abundance was equally high in the wildflower and pollen and nectar margins. In 2006 bees were significantly more abundant in the wildflower compared with the pollen and nectar treatment. Overall there was a highly significant increase in bee abundance from 5.8 per visit in 2002 to 9.0 in 2003 and then a steady decline to 1.2 in 2006. The significant year × treatment interaction reflected the marked decline in bee abundance in the pollen and nectar treatment after year 3. The abundance of critically important reproductive castes (queens and males) was significantly higher in the wildflower and pollen and nectar margins compared with all other treatments.

Species richness of bees per visit was significantly higher in the wildflower and pollen and nectar margins compared with the other treatments (Table 8; Fig. 10b). Richness was also higher in the non-crop margins (tussocky grass and natural regeneration) compared with the cropped treatments. In year 1 richness significantly higher in the Pollen and nectar margin compared the other treatments. However, after year 3 richness was significantly higher in the wildflower margins compared the other treatments. Finally, overall species richness of rare (UKBAP) bumblebees was significantly higher in the pollen and nectar margins compared with the cropped treatments and the tussocky grass margins.

Abundance of short- and long-tongued bees per visit was significantly higher in the pollen and nectar margins followed by the wildflower margins compared with all other treatments (Table 9). Abundance of short-tongued bees was also significantly higher in the natural regeneration margins compared with the cropped treatments. Finally, the abundance of Cuckoo bees was significantly higher in the wildflower, and pollen and nectar margins compared with the cropped treatments.

There was a highly significant positive relationship between log bee abundance and flower abundance on the field margins treatments (Fig. 11; $F_{1,34}$ = 141.29; P<0.001; R^2 = 80.6%). Flower and bee abundance were highest in the wildflower, and pollen and nectar margins, and lowest in the crop and conservation headland. Long-tongued bee species (e.g. *Bombus hortorum, B. pascuorum*) foraged preferentially on the sown legume *Trifolium pratense* (Fig. 12). In contrast, bees with intermediate tongue length (*B. lapidarius*) foraged on a mixture of sown legumes, including *T. pratense, Lotus corniculatus* and *T. hybridum*. Short-tongued bee species (*B. pratorum, B. terrestris / lucorum*) foraged on a wider range of sown (e.g. *T. hybridum, Rhinathus minor*) and unsown species (e.g. *Cirsium vulgare, C. arvense*).

There were large differences in the timing of flower resource availability between the wildflower and pollen and nectar margins (Fig. 13a). In early summer (May-June bee forage flowers were more abundant on the wildflower margins compared with the pollen and nectar margins. In late summer (July-August) the pattern was reversed. There were small differences in the abundance of bees in early summer between the two margins types (Fig. 13b). However, there were significantly more bees on the pollen and nectar margin in late summer. These seasonal differences in flower and bee abundance can be partly explained by differences in the flowering time of native compared to agricultural varieties of the key bee forage species *Trifoilum pratense* and *Lotus corniculatus* sown in the different margin treatments (Fig. 14a,b). Native varieties of these legume species sown in the wildflower margins flowered markedly earlier than agricultural varieties sown in the pollen and nectar margins.

A total of 9,076 butterflies were recorded on the margin treatments during the experiment, representing 25 species. The most abundant of these were *Maniola jurtina* (Meadow Brown; n=1952), *P. rapae* (Small White; n=1331), *P. brassicae* (Large White; n=931), *Cynthia cardui* (Painted Lady; n=725), and *Polyommatus icarus* (Common Blue; n=690). Several declining species were recorded, including *Lasiommata megera* (Wall Brown; n=26) and *Coenonympha pamphilus* (Small Heath; n=12). Over the 5 years total butterfly abundance per visit was significantly higher in the wildflower, and pollen and nectar margins compared with all other treatments (Table 10). Abundance in the other non-cropped treatments (tussocky grass and natural regeneration) was also significantly higher than for the cropped treatments. This pattern was relatively consistent with the exception of year 2 when abundance was significantly higher in the pollen and nectar treatment followed by the wildflower margins. Similarly, total abundance of immobile butterfly species was significantly higher in the pollen and nectar and wildflower margins compared with all other treatments. Numbers were also higher in the tussocky and natural regeneration margins compared with the crop. Treatment effects were less clear cut for the mobile butterflies. Overall abundance was significantly higher in the pollen and nectar margins, followed by the wildflower and natural regeneration treatments. However, the intensity of treatment effects diminished during the course of the experiment, so that there were no significant differences between treatments by year 5. In all cases, the significant time effects reflected the increase in butterfly abundance after year 1 followed by a gradual decline. There was a significant decline in butterfly abundance on the pollen and nectar margins relative to the other treatments.

Overall species richness of butterflies per visit was significantly higher in the wildflower and pollen and nectar margins, followed by the natural regeneration and tussocky grass margins compared with the cropped treatments (Table 11). This pattern was fairly consistent throughout the experiment. Similarly, richness of both mobile and immobile species was significantly higher in the wildflower, and pollen and nectar margins compared with all other treatments. Species richness of immobile species was also significantly higher in the remaining non-crop margin type compared with the cropped treatments. In the case of mobile species, richness was only significantly higher in the natural regeneration treatment compared with the crop. In all cases, there was a significant increase in species richness followed by a gradual decline with time. Once again richness declined more markedly in the pollen and nectar margins compared with the other treatments.

SOIL INVERTEBRATES

Soil cores from the non-crop margin treatments contained a significantly higher total number of invertebrates from a greater number of families and groups compared with the cropped treatments (Table 12). Importantly, the abundance of earthworms (Oligochaeta) was significantly higher in the three uncultivated margins treatments sown with perennial seed mixtures compared with the cultivated margin types (Fig. 14). Cores from the tussocky grass margins contained a significantly higher abundance of Araneae, Isopoda, Lepidoptera larvae, Diptera, Carabidae, and Hemiptera compared with the crop and conservation headlands. Similarly, abundance of Staphylinidae was significantly higher in the tussocky margins compared with the crop. The wildflower margins contained a significantly higher abundance of Prosobranchia with the natural regeneration margins and cropped treatments. Finally, the abundance of Pulmonata significantly higher in the wildflower margins compared with conservation headlands.

SOIL SURFACE ACTIVE INVERTEBRATES

Spring pitfall trapping recorded a total of 13,833 invertebrates comprising 28 families and 250 species. Autumn trapping resulted in 6,222 invertebrates comprising 27 families and 200 species. A total of 159 species were recorded in both spring and autumn trapping sessions. Overall species richness and total abundance of invertebrates caught in the spring was significantly lower in the tussocky grass margins compared with all other treatments (richness $F_{5,25}$=8.05; P<0.001; abundance $F_{5,25}$=6.13; P<0.001) (Fig. 17a,b). There was also a marked decline in species richness over the first 2 years ($F_{4,108}$=34.72; P<0.001), with numbers falling in the margins sown with perennial seed mixtures ($F_{20,108}$=2.81; P<0.001). There were significant, but smaller declines in abundance over the first 2 years ($F_{4,108}$=6.19; P<0.001) in all treatments. Closer analysis of feeding guilds showed significantly lower species richness and abundance of predators and seed predators in tussocky margins in the spring compared with most other margin types (Fig. 17a,b; Table 13a,b). In addition, abundance of decomposers was significantly lower in the crop compared with all other treatments except conservation headland. There was a highly significant increase in both the number and species richness of decomposers with time. In contrast, number and diversity of seed predators declined markedly in the perennial margins treatments after year 1 and the number and diversity of predators after year 2.

In the autumn total species richness over the four years was once again significantly lower in the tussocky margins compared with all other types ($F_{5,25}$=2.28; P<0.05) (Fig. 18a). This reflected significantly lower richness of predators and seed predators in this treatment compared with natural regeneration and conservation headlands (Fig. 18a; Table 14a). Richness of decomposers was also significantly higher in the wildflower margins compared with the crop and conservation headland. Overall species richness, together with that of decomposer and predators, showed small, but significant increases with time in all treatments ($F_{4,108}$=5.68; P<0.001). Total abundance of invertebrates was significantly higher in all the non-crop margins treatments compared with the crop ($F_{5,25}$=5.62; P<0.001) (Fig. 18b). Abundance was also higher in the wildflower and natural regeneration margins compared with the conservation headland. Overall abundance of seed predators was significantly higher in the natural regeneration margins compared with all treatments except wildflower and conservation headland (Fig. 18b; Table 14b). Abundance of decomposers was significantly higher in all non-crop margin treatment compared with the crop. Also, abundance was higher in all margins sown with perennial seed mixtures compared with conservation headlands. Overall abundance, particularly that of decomposers and predators, increased significantly in all treatments with time ($F_{4,108}$ = 6.79; P<0.001).

CANOPY ACTIVE INSECTS

Summer sweep net sampling recorded a total of 194,745 canopy active invertebrates between 2003 and 2006 comprising 185 families and 728 species. Suction sampling recorded 56,147 invertebrates comprising 182 families and 623 species. A total of 371 species were common to both sampling methodologies. Species richness of the combined sample was significantly higher in the wildflower treatment compared with all others ($F_{5,25}$=37.27; P<0.001) (Fig. 19a). Richness was also higher in the other non-crop margin types compared with the cropped treatments. There was no significant change in overall richness with year ($F_{3,78}$=2.41; P>0.05) or any year × treatment interaction ($F_{15,78}$=1.94; P>0.05). Analysis of feeding guilds confirmed a similar pattern (Fig. 19a; Table 15a). Richness of decomposers was significantly higher in the wildflower and pollen and nectar margins compared with all other treatments. Decomposer diversity was also significantly higher the natural regeneration margin compared with the crop. Richness of herbivores was significantly higher in the wildflower margins compared with all other treatments except pollen and nectar. Herbivore richness was higher in the other non-crop margin treatments compared with the cropped treatments. Richness of pollinating insects was significantly higher in the wildflower margins compared with all other treatments except natural regeneration. Pollinator diversity was higher in the non-crop margins compared with the crop. Richness of predatory invertebrate was significantly higher in the wildflower margins compared with the cropped treatments. Diversity of parasitoids was significantly higher in the wildflower and pollen and nectar margins compared with the cropped treatments.

Total abundance of invertebrates caught by sweep netting and suction sampling was significantly higher in the wildflower, pollen and nectar and natural regeneration margins compared with the crop ($F_{5,25}$=6.60; P<0.001) (Fig. 19b). Abundance in the tussocky margins and conservation headlands was no different from the crop. There was no significant change in overall abundance with year ($F_{3,78}$=2.73; P>0.05) or any year × treatment interaction ($F_{15,78}$=0.76; P>0.05). Abundance of decomposers was significantly higher in the wildflower and pollen and nectar treatments compared with all other treatments (Fig. 19b; Table 15b). Decomposer abundance was also significantly higher in the other non-crop margin treatments compared with the crop. Herbivore abundance was significantly higher in the pollen and nectar, and wildflower treatments compared with all other treatments. Abundance of herbivores was also significantly higher in the non-cropped margins compared with the cropped treatments. Abundance of pollinators was significantly higher in the wildflower treatment compared with all others except the natural regeneration and pollen and nectar margins. Abundance was also significantly higher in the non-cropped margins compared with the cropped treatments. Predator abundance was significantly higher in the wildflower margins compared with all other treatments except the tussocky margins. Abundance in the other non-cropped margins was significantly higher than the crop. Finally, there was no significant difference in the abundance of parasitoids between treatments.

WINTER BIRD ABUNDANCE

A total of 3,284 birds representing 23 species were recorded on the Wild Bird Seed mixture patches and adjacent crop over the five years. Linnet (*Acanthis cannabina*) was the most abundant species (43%), followed by Greenfinch, (*Carduelis chloris*, 27%), Chaffinch (*Fringilla coelebs*, 7%) and Skylark (*Alauda arvensis*, 6%). Over 95% of the birds counted were recorded on the wild bird seed (WBS) mixture patch compared with the adjacent crop. Species richness, and total abundance of all birds, Granivorous passerines, and Farmland Bird Index species were all significantly higher in the WBS patches compared with the adjacent crops on each visit between December and March (Table 16a; Figs. 20a & 21a). However, the magnitude of these differences diminished considerably after the December visit for Farmland Bird Index species and after January for both total abundance and Passerine abundance. The magnitude of differences in species richness remained large until after the February visit. Numbers of Skylark were significantly higher in the WBS patch overall and for the December and February visits only.

Species richness, total abundance of all birds, Granivorous passerines, and Farmland Bird Index species were significantly higher in the WBS patches compared with the adjacent crops every winter between 2002/3 and 2006/7 (Table 16b; Figs. 20b & 21b). However, the magnitude of these differences diminished considerably after winter 2004/5 for total abundance, and number of Granivorous passerines and Farmland Bird Index species. This corresponded to a marked decline in the cover of the sown seed-bearing crop species (Fig. 22). Considerable differences remained in species richness up to 2005/6. Numbers of Skylark were only significantly higher on the WBS patch in 2006/7 and overall.

SMALL MAMMAL UTILISATION

A total of 368 individuals were caught in the wild bird seed (WBS) mix, adjacent crops and field margins, including 213 animals trapped in the winter of 2004 and 155 trapped in summer of 2005. Virtually all (93%) of small mammal captures were Wood Mouse *(Apodemus sylvaticus*). Bank Vole (*Clethrionomys glareolus*) and Field Vole (*Microtus agrestis*) accounted for the remaining 7% of catches, primarily on the field margins. There were no significant difference in the species richness of small mammal catches between the three habitat types in winter ($F_{2,6}$ = 0.27, $P > 0.05$). However, species richness was significantly higher in the field margin compared with the WBS patch in the summer ($F_{2,6}$ = 11.40, $P < 0.01$). Small mammal activity was significantly higher in the WBS patch compared with the crop and field margin during the winter months (Fig. 23) ($F_{2,6}$ = 14.10, $P < 0.01$). However, during the summer months the pattern of use was reversed with activity significantly higher in both the crop and field margin compared with the WBS patch ($F_{2,6}$ = 15.51, $P < 0.01$).

Discussion

EXTENSIFICATION OF MANAGEMENT *VS.* CREATION OF PROTECTED WILDLIFE HABITATS

The results of this long-term, multi-site experiment showed clear and consistent responses of soil, flora and fauna to a range of agri-environment scheme options (Fig. 2a). The inclusion of the conventionally managed crop as a control confirmed the detrimental effects of intensive agricultural management on biodiversity and many ecosystem functions (e.g. Tscharntke *et al.* 2005), and is an essential benchmark for such comparative studies (Perry *et al*. 2003). The extensification of management inputs into the crop as prescribed by the conservation headland treatment resulted in a small increase in annual plant diversity (Critchley *et al*. 2004), but this did not translate into a significant increase in overall flower abundance or diversity of associated invertebrates (Pywell *et al*. 2005b). Measures of biodiversity were frequently high in the conservation headlands, but often very variable (Fig. 2b). This reflected the relatively poor performance of this option on heavy soils where there was a large seed bank of highly competitive grass weeds, such as *Alopecurus myosuroides*, which further reduced plant diversity. It is also likely that continued, large inputs of inorganic fertiliser to this treatment resulted in high levels of competition from the crop which further reduced plant diversity (Mountford, Lakhani & Kirkham 1993). Indeed conservation headlands without fertiliser addition have proved to be an effective means of conserving declining arable plants (Walker *et al*. 2007), particularly on lighter soils.

The results clearly demonstrate that the most effective means of enhancing biodiversity in intensively managed arable systems is the complete removal of land from production and the creation of protected wildlife habitats (Feber, Smith & Macdonald 1996; Meek *et al*. 2002; Asteraki *et al*. 2004; Pywell *et al*. 2005b), thus proving the first hypothesis. It is possible to reliably create a diverse range of wildlife habitats despite high residual soil fertility and a large seed bank of competitive species (BD1404; Pywell *et al*. 2002). Five years of cutting and removal of vegetation failed to reduce the concentration of major nutrients compared with the conventionally managed crop (BD1425; Marrs *et al*. 1998; Pywell *et al*. 2007a). This confirms the intransigent nature of residual soil nutrient pools, particularly those of phosphorous and potassium, but suggests that soil fertility may not be a major constraint on the restoration of botanical diversity provided suitable species are sown and appropriate management applied (Pywell *et al*. 2002; 2007a). Allowing natural regeneration of vegetation at the field margin is a simple and popular management strategy under the agri-environment schemes (Stevenson 2007). Our results showed that a diverse community of annual plants rapidly colonised from the seed bank and hedge bottom. This provided good habitat for soil surface active invertebrates (Meek *et al*. 2002), and subsequent colonisation by perennial forbs, such as *Cirsium* spp., in later years proved attractive to pollinating insects (Kells, Holland & Goulson 2001; Pywell *et al*. 2006). However, the outcome of this management strategy was variable between sites (Fig. 2b), depending on local species pool and management history, and other studies have shown that succession rapidly takes place to a species-poor, perennial grass sward in the absence of annual cultivation (Carvell *et al*. 2004). Furthermore, this treatment served as a reservoir of undesirable agricultural weeds which spread into the crop (Meek *et al*. 2007).

Sowing farmland with seed mixtures is a more effective and reliable means of directing succession to a desired endpoint for the creation of specific wildlife habitats (BD1404; BD1425; Pywell *et al*. 2002; 2007a). Sowing a simple, low-cost mixture of tussocky grass species is the most popular means of achieving this under the agri-environment schemes (Stevenson 2007). The competitive, generalist grass species rapidly established on the fertile ex-arable soils and were effective at excluding undesirable arable weed species (Critchley *et al*. 2004). This consistently resulted in a structurally complex, but very species poor-vegetation. However, this dense, sheltered vegetation did provide an effective physical barrier against the drift of pesticide and fertiliser into the hedge bottom (Miller & Lane 1999). It was also good habitat for hibernating carabid and staphylinid beetles, and spiders, and canopy-active predatory insects in the summer (Collins *et al.* 2003a,b; Pywell *et al*. 2005a). The low densities of ground-active invertebrate probably reflects their severely restricted activity in such dense vegetation. The addition of perennial wildflowers or legume species to the seed mixture increased the cost, but the resultant diverse vegetation had significant benefits for many invertebrate groups, particularly detrivores, herbivores and pollinators (e.g. Lagerlöf *et al.* 1992; Feber, Smith & Macdonald 1996; Meek *et al.* 2002; Carvell *et al*. 2004; Pywell *et al*. 2005b), especially if the margin occupies a sunny, sheltered position (Pywell *et al.* 2004).

TARGETED *VS.* GENERALIST MANAGEMENT PRESCRIPTIONS

This study provided good evidence that three of the management prescriptions which were specifically focused on declining farmland taxa (cultivated natural regeneration, pollen and nectar, and wild bird seed mixtures) were considerably more effective in enhancing both the target taxa and associated biodiversity than those designed to deliver a broader range of environmental benefits (conservation headland, tussocky grass margin). All three options were developed from an evidence-based understanding of the ecology and habitat requirements of the target species. Declining arable plant species are known to be associated with low intensity cropping systems which provide open, competition free habitat (Andreasen *et al*. 1996; Marshall *et al*. 2003), particularly at the field edge (Wilson & Aebischer 1995). Annual, light cultivation of field margins removed from agricultural production is the best means of re-creating these environmental conditions and maintaining an open, diverse community of annual plants (Critchley *et al*. 2004; Walker *et al*. 2007).

Recent research has shown a significant reduction in the abundance of key bumblebee forage species in the wider countryside, especially members of the Fabaceae (legumes), Asteraceae (thistles and daisies) and Lamiaceae (mints) (Carvell *et al*. 2006a). Sowing simple mixtures of pollen- and nectar-rich legume species proved to be the most effective and reliable means of providing high quality late-summer foraging habitat for bumblebees (Carvell *et al*. 2004, 2007; Pywell *et al*. 2006), including rare species (Carvell *et al*. 2006b).

Finally, there is good evidence that increased winter mortality is a key factor causing serious declines in farmland bird populations (e.g. Peach *et al*. 1999; Siriwardena *et al*. 2000). This has been linked to the loss of winter food resources caused by highly efficient and intensive modern agricultural practices, and in particular the decline of winter stubbles and mixed farming (Stoate *et al*. 2004). Field experiments and monitoring have demonstrated that sowing simple mixtures of seed-bearing crops is an effective means of supplementing the over-winter food supply for farmland birds (Stoate *et al*. 2004; Bradbury *et al.* 2004). Finally, there is evidence of potentially additive or synergistic benefits of these targeted habitats on other declining taxa. For example, the annual cultivation of the wild bird seed mixture patches provided good habitat for declining arable plants, bumblebees and small mammals (Carvell *et al*. 2006c; Pywell *et al*. 2007b).

MAINTENANCE OF HABITAT QUALITY IN THE LONGER TERM

The results showed serious declines in the quality of two of the targeted habitats after three years (pollen and nectar and wild bird seed mixtures), confirming the value of long-term experimentation. This could have serious detrimental effects on populations of farmland birds and bumblebees in the wider countryside, and has important implications for future agri-environment scheme policy and advice. The cover of sown *Trifolium* species declined by over 80% after year 3 (Fig. 8) and was replaced by grasses. *Trifolium pratense* and *T. hybridum* are short-lived perennials which are well adapted to fertile ex-arable soils, but do not persist well under cutting or grazing management (Frame, Charlton & Laidlaw 1998), due to low rates of seedling regeneration (*R.F Pywell unpublished data*; BD1623). Importantly, the species-rich wildflower margins maintained a consistently high supply of pollen and nectar resources over the five year period. They also contained both early- and late-flowering species which are important for bumblebee reproductive castes. Similarly, the establishment and cover of seed-bearing crop species declined by and average of 76% after year 3 (Fig. 23) due to competition from weed species and herbivory by insect pests, such as flea beetles (*Phyllotreta* spp.) and pollen beetles (*Meligethes aeneus*) (BD1623; Pywell *et al*. 2007b).

ENHANCED DELIVERY OF ECOSYSTEM FUNCTIONS AND SERVICES

In this study we examined the potential of agri-environment scheme options to increase the efficiency of delivery of key ecosystem functions and services, thus mitigating some of the detrimental effects of intensive agriculture (Hector & Bagchi 2007). Much of the global carbon pool is held in the soil (Batjes 1996). Increased loss of soil carbon to the atmosphere under rising temperature regimes is therefore of critical concern (Knorr *et al*. 2005; Powlson 2005). A recent study has estimated the mean loss of carbon from soils in England and Wales to be 0.6% year^{-1} (relative to the existing carbon content) (Bellamy *et al*. 2005). These losses are irrespective of land use type and are thought to be driven by rising temperature increasing the rate of organic matter decomposition by microbial communities. The significant increase in soil organic matter (21% relative to the crop) in the wildflower margins suggest there is considerable potential to off-set these losses of carbon though existing agri-environment scheme polices. This rapid accumulation of carbon is likely to reflect the cessation of disturbance by cultivation, together with the co-existence of species with different growth rates and root architecture (De Deyn, Cornelissen & Bardgett 2007). In addition, our results showed that removal of land from production and cultivation increased the abundance of ecosystem engineers, such as earthworms and other soil macro-invertebrates, which re-distribute carbon through the soil profile and enhance the rate of nutrient cycling (Lavelle *et al.* 1997).

Sowing diverse mixtures of wildflowers, and pollen- and nectar-rich legumes species significantly enhanced both the diversity and abundance of all insect pollinators, including bumblebees. This is likely to increase the resilience of pollination services for nearby crop and wildflower communities to environmental perturbations and disease (Daily 1997; Ghazoul 2005). Finally, there is evidence that the complexity and therefore the stability of invertebrate food webs are higher in the non-cropped margins, and particularly those sown with wildflowers. This will have important implications for the regulation of pest species and the strength of trophic cascades (e.g. Strong 1992; Shurin *et al.* 2002).

This study provides the first comprehensive, long-term assessment of the effectiveness of UK agri-environment scheme prescriptions for arable land. We can conclude that complete removal of land from production to create protected wildlife areas is the most practical and effective means of enhancing biodiversity, and the delivery of key ecosystem functions and services. Sowing seed mixtures is an effective and reproducible means of directing succession to a desired endpoint for the creation of specific wildlife habitats. Management prescriptions specifically targeted to the requirements of declining taxa (arable plants, bees and birds) were more cost-effective than those designed to deliver a broader range of environmental benefits. However, it was not possible to maintain the quality of some of these habitats *in situ* for long periods. It is therefore recommended that these are treated as short-lived, rotational options which are re-established every 2-3 years on new areas of farmland. The cessation of cultivation and the creation of species-rich vegetation significantly increased diversity of soil ecosystem engineers. This had important, positive benefits on the soil carbon cycle. Similarly, creation of species-rich field margins resulted in the largest increases in trophic complexity. This is likely to increase the efficiency of pollination and pest control services, and their resilience of to environmental perturbations. In conclusion, no single management prescription fulfilled all the required functions. Nevertheless, field margins sown with a diverse mixture of wildflowers exhibited the greatest multi-functionality. They also appeared to be the most effective means of increasing the efficiency of ecosystem service delivery. The best strategy would therefore to promote greater uptake of this particular option which is currently rare in the countryside, whilst at the same time maximising habitat heterogeneity by encouraging the creation as a wide variety of other habitat types as possible.

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Introduction

Intensive agricultural practices have highly detrimental impacts on biodiversity (e.g. Tapper & Barnes 1986; Sutcliffe & Kay 2000; Donald 2001; Robinson & Sutherland 2002; Steffan-Dewenter *et al*. 2005). Indeed, within certain taxa, such as birds (Gregory, Noble & Custance 2004) and plants (Preston *et al*. 2002), the fastest declining species in the UK over the last few decades have been those associated with farmland. The two primary drivers for this are, firstly the trend for simplified cropping systems applied to increasingly consolidated land parcels leading to loss of non-crop habitat, such as hedgerows and ponds; and secondly, the intensification of management practices within the cropping systems themselves, including the increased use of pesticides and fertilisers, and shorter fallow periods (Stoate *et al*. 2001). The resultant loss of species and habitats, together with the associated pollution and eutrophication may also serve to perturb key ecosystem functions, including pollination, natural regulation of pest species, carbon sequestration and soil nutrient cycling (Hector & Bagchi 2007).

The UK Entry Level Stewardship (ELS) agri-environment scheme (Anon. 2005) recognises that the impacts of modern agriculture on biodiversity and ecosystem function can be mitigated through approaches which either decrease the intensity of agricultural management on farmed land (‘extensification’) or protect areas from intensive farming practices (Bignal 1998). There is now a large body of research on the effectiveness of these different management strategies for conserving different taxa (reviewed by Marshall & Moonen 2002; Vickery *et al*. 2004). However, considerably less is known about their effectiveness in promoting key ecosystem functions and services. On arable farmland in the UK the most popular means of enhancing biodiversity by extensification of management is through conservation headlands (Stevenson 2007) which are cereal field margins (usually about 6 m wide) which are selectively sprayed with pesticides (Sotherton 1991). This approach has proved to be beneficial to broad-leaved annual plants (Wilson 1990), butterflies (Dover 1997), bumblebees (Kells, Holland & Goulson 2001) and birds (Rands 1995). The most popular means of protecting biodiversity by removal of land from production is by creating tall grassy strips at the field margin (Stevenson 2007). This dense, sheltered vegetation is known to provide important habitat for hibernating carabid and staphylinid beetles, spiders, small mammals, nesting bumblebees and certain breeding birds (e.g. Smith *et al*. 1993; Thomas *et al*. 1992; Collins *et al.*, 2003a,b; Kells & Goulson 2003; Shore *et al*. 2005; Pywell *et al*. 2005a). Similarly, research has shown that sowing non-crop field margins with perennial wildflowers can significantly enhance their value for butterflies, bumblebees, honeybees, hoverflies and other invertebrates (e.g. Lagerlöf *et al.* 1992; Feber *et al.* 1996; Meek *et al.* 2002; Carvell *et al*. 2004; Pywell *et al*. 2005b).

More recent prescriptions have been specifically developed to address the requirements of declining farmland taxa. One of the most popular of these ‘targeted’ prescriptions involves sowing mixtures of seed-bearing crops to supplement the over-winter food supply for declining farmland birds to counter winter mortality (Stoate *et al*. 2004; Bradbury *et al*. 2004). Similarly, research has shown that sowing field margins with simple mixtures of pollen- and nectar-rich legume species is a cost-effective means of providing late-summer foraging habitat for bumblebees (Carvell *et al.* 2007; Pywell *et al*. 2006). Finally, uncropped, annually cultivated margins have proved an effective means of conserving populations of declining arable plant species (Walker *et al*. 2007).

To date there has been few detailed comparative study of these different approaches to the enhancement of biodiversity on arable land promoted under the agri-environment schemes (Kleijn & Sutherland 2003). In this study we present the results of a multi-site experiment which compares the effects of six widespread crop and field margin management strategies on a broad range of taxa and ecosystem functions over five years. This enabled us to test the following hypotheses:

H1: Extensification of arable land management results in greater biodiversity, and a more efficient delivery of a wider range of ecosystem services. However, complete removal from crop production (i.e. protected wildlife areas) is a more practical and effective means of enhancing biodiversity and delivering these key functions and services;

H2: Management prescriptions specifically targeted to the requirements of declining taxa are more effective than those designed to deliver a broader range of environmental benefits;

H3: The positive effects of management prescriptions on different taxa are reproducible over a wide variety of locations and soil types, and these patterns persist or strengthen over time;
H4: Soil biodiversity is positively correlated to increases in above-ground biodiversity, and has a potentially important impact on ecosystem function; and,
H5: Sowing seed mixtures to create species-rich vegetation on land removed from production will result in the greatest increases in trophic complexity in above- and below-ground food webs.

The results are discussed in the context of (i) the ecological role of the different habitats in the conservation of a range of taxa, and (ii) the implications for future agri-environment scheme policies aimed at the enhancement of biodiversity on farmland.

Methods

STUDY SITES AND EXPERIMENTAL TREATMENTS

The experiment was conducted at six sites across central and eastern England on a range of soils (Fig. 1): clay at Abbots Hall, Essex (51°48'N, 0°51'E), sandy loam (over chalk) at Whittlesford, Cambridgeshire (52°6'N, 0°07'E), calcareous clay at Colworth, Bedfordshire (52°15'N, 0°35'W), sandy loam at Little Wittenham, Oxfordshire (51°38'N, 1°12'W), clay with flints (over chalk) at Marlow, Buckinghamshire (51°36'N, 0°48'W), and variable loam at Westow, Yorkshire (54°5'N, 0°49'W). In September 2001 six contiguous plots, each measuring 50 m long and 6 m wide, were established along the east- and west-facing margins (replicates) of the same arable field at each site. Each margin was situated adjacent to a hedge typically 2 m high. Experimental treatments representing one of five ELS field margin management prescriptions (Anon. 2005; Appendix 1, Table 1) were assigned to plots at random, with the exception of the crop and conservation headland which were assigned randomly to either end of each replicate to enable farming operations. In addition, a rectangular, field centre patch of 0.3 ha was sown each spring with a mixture of four seed-bearing crop species to provide winter food resources of declining farmland bird species.

The control treatment was a winter-sown cereal (wheat, barley or oats) grown with conventional inputs of fertiliser and pesticide. Broad-leaved break crops of oilseed rape, peas or sugar beet were grown on just 6 occasions on four sites over the six years of the project (see Appendix 2 for full details). Data for the crop and conservation headland treatments were excluded from the analyses for specific sites in break crop years. The conservation headland treatment comprised growing a cereal crop without application of insecticides and only selective herbicides (Sotherton 1991). This was to allow populations of broad-leaved plants and their associated insects to develop which provided food for farmland birds and benefited declining arable plant species. The remaining treatments required the complete removal of land from arable production to create a range of protected wildlife habitats. The least interventionist of these was natural regeneration of vegetation from the seed bank and hedge bottom. This treatment was cut and lightly cultivated (to a depth of *c.* 15 cm) each autumn to maintain an open vegetation community dominated by annual species which provided habitat for invertebrates and food resources for seed-eating birds. In the remaining treatments seed mixtures were sown to direct succession to a desired end-point. The simplest of these involved sowing a low cost mixture of six fine- and broad-leaved grass species at 20 kg ha^{-1} (£60 ha^{-1}; €70 ha^{-1}) to created tall, dense tussocky grass strip (see Appendix 3 for seed mixture). This vegetation was cut in the establishment year to control volunteer crops and undesirable species, but subsequently unmanaged. This treatment had a number of aims, including protection of boundary features against pesticide and fertiliser drift, provision of overwintering habitat for invertebrates, nesting sites for bumblebees and habitat for small mammals, and supply of food resources for seed-feeding birds. The pollen and nectar seed mixture comprised sowing four agricultural varieties of legumes with three fine-leaved grass species at 20 kg ha^{-1} (£90 ha^{-1}; €111 ha^{-1}) specifically designed to provide mid- to late-season foraging resources for pollinating insects, particularly bumblebees and butterflies (Carvell *et al*. 2007; Pywell *et al*. 2006). The wildflower treatment required sowing 21 species of native forbs comprising a range of functional types with three fine-leaved grass species at 37.2 kg

ha^{-1} (£891 ha^{-1}; €1098 ha^{-1}) to provide vegetation with both a diverse structure and composition for the widest range of invertebrate species. Finally, in the spring of each year a mixture of four annual seed-bearing crops was sown at 7.5 kg ha^{-1} (£50 ha^{-1}; €62 ha^{-1}) in the field centre wild bird seed (WBS) mixture plots to provide late winter food resources for seed-eating birds.

In the establishment year the sown habitats were managed by cutting and removal of herbage in May and September to reduce competition from crop volunteers and other undesirable species. In subsequent years the pollen and nectar and wildflower treatments were always cut and removed in September with an occasional cut in April if required. In addition, at two sites in the first year a graminicide (Fusilade Max: fluazifop-P-butyl) was applied at half rate (0.8 l in 200 l of water ha^{-1}) to the pollen and nectar and wildflower margins to reduce competition from the annual grass weeds, *Anisantha sterilis* and *Alopecurus myosuroides*. Mollusc herbivory in the sown treatments was reduced by two applications of baited pellets containing 4% w/w metaldyhyde at 7.5 kg ha^{-1} at four sites on heavy soil in the spring of year 1. Similar applications were made to the WBS mixture patches in the spring at three sites on heavy soil. Other invertebrate pests, particularly flea beetles (*Phyllotreta* spp.) (Coleoptera: Chrysomelidae) and pollen beetles (*Meligethes aeneus*) (Coleoptera: Nitidulidae), were controlled in the WBS patches by one or two applications of synthetic pyrethroid pesticide during the spring and summer (following recommendations from BD1623). This typically comprised the application of EC 100 g l^{-1} cypermethrin A.I. applied at 250 ml ha^{-1} or EC 240 g l^{-1} tau-fluvalinate A.I. applied at 200 ml ha^{-1} (BD1623).

MONITORING

Soil nutrients

In January 2006 four soil cores (150 mm deep × 70 mm wide × 140 mm long) were collected using a spade along a zig-zag transect through the centre of each plot, avoiding a 1 m buffer around the edge. The cores were bulked, thoroughly mixed for each plot and analysed for Olsen extractable phosphorous (P), exchangeable potassium (K), magnesium (Mg) and total nitrogen (N%) using standard methods (Allen *et al*. 1974; MAFF 1986). At the same time 10 soil cores were collected in the same zig-zag pattern from each plot to a depth of 100 mm using a 20 mm diameter gouge auger. Each core was divided into two depth fractions (0-5 cm and 6- 10 cm) and placed into separate polythene bags. Samples for each plot and depth fraction were bulked and thoroughly mixed. Total carbon content was estimated by loss on ignition (%LOI) in the muffle furnace at 375°C for 16 hours (Allen *et al*. 1974).

Vegetation composition and structure

Between late June and early July of each year vegetation composition of each treatment was recorded from five 1 × 1 m quadrats placed at random in each plot, avoiding a 1 m edge buffer. Percentage cover of all vascular plant species and bare soil was estimated as a vertical projection. Finally, cover abundance of all species present in the treatment plot was estimated each year using the DAFOR score (Kershaw & Looney 1985). Plant nomenclature followed Stace (1997).

Height and structure of the vegetation was recorded from ten drop disk measurements (diameter 300 mm, weight 200 g) (Stewart, Bourn & Thomas 2001). Both mean sward height and the variation in sward height as expressed by standard deviation of the mean were calculated. Finally, drop disk measurements were used to estimate vegetation production (g m^{-2}) in each treatment using a simple linear regression model developed from a grassland restoration experiment sown with similar species at Little Wittenham, Oxfordshire (51°38'N, 1°12'W) (Coulson *et al*. 2001). In this study a highly significant relationship was found between mean biomass (based on five 40 × 40 cm quadrats) and mean vegetation height (based on 20 drop disks 300 mm diameter, 200 g), namely biomass m^{-2} = 23.53 + 14.14 Sward ht (cm); $F_{1,19}$ = 16.56; P<0.001; R^2 = 48%; *R.F.Pywell unpublished data;* see Appendix 4 for details).

Flower resources

The forb flower resource was estimated for each treatment plot (excluding the WBS plots) following each bumblebee and butterfly transect count. All flowering forbs were first identified to species and the approximate abundance of single flowers and multi-flowered stems (racemes, corymbs, e.g. *Trifolium pratense*; capitulums, e.g. *Centaurea nigra*; umbels, e.g. *Daucus carota*) was scored using a simple floristic index (Carvell *et al*. 2004; Pywell *et al*. 2005b, 2006): 1. Rare (approx. 1 – 25 flowers per 300 m^2 plot); 2. Occasional (approx. 26 - 200 flowers); 3. Frequent (approx. 201 - 1000 flowers); 4. Abundant (approx. 1001 - 5000 flowers); 5. Super-abundant (more than 5001 flowers).

Pollinator transects

The abundance and diversity of bumblebees and butterflies were recorded from transect walks through the centre of each field margin plot (excluding WBS mixture plots) on between seven and nine occasions between May and September each year (Banaszak 1980; Pywell *et al*. 2005b). Walks were carried out between 10.00 am and 17.00 pm when weather conditions conformed to the Butterfly Monitoring Scheme (BMS) rules (temperature above 13°C with at least 60% clear sky, or 17°C in any sky conditions; no count at all if raining) (Pollard & Yates 1993). The shade (ambient) temperature, percentage sunshine and wind speed were recorded at the end of each transect walk. Butterflies and foraging bumblebees were recorded to species level across the entire plot width. In addition, bees were further sub-divided into caste where possible (following Prŷs-Jones & Corbet 1991). Voucher specimens of rare species were collected for verification. Workers of *Bombus terrestris* and *B. lucorum* were collectively recorded as these cannot be reliably distinguished in the field. The cuckoo bumblebees (subgenus *Psithyrus* sp.), which are brood parasites of true *Bombus* species, were counted together as a group for analysis, but honeybees and solitary species were not noted. The flowering plant each bee was first seen to visit was also recorded to species level.

Soil invertebrates

In January 2006 four soil cores (150 mm deep × 70 mm wide × 140 mm long) were collected using a spade along a zig-zag walk through the centre of each plot. Each core was stored in a sealed and labelled polythene bag at 3°C prior to sorting. Cores were placed in a warm room (18°C) for 12-18 hours prior to sorting to encourage invertebrate activity and therefore increase the probability of catching individuals by hand sorting. Each core was placed into large, deep tray and broken up by hand (Thomas *et al.* 1992). The fragments of soil and vegetation were thoroughly searched for invertebrates for a fixed period of ten minutes. All invertebrate species were counted and identified to phyla, order or sub-order level with the exception of Coleoptera which were identified to family level.

Soil surface active invertebrates

The activity and density of soil surface active invertebrates was recorded using pitfall traps (8 cm diameter × 11 cm deep plastic cups) sunk into the ground with the top level with the soil surface (Luff 1996). Each trap was one-third filled with a preservative solution of propylene glycol diluted 1:1 with water. Rain shelters (12 cm diameter) were placed over each trap to prevent flooring. Eight traps were set at 5 m spacing placed along the centre line of each plot. Traps were opened for 22 days between late April and May, and again between early and late October each year. All traps from each plot were combined and contents counted and identified to the appropriate taxonomic level under a microscope. Nomenclature followed Luff & Duff (2001) for Carabidae, Lott & Duff (2003) for Staphylinidae, and Roberts (1993) for Araneae.

Canopy active invertebrates

The abundance and diversity of canopy active invertebrates were sampled in each plot in early July of each year from 2003 onwards using two complementary approaches (Standen 2000). Sampling was undertaken between 10.00 am and 17.00 pm when the vegetation and soil were dry. Firstly, a sample was collected using a Vortis™ suction sampler (www.burkard.co.uk) (Arnold 1994). Each sample comprised nine 10-s 'sucks' collected in a zig-zag pattern through each plot (avoiding a 1 m edge buffer), giving a total sample area of 0.174 m^2. Secondly, a standard sweep net of 0.46 m diameter with a 0.7 m handle was vigorously swept through the vegetation canopy along the centre line of each plot. Sampling was undertaken by the same individual on all occasions. One sample unit comprised 35 strokes of approximately 1 m width at 1 m intervals giving a total area swept of *c.*16 m^2 per sample. The contents of each sample were transferred to separate, labelled plastic bag and immediately placed in a cool box. All samples were killed by freezing within 6 h of collection. The contents of each sample were counted and identified to the appropriate taxonomic level under a microscope. Nomenclature for Chrysomelidae followed Strejcek (1993), Morris (2003) for Curculionoidea, Heteroptera followed Southwood & Leston (1959), LeQuesne & Payne (1981) for Auchenorrhyncha, and Chandler (1998) for Diptera.

Winter bird abundance

Bird counts were made monthly between December and March of each year on the WBS mixture plots and an equivalent area of crop in the field centre. This was achieved by firstly observing bird utilisation of the two areas from a distant vantage point, avoiding disturbance of the birds, for a fixed 20 minute period and then walking a transect through the middle of both plots to flush out any remaining birds (modified after Perkins *et al*. 2000). Counts were not made in adverse weather conditions (heavy rain, strong winds or poor visibility).

Small mammal utilisation

Small mammal activity and utilisation of the WBS mixture patches, adjacent crop and field margins were recorded by live-trapping using Longworth traps over a one week period at five sites in November/December 2004 and again in late May/early June 2005. The Abbots Hall site was excluded from the sample due to poor establishment of the WBS treatment in that year. At each site trapping was carried out simultaneously on all three habitats Traps were baited with wheat or maize, casters (fly pupae) and apple or carrot (Shore *et al.* 2005). Traps were laid in a grid with 12 m spacing which typically comprised two lines of 13 traps each in the WBS patch, with an identical grid either side of the patch in the equivalent crop. In addition, a line of 18 traps was placed along one of the field margin replicates. Traps were set on pre-bait for three nights and then set to catch for three nights with trap rounds carried out each morning and evening. Captured animals were identified, sexed, weighed and individually marked for identification purposes with a unique microchip (www.avidcanada.com) before being released.

STATISTICAL ANALYSIS

Response variables

A total of 1776 response variables for soil, flora and fauna were calculated and analysed in order to test the research hypotheses. These included site by treatment means for selected species, and calculated groupings based on ecological function, taxonomy and conservation status. Mean values were calculated for both individual years and across all years (1186 variables). Logarithmic or arcsine transformations were undertaken on count and percentage cover data respectively to achieve normality of residuals as required. Species richness data were untransformed.

Mean percentage cover of plant species were calculated for each site and treatment in each year. In addition, summary variables of mean cover of sown and unsown forbs and grasses were calculated, together with total species number (richness) per m^{-2}, richness of annuals, perennials, grasses and forbs. Finally, the conservation status of arable plant species was determined from Wilson & King (2003). Mean diversity of declining arable plants was calculated both per m^{-2} and per plot based on DAFOR scores. The median of the flower abundance range class (1-5) was calculated for each species and averaged for each treatment plot per visit. From this total abundance and species richness of flowers per visit were calculated, together with abundance of flowers of key plant families, and the sub-groupings of sown and unsown species, and bee forage species.

Mean counts of individual bumblebee species were calculated per visit for each treatment at each site and year. In addition, total abundance and species richness of all bees, rare bees, reproductives (males and queens) and *Psithyrus* spp. were calculated. The functional classification of short-tongued (*B. terrestris/lucorum*, *B. pratorum* and *B. lapidarius*) and long-tongued species (*B. pascuorum, B. hortorum, B. muscorum, B. ruderatus*) (Goulson *et al*. 2004) were applied to these data. Similarly, counts of individual butterfly species were calculated per visit, together with total abundance and richness, and the functional classifications of mobile and immobile species (Warren 1992).

Spring and autumn counts of soil surface active invertebrates caught by pitfall trapping were analysed separately. Counts from all eight traps were summed for each treatment plot. Mean total abundance and species richness were calculated for each site, treatment and year. In addition, abundance and richness were calculated for individual families and the functional groupings of decomposer, herbivore, seed predator and predator (beneficial). Summer counts of canopy-active insects derived from vacuum and sweep net sampling were combined for analysis. Mean total abundance and species richness were calculated. In addition, abundance and richness were calculated for individual families, and the functional groupings of decomposer, herbivore, nectar feeder, pollen-feeder, pollinator, seed predator, predator and parasite.

Total abundance and species richness of birds were calculated for each WBS mixture patch and the equivalent area of crop, both for each month and for each year. In addition, the data were classified into the functional sub-groups of granivorous passerines (Bradbury *et al*. 2004) and species comprising the Farmland Bird Index (Gregory, Noble & Custance 2004). The abundance and species richness of small mammal was calculated for each site and habitat for each season (summer / winter). A factor was applied to correct for small differences in trapping effort between sites and the catches per 100 trap nights were calculated.

Data analysis

Three main approaches to data analysis were used to address the research hypotheses: 1) an oversites analysis of variance (ANOVA) with site and treatment in the model and Tukey's pairwise comparison tests to investigate the magnitude and generality of within-year treatment effects; 2) ANOVA with repeated measures to test for average treatment effects across all years, to determine how these changed over time, and to investigate treatment × time interactions. The Geisser-Greenhouse method (Maxwell & Delaney 1990) was used to calculated ε values for adjustment of degrees of freedom according to the amount by which the population covariance matrix departs from homogeneity; and 3) a meta analysis of significant and highest ranked treatment effects averaged across all years to provide a broad comparison between all treatments. In addition, linear regression was used to investigate the relationship between key factors, such as the log-transformed abundance of bees and dicot flowers. All analyses were undertaken using GenStat® 7.0 for Windows (Payne *et al*. 2002).

Results

OVERALL TREATMENT EFFECTS

Significant treatment differences were detected in 37% of the ANOVA tests carried out on the 1186 variables averaged across all years. Field margins sown with the wildflower seed mixture had the highest proportion (14.9%) of significant tests compared with the other treatments (Fig. 2a), followed by pollen & nectar (7.0%), tussocky grass (6.6%) and natural regeneration (6.2%) margins. The conservation headland (1.9%) and crop (1.0%) treatments had a considerably lower proportion of significant tests than expected by chance alone (5%). Vegetation variables accounted for a high proportion of significant tests in the wildflower and natural regeneration treatments. Soil invertebrate variables accounted for a high proportion of significant tests in the tussocky grass and wildflower treatments. Soil surface active invertebrates accounted for a high proportion of significant tests in the conservation headland, natural regeneration and wildflower treatments. Pollinators accounted for a high proportion of the significant tests in the pollen and nectar, and wildflower treatments. Finally, canopy active invertebrates accounted for a high proportion of the significant tests in the wildflower, tussocky and pollen and nectar treatments.

Wildflower margins had the highest proportion (24.7%) of top ranked variables regardless of significance (Fig. 2b), followed by natural regeneration (20.6%), pollen and nectar (18.6%), tussocky grass (15.8%) and conservation headland (14.1%). Once again the crop treatment had the lowest proportion of top ranked variables (6.3%). The proportion of top ranked variables accounted for by different taxa and functional groupings for each treatment was broadly the same as for the significant tests.

SOIL NUTRIENTS

After 5 years there were no significant differences in soil pH or the concentrations of macro nutrients (P. K, Mg, %N) between the different field margin treatments and the conventionally managed crop (Table 2). However, there were significant treatment differences in the accumulation of soil organic matter as estimated by percentage loss on ignition (Fig. 3). Sowing field margins with the wildflower and pollen and nectar seed mixtures resulted in significant (ANOVA $F_{5,20}$=8.91; *P*<0.001) increases (25% and 18% respectively) in %LOI values in the 0-5 cm depth fraction compared with the conventional crop and conservation headland. Similarly, %LOI was significantly higher in the wildflower margin compared with the annually cultivated Natural regeneration. In contrast, there were no significant differences in %LOI between treatments of the 6-10 cm depth fraction ($F_{5,20}$=1.22; *P*>0.05). Finally, when %LOI was averaged for the 0-10 cm depth fraction, values were significantly higher in the wildflower treatment (21%) compared with the crop, conservation headland and natural regeneration margins ($F_{5,20}$=3.72; *P*<0.05).

VEGETATION STRUCTURE AND COMPOSITION

Vegetation was significantly taller in the crop and conservation headland compared with the non-crop margin treatments both overall and in individual years except 2006 (Table 3). There were significant differences in vegetation height between years, particularly crop and conservation headlands. In addition, variation in vegetation height was significantly greater in the natural regeneration margin compared with the cropped treatments. Variability in vegetation structure diminished rapidly after year 1. Finally, there were large significant differences in estimated productivity between treatments (Fig. 4), with biomass significantly higher in the crop and conservation headland compared with the non-crop treatments.

Vegetation species richness was significantly higher in the wildflower followed by the natural regeneration margins compared with all other treatments (Table 4). Species richness of the other non-cropped margins was significantly higher than the crop. There was a small but significant decline in species richness with time, reflecting the loss of annual species after the first year (10.6 m^{-2} in 2002 to 9.4 m^{-2} in 2006). The significant time × treatment interaction reflected the greater magnitude of this effect in the margins sown with perennial seed mixtures compared with the annually cultivated treatments. Richness of annual species was significantly higher in the natural regeneration margins compared with all other treatments. Annuals were also more diverse in the conservation headland compared with the perennial margins (Fig. 5a). Richness of annual species declined more rapidly with time in the margins sown with perennial seed mixtures compared with a gradual increase in the natural regeneration treatment. Similarly, richness of perennial was significantly higher in the wildflower treatment compared with all others, followed by the pollen and nectar and tussocky margins (Fig. 5b). After 5 years the Natural regeneration treatment contained significantly more perennial species than the two cropped treatments. There was no significant time or time × treatment interactions for perennial species. Diversity of grasses was significantly higher in the non-crop margin treatments compared with the cropped treatments (Table 4). Diversity of grasses significantly declined with time in the tussocky margins, but increased in the pollen and nectar treatment. Finally, richness of forbs was significantly higher in the wildflower treatment compared with all others, followed by natural regeneration. Forb richness was lowest in the crop and tussocky margins. There was a significant decline in forb richness with time reflecting the loss of annual species after year 1. The decline of forb richness was significantly higher in the pollen and nectar margins, so that after 2004 there were no more forb species in this treatment compared with the crop. The richness of sown species remained relatively stable in the wildflower treatment and there was no significant change with time ($F_{4, 20}$=2.05; P<0.05; Fig. 6). Finally, there were no significant differences in species richness of declining arable plants per m^{-2} ($F_{5,25}$=1.16, P>0.05). However, richness of these species at the plot scale was significantly higher ($F_{5,25}$=3.86, P<0.01) in the annually cultivated natural regeneration margins compared with all other treatments except pollen and nectar (Fig. 7).

Cover of sown grasses was significantly higher in the tussocky grass margins, followed by the pollen and nectar and wildflower treatments compared with all others (Table 5). There was a significant increase in grass cover in the pollen and nectar margins and a decline in the wildflower margins with time compared to other treatments. Cover of sown forbs was significantly higher in the wildflower followed by the pollen and nectar treatments compared with all others. There was a significant decline in sown forb cover with time. This was most marked in the pollen and nectar treatment where cover declined rapidly after year 3 (Fig. 8). Cover of unsown grasses was significantly higher in the conservation headland compared with all other treatments except the crop. Cover was next highest in the natural regeneration treatment compared with all others. Cover of unsown grasses remained relatively stable with time and there was no significant year effect. Cover of unsown forbs was significantly higher in the natural regeneration compared with all other treatments. Finally, cover of bare ground was significantly higher in the crop and conservation headland, followed by natural regeneration compared with all other treatments.

FLOWER RESOURCES

There were highly significant differences in the abundance per m^{-2} of forb flowers between treatments in all years and overall (Table 6; Fig. 9). In year 1 flower abundance was significantly higher in the pollen and nectar margins compared with all others. Abundance was also higher in the wildflower margins compared with all treatments except natural regeneration. In years 2 and 3 abundance was significantly higher in the wildflower, and pollen and nectar margins compared with all others. However, from year 4 onwards flower abundance was significantly higher in the wildflower treatment compared with all others. There was no difference in abundance between the pollen and nectar margins and the other treatments. Flower abundance declined significantly with time from 9.2 per m^{-2} in 2002 to 4.4 m^{-2} in 2006. Much of this was due to the dramatic loss of flowers, particularly of sown species, in the pollen and nectar treatment (21.4 m^{-2} in 2002 to 3.0 m^{-2} in 2006). The abundance of flowers of sown species showed a virtually identical pattern of response. Abundance of flowers of unsown species was consistently and significantly higher in the natural regeneration compared with all other treatments. There was a significant decline in unsown flower abundance after year 1 which was more marked in the treatments sown with perennial seed mixtures. Finally, species richness of the flower resource was significantly higher in the wildflower treatment compared with all others in every year and overall. Richness was next highest in the natural regeneration and pollen and nectar treatments compared with all others.

The abundance of Asteraceae (Thistles and Daisies) flowers was significantly higher in the wildflower margins followed by natural regeneration compared with all other treatments (Table 7). Abundance of Fabaceae (Legumes) flowers was significantly higher in the pollen and nectar margins compared with all others followed by the wildflower treatment. Abundance of bee forage flowers was significantly higher in the wildflower margins, followed by the pollen and nectar margins compared with all other treatments.

POLLINATOR TRANSECTS

A total of 15,722 bumblebees were recorded on the field margin treatments during the experiment, representing nine species of *Bombus* and three species of *Psithyrus*. *B. lapidarius* was the most common bee (n=6815) closely followed by *B. pascuorum* (n=6066). Three rare bee species were recorded: *B. muscorum* (n=40); *B. ruderarius* (n=17); and *B. ruderatus* (n=148). Over the five years mean bumblebee counts per visit were significantly higher in the pollen and nectar treatment compared all other treatments (Table 8; Fig. 10a). Bee counts were also significantly higher in the wildflower margins compared with the remaining treatments except natural regeneration. In years 1 to 3 there were significantly more bees recorded per visit on the pollen and nectar margins compared with all other treatments. In year 4 bee abundance was equally high in the wildflower and pollen and nectar margins. In 2006 bees were significantly more abundant in the wildflower compared with the pollen and nectar treatment. Overall there was a highly significant increase in bee abundance from 5.8 per visit in 2002 to 9.0 in 2003 and then a steady decline to 1.2 in 2006. The significant year × treatment interaction reflected the marked decline in bee abundance in the pollen and nectar treatment after year 3. The abundance of critically important reproductive castes (queens and males) was significantly higher in the wildflower and pollen and nectar margins compared with all other treatments.

Species richness of bees per visit was significantly higher in the wildflower and pollen and nectar margins compared with the other treatments (Table 8; Fig. 10b). Richness was also higher in the non-crop margins (tussocky grass and natural regeneration) compared with the cropped treatments. In year 1 richness significantly higher in the Pollen and nectar margin compared the other treatments. However, after year 3 richness was significantly higher in the wildflower margins compared the other treatments. Finally, overall species richness of rare (UKBAP) bumblebees was significantly higher in the pollen and nectar margins compared with the cropped treatments and the tussocky grass margins.

Abundance of short- and long-tongued bees per visit was significantly higher in the pollen and nectar margins followed by the wildflower margins compared with all other treatments (Table 9). Abundance of short-tongued bees was also significantly higher in the natural regeneration margins compared with the cropped treatments. Finally, the abundance of Cuckoo bees was significantly higher in the wildflower, and pollen and nectar margins compared with the cropped treatments.

There was a highly significant positive relationship between log bee abundance and flower abundance on the field margins treatments (Fig. 11; $F_{1,34}$ = 141.29; P<0.001; R^2 = 80.6%). Flower and bee abundance were highest in the wildflower, and pollen and nectar margins, and lowest in the crop and conservation headland. Long-tongued bee species (e.g. *Bombus hortorum, B. pascuorum*) foraged preferentially on the sown legume *Trifolium pratense* (Fig. 12). In contrast, bees with intermediate tongue length (*B. lapidarius*) foraged on a mixture of sown legumes, including *T. pratense, Lotus corniculatus* and *T. hybridum*. Short-tongued bee species (*B. pratorum, B. terrestris / lucorum*) foraged on a wider range of sown (e.g. *T. hybridum, Rhinathus minor*) and unsown species (e.g. *Cirsium vulgare, C. arvense*).

There were large differences in the timing of flower resource availability between the wildflower and pollen and nectar margins (Fig. 13a). In early summer (May-June bee forage flowers were more abundant on the wildflower margins compared with the pollen and nectar margins. In late summer (July-August) the pattern was reversed. There were small differences in the abundance of bees in early summer between the two margins types (Fig. 13b). However, there were significantly more bees on the pollen and nectar margin in late summer. These seasonal differences in flower and bee abundance can be partly explained by differences in the flowering time of native compared to agricultural varieties of the key bee forage species *Trifoilum pratense* and *Lotus corniculatus* sown in the different margin treatments (Fig. 14a,b). Native varieties of these legume species sown in the wildflower margins flowered markedly earlier than agricultural varieties sown in the pollen and nectar margins.

A total of 9,076 butterflies were recorded on the margin treatments during the experiment, representing 25 species. The most abundant of these were *Maniola jurtina* (Meadow Brown; n=1952), *P. rapae* (Small White; n=1331), *P. brassicae* (Large White; n=931), *Cynthia cardui* (Painted Lady; n=725), and *Polyommatus icarus* (Common Blue; n=690). Several declining species were recorded, including *Lasiommata megera* (Wall Brown; n=26) and *Coenonympha pamphilus* (Small Heath; n=12). Over the 5 years total butterfly abundance per visit was significantly higher in the wildflower, and pollen and nectar margins compared with all other treatments (Table 10). Abundance in the other non-cropped treatments (tussocky grass and natural regeneration) was also significantly higher than for the cropped treatments. This pattern was relatively consistent with the exception of year 2 when abundance was significantly higher in the pollen and nectar treatment followed by the wildflower margins. Similarly, total abundance of immobile butterfly species was significantly higher in the pollen and nectar and wildflower margins compared with all other treatments. Numbers were also higher in the tussocky and natural regeneration margins compared with the crop. Treatment effects were less clear cut for the mobile butterflies. Overall abundance was significantly higher in the pollen and nectar margins, followed by the wildflower and natural regeneration treatments. However, the intensity of treatment effects diminished during the course of the experiment, so that there were no significant differences between treatments by year 5. In all cases, the significant time effects reflected the increase in butterfly abundance after year 1 followed by a gradual decline. There was a significant decline in butterfly abundance on the pollen and nectar margins relative to the other treatments.

Overall species richness of butterflies per visit was significantly higher in the wildflower and pollen and nectar margins, followed by the natural regeneration and tussocky grass margins compared with the cropped treatments (Table 11). This pattern was fairly consistent throughout the experiment. Similarly, richness of both mobile and immobile species was significantly higher in the wildflower, and pollen and nectar margins compared with all other treatments. Species richness of immobile species was also significantly higher in the remaining non-crop margin type compared with the cropped treatments. In the case of mobile species, richness was only significantly higher in the natural regeneration treatment compared with the crop. In all cases, there was a significant increase in species richness followed by a gradual decline with time. Once again richness declined more markedly in the pollen and nectar margins compared with the other treatments.

SOIL INVERTEBRATES

Soil cores from the non-crop margin treatments contained a significantly higher total number of invertebrates from a greater number of families and groups compared with the cropped treatments (Table 12). Importantly, the abundance of earthworms (Oligochaeta) was significantly higher in the three uncultivated margins treatments sown with perennial seed mixtures compared with the cultivated margin types (Fig. 14). Cores from the tussocky grass margins contained a significantly higher abundance of Araneae, Isopoda, Lepidoptera larvae, Diptera, Carabidae, and Hemiptera compared with the crop and conservation headlands. Similarly, abundance of Staphylinidae was significantly higher in the tussocky margins compared with the crop. The wildflower margins contained a significantly higher abundance of Prosobranchia with the natural regeneration margins and cropped treatments. Finally, the abundance of Pulmonata significantly higher in the wildflower margins compared with conservation headlands.

SOIL SURFACE ACTIVE INVERTEBRATES

Spring pitfall trapping recorded a total of 13,833 invertebrates comprising 28 families and 250 species. Autumn trapping resulted in 6,222 invertebrates comprising 27 families and 200 species. A total of 159 species were recorded in both spring and autumn trapping sessions. Overall species richness and total abundance of invertebrates caught in the spring was significantly lower in the tussocky grass margins compared with all other treatments (richness $F_{5,25}$=8.05; P<0.001; abundance $F_{5,25}$=6.13; P<0.001) (Fig. 17a,b). There was also a marked decline in species richness over the first 2 years ($F_{4,108}$=34.72; P<0.001), with numbers falling in the margins sown with perennial seed mixtures ($F_{20,108}$=2.81; P<0.001). There were significant, but smaller declines in abundance over the first 2 years ($F_{4,108}$=6.19; P<0.001) in all treatments. Closer analysis of feeding guilds showed significantly lower species richness and abundance of predators and seed predators in tussocky margins in the spring compared with most other margin types (Fig. 17a,b; Table 13a,b). In addition, abundance of decomposers was significantly lower in the crop compared with all other treatments except conservation headland. There was a highly significant increase in both the number and species richness of decomposers with time. In contrast, number and diversity of seed predators declined markedly in the perennial margins treatments after year 1 and the number and diversity of predators after year 2.

In the autumn total species richness over the four years was once again significantly lower in the tussocky margins compared with all other types ($F_{5,25}$=2.28; P<0.05) (Fig. 18a). This reflected significantly lower richness of predators and seed predators in this treatment compared with natural regeneration and conservation headlands (Fig. 18a; Table 14a). Richness of decomposers was also significantly higher in the wildflower margins compared with the crop and conservation headland. Overall species richness, together with that of decomposer and predators, showed small, but significant increases with time in all treatments ($F_{4,108}$=5.68; P<0.001). Total abundance of invertebrates was significantly higher in all the non-crop margins treatments compared with the crop ($F_{5,25}$=5.62; P<0.001) (Fig. 18b). Abundance was also higher in the wildflower and natural regeneration margins compared with the conservation headland. Overall abundance of seed predators was significantly higher in the natural regeneration margins compared with all treatments except wildflower and conservation headland (Fig. 18b; Table 14b). Abundance of decomposers was significantly higher in all non-crop margin treatment compared with the crop. Also, abundance was higher in all margins sown with perennial seed mixtures compared with conservation headlands.

Overall abundance, particularly that of decomposers and predators, increased significantly in all treatments with time ($F_{4,108}$ = 6.79; P<0.001).

CANOPY ACTIVE INSECTS

Summer sweep net sampling recorded a total of 194,745 canopy active invertebrates between 2003 and 2006 comprising 185 families and 728 species. Suction sampling recorded 56,147 invertebrates comprising 182 families and 623 species. A total of 371 species were common to both sampling methodologies. Species richness of the combined sample was significantly higher in the wildflower treatment compared with all others ($F_{5,25}$=37.27; P<0.001) (Fig. 19a). Richness was also higher in the other non-crop margin types compared with the cropped treatments. There was no significant change in overall richness with year ($F_{3,78}$=2.41; P>0.05) or any year × treatment interaction ($F_{15,78}$=1.94; P>0.05). Analysis of feeding guilds confirmed a similar pattern (Fig. 19a; Table 15a). Richness of decomposers was significantly higher in the wildflower and pollen and nectar margins compared with all other treatments. Decomposer diversity was also significantly higher the natural regeneration margin compared with the crop. Richness of herbivores was significantly higher in the wildflower margins compared with all other treatments except pollen and nectar. Herbivore richness was higher in the other non-crop margin treatments compared with the cropped treatments. Richness of pollinating insects was significantly higher in the wildflower margins compared with all other treatments except natural regeneration. Pollinator diversity was higher in the non-crop margins compared with the crop. Richness of predatory invertebrate was significantly higher in the wildflower margins compared with the cropped treatments. Diversity of parasitoids was significantly higher in the wildflower and pollen and nectar margins compared with the cropped treatments.

Total abundance of invertebrates caught by sweep netting and suction sampling was significantly higher in the wildflower, pollen and nectar and natural regeneration margins compared with the crop ($F_{5,25}$=6.60; P<0.001) (Fig. 19b). Abundance in the tussocky margins and conservation headlands was no different from the crop. There was no significant change in overall abundance with year ($F_{3,78}$=2.73; P>0.05) or any year × treatment interaction ($F_{15,78}$=0.76; P>0.05). Abundance of decomposers was significantly higher in the wildflower and pollen and nectar treatments compared with all other treatments (Fig. 19b; Table 15b). Decomposer abundance was also significantly higher in the other non-crop margin treatments compared with the crop. Herbivore abundance was significantly higher in the pollen and nectar, and wildflower treatments compared with all other treatments. Abundance of herbivores was also significantly higher in the non-cropped margins compared with the cropped treatments. Abundance of pollinators was significantly higher in the wildflower treatment compared with all others except the natural regeneration and pollen and nectar margins. Abundance was also significantly higher in the non-cropped margins compared with the cropped treatments. Predator abundance was significantly higher in the wildflower margins compared with all other treatments except the tussocky margins. Abundance in the other non-cropped margins was significantly higher than the crop. Finally, there was no significant difference in the abundance of parasitoids between treatments.

WINTER BIRD ABUNDANCE

A total of 3,284 birds representing 23 species were recorded on the Wild Bird Seed mixture patches and adjacent crop over the five years. Linnet (*Acanthis cannabina*) was the most abundant species (43%), followed by Greenfinch, (*Carduelis chloris*, 27%), Chaffinch (*Fringilla coelebs*, 7%) and Skylark (*Alauda arvensis*, 6%). Over 95% of the birds counted were recorded on the wild bird seed (WBS) mixture patch compared with the adjacent crop. Species richness, and total abundance of all birds, Granivorous passerines, and Farmland Bird Index species were all significantly higher in the WBS patches compared with the adjacent crops on each visit between December and March (Table 16a; Figs. 20a & 21a). However, the magnitude of these differences diminished considerably after the December visit for Farmland Bird Index species and after January for both total abundance and Passerine abundance. The magnitude of differences in species richness remained large until after the February visit. Numbers of Skylark were significantly higher in the WBS patch overall and for the December and February visits only.

Species richness, total abundance of all birds, Granivorous passerines, and Farmland Bird Index species were significantly higher in the WBS patches compared with the adjacent crops every winter between 2002/3 and 2006/7 (Table 16b; Figs. 20b & 21b). However, the magnitude of these differences diminished considerably after winter 2004/5 for total abundance, and number of Granivorous passerines and Farmland Bird Index species. This corresponded to a marked decline in the cover of the sown seed-bearing crop species (Fig. 22). Considerable differences remained in species richness up to 2005/6. Numbers of Skylark were only significantly higher on the WBS patch in 2006/7 and overall.

SMALL MAMMAL UTILISATION

A total of 368 individuals were caught in the wild bird seed (WBS) mix, adjacent crops and field margins, including 213 animals trapped in the winter of 2004 and 155 trapped in summer of 2005. Virtually all (93%) of small mammal captures were Wood Mouse *(Apodemus sylvaticus*). Bank Vole (*Clethrionomys glareolus*) and Field Vole (*Microtus agrestis*) accounted for the remaining 7% of catches, primarily on the field margins. There were no significant difference in the species richness of small mammal catches between the three habitat types in winter ($F_{2,6}$ = 0.27, $P > 0.05$). However, species richness was significantly higher in the field margin compared with the WBS patch in the summer ($F_{2,6}$ = 11.40, $P < 0.01$). Small mammal activity was significantly higher in the WBS patch compared with the crop and field margin during the winter months (Fig. 23) ($F_{2,6}$ = 14.10, $P < 0.01$). However, during the summer months the pattern of use was reversed with activity significantly higher in both the crop and field margin compared with the WBS patch ($F_{2,6}$ = 15.51, $P < 0.01$).

Discussion

EXTENSIFICATION OF MANAGEMENT *VS.* CREATION OF PROTECTED WILDLIFE HABITATS

The results of this long-term, multi-site experiment showed clear and consistent responses of soil, flora and fauna to a range of agri-environment scheme options (Fig. 2a). The inclusion of the conventionally managed crop as a control confirmed the detrimental effects of intensive agricultural management on biodiversity and many ecosystem functions (e.g. Tscharntke *et al.* 2005), and is an essential benchmark for such comparative studies (Perry *et al*. 2003). The extensification of management inputs into the crop as prescribed by the conservation headland treatment resulted in a small increase in annual plant diversity (Critchley *et al*. 2004), but this did not translate into a significant increase in overall flower abundance or diversity of associated invertebrates (Pywell *et al*. 2005b). Measures of biodiversity were frequently high in the conservation headlands, but often very variable (Fig. 2b). This reflected the relatively poor performance of this option on heavy soils where there was a large seed bank of highly competitive grass weeds, such as *Alopecurus myosuroides*, which further reduced plant diversity. It is also likely that continued, large inputs of inorganic fertiliser to this treatment resulted in high levels of competition from the crop which further reduced plant diversity (Mountford, Lakhani & Kirkham 1993). Indeed conservation headlands without fertiliser addition have proved to be an effective means of conserving declining arable plants (Walker *et al*. 2007), particularly on lighter soils.

The results clearly demonstrate that the most effective means of enhancing biodiversity in intensively managed arable systems is the complete removal of land from production and the creation of protected wildlife habitats (Feber, Smith & Macdonald 1996; Meek *et al*. 2002; Asteraki *et al*. 2004; Pywell *et al*. 2005b), thus proving the first hypothesis. It is possible to reliably create a diverse range of wildlife habitats despite high residual soil fertility and a large seed bank of competitive species (BD1404; Pywell *et al*. 2002). Five years of cutting and removal of vegetation failed to reduce the concentration of major nutrients compared with the conventionally managed crop (BD1425; Marrs *et al*. 1998; Pywell *et al*. 2007a). This confirms the intransigent nature of residual soil nutrient pools, particularly those of phosphorous and potassium, but suggests that soil fertility may not be a major constraint on the restoration of botanical diversity provided suitable species are sown and appropriate management applied (Pywell *et al*. 2002; 2007a). Allowing natural regeneration of vegetation at the field margin is a simple and popular management strategy under the agri-environment schemes (Stevenson 2007). Our results showed that a diverse community of annual plants rapidly colonised from the seed bank and hedge bottom. This provided good habitat for soil surface active invertebrates (Meek *et al*. 2002), and subsequent colonisation by perennial forbs, such as *Cirsium* spp., in later years proved attractive to pollinating insects (Kells, Holland & Goulson 2001; Pywell *et al*. 2006). However, the outcome of this management strategy was variable between sites (Fig. 2b), depending on local species pool and management history, and other studies have shown that succession rapidly takes place to a species-poor, perennial grass sward in the absence of annual cultivation (Carvell *et al*. 2004). Furthermore, this treatment served as a reservoir of undesirable agricultural weeds which spread into the crop (Meek *et al*. 2007).

Sowing farmland with seed mixtures is a more effective and reliable means of directing succession to a desired endpoint for the creation of specific wildlife habitats (BD1404; BD1425; Pywell *et al*. 2002; 2007a). Sowing a simple, low-cost mixture of tussocky grass species is the most popular means of achieving this under the agri-environment schemes (Stevenson 2007). The competitive, generalist grass species rapidly established on the fertile ex-arable soils and were effective at excluding undesirable arable weed species (Critchley *et al*. 2004). This consistently resulted in a structurally complex, but very species poor-vegetation. However, this dense, sheltered vegetation did provide an effective physical barrier against the drift of pesticide and fertiliser into the hedge bottom (Miller & Lane 1999). It was also good habitat for hibernating carabid and staphylinid beetles, and spiders, and canopy-active predatory insects in the summer (Collins *et al.* 2003a,b; Pywell *et al*. 2005a). The low densities of ground-active invertebrate probably reflects their severely restricted activity in such dense vegetation. The addition of perennial wildflowers or legume species to the seed mixture increased the cost, but the resultant diverse vegetation had significant benefits for many invertebrate groups, particularly detrivores, herbivores and pollinators (e.g. Lagerlöf *et al.* 1992; Feber, Smith & Macdonald 1996; Meek *et al.* 2002; Carvell *et al*. 2004; Pywell *et al*. 2005b), especially if the margin occupies a sunny, sheltered position (Pywell *et al.* 2004).

TARGETED *VS.* GENERALIST MANAGEMENT PRESCRIPTIONS

This study provided good evidence that three of the management prescriptions which were specifically focused on declining farmland taxa (cultivated natural regeneration, pollen and nectar, and wild bird seed mixtures) were considerably more effective in enhancing both the target taxa and associated biodiversity than those designed to deliver a broader range of environmental benefits (conservation headland, tussocky grass margin). All three options were developed from an evidence-based understanding of the ecology and habitat requirements of the target species. Declining arable plant species are known to be associated with low intensity cropping systems which provide open, competition free habitat (Andreasen *et al*. 1996; Marshall *et al*. 2003), particularly at the field edge (Wilson & Aebischer 1995). Annual, light cultivation of field margins removed from agricultural production is the best means of re-creating these environmental conditions and maintaining an open, diverse community of annual plants (Critchley *et al*. 2004; Walker *et al*. 2007).

Recent research has shown a significant reduction in the abundance of key bumblebee forage species in the wider countryside, especially members of the Fabaceae (legumes), Asteraceae (thistles and daisies) and Lamiaceae (mints) (Carvell *et al*. 2006a). Sowing simple mixtures of pollen- and nectar-rich legume species proved to be the most effective and reliable means of providing high quality late-summer foraging habitat for bumblebees (Carvell *et al*. 2004, 2007; Pywell *et al*. 2006), including rare species (Carvell *et al*. 2006b).

Finally, there is good evidence that increased winter mortality is a key factor causing serious declines in farmland bird populations (e.g. Peach *et al*. 1999; Siriwardena *et al*. 2000). This has been linked to the loss of winter food resources caused by highly efficient and intensive modern agricultural practices, and in particular the decline of winter stubbles and mixed farming (Stoate *et al*. 2004). Field experiments and monitoring have demonstrated that sowing simple mixtures of seed-bearing crops is an effective means of supplementing the over-winter food supply for farmland birds (Stoate *et al*. 2004; Bradbury *et al.* 2004). Finally, there is evidence of potentially additive or synergistic benefits of these targeted habitats on other declining taxa. For example, the annual cultivation of the wild bird seed mixture patches provided good habitat for declining arable plants, bumblebees and small mammals (Carvell *et al*. 2006c; Pywell *et al*. 2007b).

MAINTENANCE OF HABITAT QUALITY IN THE LONGER TERM

The results showed serious declines in the quality of two of the targeted habitats after three years (pollen and nectar and wild bird seed mixtures), confirming the value of long-term experimentation. This could have serious detrimental effects on populations of farmland birds and bumblebees in the wider countryside, and has important implications for future agri-environment scheme policy and advice. The cover of sown *Trifolium* species declined by over 80% after year 3 (Fig. 8) and was replaced by grasses. *Trifolium pratense* and *T. hybridum* are short-lived perennials which are well adapted to fertile ex-arable soils, but do not persist well under cutting or grazing management (Frame, Charlton & Laidlaw 1998), due to low rates of seedling regeneration (*R.F Pywell unpublished data*; BD1623). Importantly, the species-rich wildflower margins maintained a consistently high supply of pollen and nectar resources over the five year period. They also contained both early- and late-flowering species which are important for bumblebee reproductive castes. Similarly, the establishment and cover of seed-bearing crop species declined by and average of 76% after year 3 (Fig. 23) due to competition from weed species and herbivory by insect pests, such as flea beetles (*Phyllotreta* spp.) and pollen beetles (*Meligethes aeneus*) (BD1623; Pywell *et al*. 2007b).

ENHANCED DELIVERY OF ECOSYSTEM FUNCTIONS AND SERVICES

In this study we examined the potential of agri-environment scheme options to increase the efficiency of delivery of key ecosystem functions and services, thus mitigating some of the detrimental effects of intensive agriculture (Hector & Bagchi 2007). Much of the global carbon pool is held in the soil (Batjes 1996). Increased loss of soil carbon to the atmosphere under rising temperature regimes is therefore of critical concern (Knorr *et al*. 2005; Powlson 2005). A recent study has estimated the mean loss of carbon from soils in England and Wales to be 0.6% $year^{-1}$ (relative to the existing carbon content) (Bellamy *et al*. 2005). These losses are irrespective of land use type and are thought to be driven by rising temperature increasing the rate of organic matter decomposition by microbial communities. The significant increase in soil organic matter (21% relative to the crop) in the wildflower margins suggest there is considerable potential to off-set these losses of carbon though existing agri-environment scheme polices. This rapid accumulation of carbon is likely to reflect the cessation of disturbance by cultivation, together with the co-existence of species with different growth rates and root architecture (De Deyn, Cornelissen & Bardgett 2007). In addition, our results showed that removal of land from production and cultivation increased the abundance of ecosystem engineers, such as earthworms and other soil macro-invertebrates, which re-distribute carbon through the soil profile and enhance the rate of nutrient cycling (Lavelle *et al.* 1997).

Sowing diverse mixtures of wildflowers, and pollen- and nectar-rich legumes species significantly enhanced both the diversity and abundance of all insect pollinators, including bumblebees. This is likely to increase the resilience of pollination services for nearby crop and wildflower communities to environmental perturbations and disease (Daily 1997; Ghazoul 2005). Finally, there is evidence that the complexity and therefore the stability of invertebrate food webs are higher in the non-cropped margins, and particularly those sown with wildflowers. This will have important implications for the regulation of pest species and the strength of trophic cascades (e.g. Strong 1992; Shurin *et al.* 2002).

CONCLUSIONS AND RECOMMENDATIONS

This study provides the first comprehensive, long-term assessment of the effectiveness of UK agri-environment scheme prescriptions for arable land. We can conclude that complete removal of land from production to create protected wildlife areas is the most practical and effective means of enhancing biodiversity, and the delivery of key ecosystem functions and services. Sowing seed mixtures is an effective and reproducible means of directing succession to a desired endpoint for the creation of specific wildlife habitats. Management prescriptions specifically targeted to the requirements of declining taxa (arable plants, bees and birds) were more cost-effective than those designed to deliver a broader range of environmental benefits. However, it was not possible to maintain the quality of some of these habitats *in situ* for long periods. It is therefore recommended that these are treated as short-lived, rotational options which are re-established every 2-3 years on new areas of farmland. The cessation of cultivation and the creation of species-rich vegetation significantly increased diversity of soil ecosystem engineers. This had important, positive benefits on the soil carbon cycle. Similarly, creation of species-rich field margins resulted in the largest increases in trophic complexity. This is likely to increase the efficiency of pollination and pest control services, and their resilience of to environmental perturbations. In conclusion, no single management prescription fulfilled all the required functions. Nevertheless, field margins sown with a diverse mixture of wildflowers exhibited the greatest multi-functionality. They also appeared to be the most effective means of increasing the efficiency of ecosystem service delivery. The best strategy would therefore to promote greater uptake of this particular option which is currently rare in the countryside, whilst at the same time maximising habitat heterogeneity by encouraging the creation as a wide variety of other habitat types as possible.

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Knowledge transfer activities

Between 2001 and 2007 the results of this and related projects (BD1623, BD1625) were disseminated to more than 3000 project officers, farmers, agronomists and scientists through organised training events and presentations given by the Wildlife Farming Company. It is estimated that agronomists and growers who attended these events are responsible for the management of more than 1,000,000 ha of farmland in the UK.

The results of BD1624 have also played a key role in the success of Operation Bumblebee (www.operationbumblebee.co.uk/) – a project run by Syngenta UK (a Buzz partner) which aims to provide farmers and advisors with the training and skills necessary to establish high quality wildlife habitat on farmland for bumblebee bees at over 1,000 locations in the UK.

Appendix 1. Tables and figures

Table 1. Details of the field margin treatments and Environmental Stewardship options.

Treatment	Description	ELS code	Points ha^{-1}
1. Crop	Conventional crop to edge.	-	-
2. Conservation headland	Crop managed with restricted herbicide and insecticide.	EF9	100
3. Natural regeneration	Cut and light cultivation annually in Sep.	EF11	400
4. Tussocky grass	5 grass species sown at 20 kg ha^{-1}. Uncut.	EE3	400
5. Pollen and nectar	4 legume and 4 fine-leaved grass species sown at 20 kg ha^{-1}. Cut annually in Sep.	EF4	450
6. Wildflower and grass	21 forb and 4 fine-leaved grass species sown at 37 kg ha^{-1}. Cut annually in Sep.	EE3 supplement	400

Table 2. Treatment effects on soil pH and nutrient concentrations.

Treatment	pH		%Nitrogen		P mg/l		K mg/l		Mg mg/l	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Crop	7.41	0.23	0.19	0.01	35.35	8.35	215.58	39.86	146.83	75.84
Conservation headland	7.39	0.24	0.20	0.01	32.42	6.15	219.00	51.73	120.83	53.59
Natural regeneration	7.24	0.20	0.19	0.02	32.57	7.68	214.75	38.11	138.58	60.17
Tussocky grass	7.09	0.32	0.19	0.02	32.60	9.08	218.92	28.15	128.33	49.54
Pollen and nectar	7.16	0.30	0.21	0.02	32.60	6.92	217.67	52.82	133.75	58.91
Wildflower	7.20	0.22	0.21	0.02	37.48	12.55	212.50	38.60	150.67	68.64
ANOVA $F_{5,25}$	2.55		1.32		0.30		0.03		1.11	
P	ns		ns		ns		ns		ns	

ns = no significant difference.

Table 3. Treatment effects on mean and standard deviation in sward height (cm). Values are estimated from ten randomly placed 30 cm diameter drop disks per plot. Means with the same letter in the same column are not significantly different (*P*> 0.05).

	Mean height (cm)					Standard deviation height (cm)				
	2003	**2004**	**2005**	**2006**	**Overall**	**2003**	**2004**	**2005**	**2006**	**Overall**
Crop	62.74ab	59.06a	72.01a	44.45	60.13a	10.76	5.47	4.69b	6.42	6.83bc
Conservation headland	66.69a	55.67a	75.13a	40.83	60.48a	10.67	5.23	5.08b	5.95	6.73c
Natural regeneration	32.08c	28.58b	29.53b	32.85	32.62b	11.22	6.72	9.12a	11.46	9.63a
Tussocky grass	24.76c	27.54b	33.61b	40.46	31.59b	7.43	5.56	8.38ab	13.15	8.63abc
Pollen and nectar	39.07c	32.02b	32.97b	26.43	30.76b	11.40	7.83	10.09a	7.78	9.27ab
Wildflower	39.70bc	31.95b	36.49b	34.39	35.63b	9.35	6.53	7.47ab	8.08	7.86abc
ANOVA F-values										
Treatment $_{5,25}$	10.75	25.17	27.01	1.20	33.12	0.97	1.53	5.93	2.74	4.45
	***	***	***	ns	***	ns	ns	***	*	**
Year $_{3,78}$					4.89					9.31
					**					***
Year × treatment $_{15,78}$					2.62					1.66
					**					ns

ns = no significant difference; * = *P* < 0.05; ** = *P* < 0.01; *** = *P* < 0.001

Table 4. Treatment effects on the mean species richness per m^{-2} of the vegetation communities between 2002 and 2006. Means with the same letter in the same column are not significantly different (P> 0.05).

	Total						Annuals					
	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall
Crop	3.3c	4.1c	4.8c	3.2e	5.5b	4.2e	2.9d	3.8b	4.5bc	3.0bc	4.8b	3.8bc
Conservation headland	6.7c	8.3b	5.3bc	5.0de	5.5b	6.2de	5.4bcd	7.9a	5.0b	4.5b	5.1b	5.6b
Natural regeneration	11.3b	12.9a	14.0a	12.1b	12.9a	12.6b	8.3a	10.2a	11.4a	7.5a	9.0a	9.3a
Tussocky grass	12.1b	7.6b	7.5bc	6.9cd	6.6b	8.1cd	5.7abc	1.2bc	1.0d	1.1c	1.1c	2.0c
Pollen and nectar	9.8b	6.8bc	9.3b	9.3bc	8.3b	8.7cd	4.1cd	0.3c	3.0cd	2.7bc	2.2bc	2.5c
Wildflower	20.2a	15.7a	16.7a	15.6a	16.9a	17.0a	6.7ab	1.1bc	1.8d	1.8c	2.7bc	2.8c
ANOVA F-values												
Treatment $_{5,25}$	67.00	25.93	28.20	40.73	21.25	65.09	10.34	35.37	44.90	15.16	15.68	35.31
	***	***	***	***	***	***	***	***	***	***	***	***
Year $_{4,108}$						5.47						11.16
						**						***
Year × treatment $_{20,108}$						3.63						7.32
						***						***

	Perennials						Grasses					
	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall
Crop	0.4d	0.4d	0.3d	0.2c	0.7c	0.4d	1.8d	2.7c	2.6cd	1.9bc	2.0b	2.2c
Conservation headland	1.3d	0.5d	0.3d	0.5c	0.4c	0.6d	3.1cd	3.7bc	2.4cd	2.6b	2.4b	2.8c
Natural regeneration	3.1c	2.7c	2.6c	4.6b	3.8b	3.4c	3.8c	4.9ab	4.7ab	5.3a	5.2a	4.8ab
Tussocky grass	6.3b	6.5b	6.5b	5.8b	5.5b	6.1b	7.1a	5.3a	5.1a	4.8a	4.7a	5.4a
Pollen and nectar	5.7b	6.4b	6.3b	6.6b	6.2b	6.2b	3.8c	3.2c	4.1abc	5.7a	5.5a	4.5ab
Wildflower	13.5a	14.6a	15.0a	13.8a	14.2a	14.2a	5.3b	3.2c	3.4bcd	4.3a	5.3a	4.3b
ANOVA F-values												
Treatment $_{5,25}$	323.29	168.26	98.78	74.57	57.04	294.38	31.01	10.43	10.71	22.22	13.24	28.23
	***	***	***	***	***	***	***	***	***	***	***	***
Year $_{4,108}$						0.15						3.17
						ns						*
Year × treatment $_{20,108}$						1.45						3.63
						ns						***

	Forbs				
	2002	2003	2004	2005	2006
Crop	1.6e	1.5c	2.2c	1.4c	3.5c
Conservation headland	3.7d	4.7c	2.9c	2.4c	3.1c
Natural regeneration	7.6b	8.1b	9.3b	6.8b	7.6b
Tussocky grass	5.0cd	2.3c	2.4c	2.1c	1.9c
Pollen and nectar	6.1bc	3.6c	5.2c	3.6c	2.9c
Wildflower	14.9a	12.5a	13.3a	11.3a	11.6a
ANOVA F-values					
Treatment $_{5,25}$	90.72	31.91	40.57	40.87	18.09
	***	***	***	***	***
Year $_{4,108}$					
Year × treatment $_{20,108}$					

ns = no significant difference; * = P < 0.05; ** = P < 0.01; *** = P < 0.001

Table 5. Treatment effects on the mean percentage cover of grasses, forbs and bare ground between 2002 and 2006. Means with the same letter in the same column are not significantly different (*P*> 0.05).

	% sown grasses						% sown forbs						%unsown grasses						%unsown forbs						% bare ground					
	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall
Crop	0.4d	0.0c	0.0d	0.0c	0.0d	0.1c	0.0c	0.0b	0.0c	0.0b	0.0b	0.0c	73.1a	63.8a	71.6ab	68.7a	51.8a	65.8ab	1.9b	1.3c	7.9b	2.2c	10.1ab	4.7b	26.3a	39.2a	25.3a	33.0a	36.9a	32.1a
Conservation headland	0.1d	0.0c	0.0d	0.0c	0.0d	0.0c	0.0c	0.0b	0.0c	0.0b	0.0b	0.0c	79.1a	74.5a	75.9a	75.6a	56.8a	72.4a	10.9b	12.4ab	12.3b	4.9c	5.6ab	9.2b	21.0abc	22.9ab	16.9ab	26.4a	38.7a	25.2a
Natural regeneration	2.6d	0.3c	0.1cd	2.3c	0.9d	1.2c	0.5c	0.9b	1.1c	15.6b	12.2b	6.1c	37.1b	62.2a	56.4b	59.6ab	50.9a	53.2b	54.3a	25.2a	34.9a	20.5a	24.9a	32.0a	24.0ab	14.6bc	11.7bc	7.9b	15.3b	14.7b
Tussocky grass	80.9a	84.0a	92.9a	83.6a	86.8a	85.6a	0.8c	0.6b	1.3c	3.7b	1.1b	1.5c	13.0c	1.9b	2.7c	6.6cd	5.8c	6.0c	18.2b	5.3c	4.6b	5.3c	7.0c	8.1b	5.7bcd	3.9c	0.2c	3.5b	1.8b	3.0c
Pollen and nectar	62.4b	30.7b	28.8b	38.9b	52.3b	42.6b	80.6a	83.6a	58.6b	17.0b	11.5b	50.3b	6.5c	0.8b	5.8c	34.2bc	25.4bc	14.5c	11.5b	1.0c	11.6b	10.4ab	9.4c	8.8b	2.0d	0.1c	1.8c	0.7b	2.9b	1.5c
Wildflower	49.9c	30.1b	19.7bc	28.2b	25.7c	30.7b	51.7b	74.2a	82.0a	69.8a	57.8a	67.1a	10.8c	0.5b	0.3c	3.9d	12.7c	5.6c	10.2b	3.2c	2.5b	3.4c	4.7c	4.8b	2.6cd	0.5c	0.2c	0.2b	2.1b	1.1c
ANOVA F-values																														
Treatment $_{5,25}$	200.83	55.71	59.85	53.48	82.45	137.45	102.75	109.66	70.22	37.25	23.08	212.62	49.07	37.05	91.10	21.35	8.94	77.89	17.15	9.76	7.52	6.33	4.00	22.94	7.02	17.94	13.24	13.02	13.21	40.96
	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	**	***	***	***	***	***	***	***
Year $_{4,108}$						8.25						9.23						1.66						7.97						2.20
						***						***						ns						***						ns
Year × treatment $_{20,108}$						5.65						14.59						2.88						2.53						1.09
						***						***						***						**						ns

ns = no significant difference; * = *P* < 0.05; ** = *P* < 0.01; *** = *P* < 0.001

Table 6. Treatment effects on mean abundance and species richness of the forb flower resource per pollinator visit between 2002 and 2006. Means with the same letter in the same column are not significantly different (*P*> 0.05).

	Total flowers m^{-2}						Sown species m^{-2}						Unsown species m^{-2}						Richness per plot					
	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall
Crop	0.2d	0.7b	1.6b	0.5b	1.7b	0.9d	0.0c	0.0b	0.0b	0.0b	0.0b	0.0c	0.2b	0.7b	1.6b	0.5b	1.7ab	0.9b	2.5e	2.3b	3.3c	2.6c	3.6b	2.9d
Conservation headland	1.4d	1.8b	2.1b	0.7b	1.1b	1.4d	0.0c	0.0b	0.0b	0.0b	0.0b	0.0c	1.4b	1.8b	2.1ab	0.7b	1.1ab	1.4b	3.3de	3.3b	3.3c	2.6c	2.8b	3.1d
Natural regeneration	11.5bc	6.7b	3.7b	10.5b	4.6b	7.4c	0.0c	0.2b	0.1b	5.7b	0.6b	1.3c	11.5a	6.5a	3.7a	4.9a	4.0a	6.1a	8.6b	7.4a	6.3b	6.6b	6.0b	7.0b
Tussocky grass	4.0cd	1.0b	0.9b	0.9b	0.7b	1.5d	0.0c	0.2b	0.4b	0.3b	0.3b	0.2c	3.9b	0.8b	0.5b	0.5b	0.5b	1.2b	5.1cd	3.7b	3.8bc	4.1bc	3.3b	4.0cd
Pollen and nectar	24.1a	23.4a	20.4a	10.5b	3.5b	16.4b	21.4a	22.8a	19.9a	9.8b	3.0b	15.4b	2.7b	0.5b	0.5b	0.7b	0.5b	1.0b	6.1c	4.8b	5.7b	5.7b	4.0b	5.3bc
Wildflower	13.7b	33.3a	25.1a	34.9a	14.5a	24.3a	10.0b	33.0a	24.8a	33.8a	13.9a	23.1a	3.7b	0.3b	0.3b	1.0b	0.6b	1.2b	11.4a	8.5a	9.8a	11.4a	9.5a	10.1a
ANOVA F-values																								
Treatment $_{5,25}$	17.84	14.73	24.34	32.47	14.13	75.95	31.43	15.76	25.58	28.26	16.47	76.70	8.44	8.48	7.94	6.98	3.54	17.26	58.39	16.95	17.82	23.53	11.24	36.42
	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	*	***	***	***	***	***	***	***
Year $_{4,108}$						5.93						6.29						9.12						6.09
						***						***						***						***
Year × treatment $_{20,108}$						4.90						5.06						2.13						2.00
						***						***						*						*

ns = no significant difference; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

Table 7. Treatment effects on mean flower abundance of the major forb families per pollinator visit between 2002 and 2006. Means with the same letter in the same column are not significantly different (*P*> 0.05).

	Asteraceae m^{-2}						**Fabaceae m^{-2}**						**Bee forage flowers m^{-2}**					
	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall
Crop	0.0	0.4b	0.3b	0.1b	0.2b	0.2c	0.0b	0.0b	0.0b	0.0b	0.0b	0.0c	0.1c	0.2b	0.7b	0.2c	0.9b	0.4c
Conservation headland	0.2	0.2b	0.5b	0.1b	0.1b	0.2c	0.0b	0.0b	0.0b	0.0b	0.0b	0.0c	0.8c	0.8b	0.5b	0.4c	0.3b	0.5c
Natural regeneration	5.4	3.8b	1.2b	2.5b	0.9b	2.8b	0.0b	0.0b	0.2b	5.1b	0.1b	1.1c	3.1bc	1.2b	1.8b	8.3bc	2.6b	3.4c
Tussocky grass	1.4	0.4b	0.4b	0.3b	0.6b	0.6c	0.0b	0.5b	0.4b	0.1b	0.0b	0.2c	1.2bc	0.8b	0.8b	0.6c	0.7b	0.8c
Pollen and nectar	0.7	0.5b	0.2b	0.5b	0.4b	0.5c	21.4a	22.8a	19.8a	9.6ab	2.9ab	15.3a	21.8a	23.1a	20.2a	10.3b	3.3b	15.7b
Wildflower	4.3	13.3a	10.2a	12.0a	3.8a	8.7a	1.6b	13.7a	12.8a	16.8a	7.5a	10.5b	8.6b	28.8a	24.3a	30.5a	12.0a	20.8a
ANOVA F-values																		
Treatment $_{5,25}$	2.59	23.98	138.40	49.09	15.21	55.33	48.17	14.58	17.07	9.38	7.03	65.00	22.38	19.46	25.73	30.80	11.90	140.36
	ns	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
Year $_{4,108}$						4.45						4.37						6.00
						*						**						***
Year × treatment $_{20,108}$						4.79						4.54						5.33
						***						***						***

ns = no significant difference; * = *P* < 0.05; ** = *P* < 0.01; *** = *P* < 0.001

Table 8. Treatment effects on mean bumblebee species richness and the abundance of different castes per visit between 2002 and 2006. Means with the same letter in the same column are not significantly different ($P > 0.05$).

	Species richness						Species richness BAP bees					
	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall
Crop	0.0d	0.0c	0.0b	0.0c	0.1bc	0.0c	0.0b	0.0	0.0	0.0	0.0b	0.0b
Conservation headland	0.0d	0.0c	0.0b	0.0c	0.0c	0.0c	0.0b	0.0	0.0	0.0	0.0b	0.0b
Natural regeneration	0.7bc	0.6bc	0.5b	1.0ab	0.3bc	0.6b	0.0b	0.0	0.0	0.3	0.0ab	0.1ab
Tussocky grass	0.3cd	0.8b	0.5b	0.3bc	0.2bc	0.4b	0.0b	0.0	0.2	0.0	0.0ab	0.0b
Pollen and nectar	2.3a	2.1a	1.8a	0.9b	0.6b	1.5a	0.5a	0.5	0.4	0.3	0.1ab	0.4a
Wildflower	0.9b	2.0a	1.8a	1.7a	1.3a	1.5a	0.0b	0.3	0.1	0.2	0.3a	0.2ab
ANOVA F-values												
Treatment $_{5,25}$	58.22	48.25	27.30	15.65	19.14	65.12	5.00	1.87	2.22	1.35	3.20	3.61
	***	***	***	***	***	***	**	ns	ns	ns	*	*
Year $_{4,108}$						10.80						0.41
						***						ns
Year × treatment $_{20,108}$						7.42						1.32
						***						ns

	Total bees						Total queens						Total males				
	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006
Crop	0.0c	0.0d	0.0c	0.0c	0.1c	0.0d	0.0b	0.0b	0.0b	0.0b	0.0	0.0b	0.0c	0.0c	0.0b	0.0b	0.0b
Conservation headland	0.1c	0.0d	0.0c	0.0c	0.0c	0.0d	0.0b	0.0b	0.0b	0.0b	0.0	0.0b	0.0c	0.0c	0.0b	0.0b	0.0b
Natural regeneration	3.6b	1.7c	1.3c	6.2ab	0.5bc	2.7c	0.0b	0.0ab	0.0b	0.1ab	0.0	0.0b	1.1ab	0.5ab	0.4ab	0.4ab	0.1b
Tussocky grass	0.9bc	2.1c	1.0c	0.7bc	0.4c	1.0c	0.0b	0.0ab	0.0ab	0.0b	0.0	0.0b	0.4ab	0.7ab	0.2ab	0.2b	0.1b
Pollen and nectar	27.6a	40.4a	20.5a	7.2a	1.9b	19.5a	0.6a	0.3ab	0.1a	0.0ab	0.0	0.2a	2.1a	1.3a	0.4ab	0.4ab	0.2a
Wildflower	2.7b	9.8b	7.6b	8.5a	4.4a	6.6b	0.0b	0.4a	0.1a	0.2a	0.0	0.2a	0.2bc	0.3bc	0.6a	0.4a	0.5a
ANOVA F-values																	
Treatment $_{5,25}$	32.21	56.98	43.36	13.36	19.02	77.47	12.85	4.49	6.29	4.50	1.21	11.69	7.24	13.11	4.47	3.31	7.95
	***	***	***	***	***	***	***	**	***	***	ns	***	***	***	**	*	***
Year $_{4,108}$						10.67						5.09					
						***						**					
Year × treatment $_{20,108}$						6.94						5.25					
						***						***					

ns = no significant difference; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

Table 9. Treatment effects on mean abundance of bumblebee feeding guilds per visit between 2002 and 2006. Means with the same letter in the same column are not significantly different ($P > 0.05$). Only species with mean total abundance of >0.5 per treatment are included.

	Short-tongued bees						**Long-tongued bees**						**Cuckoo bees**					
	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall
Crop	0.0c	0.0d	0.0b	0.0d	0.0c	0.0d	0.0c	0.0c	0.0c	0.0c	0.0b	0.0c	0.0b	0.0b	0.0b	0.0b	0.1b	0.0b
Conservation headland	0.1c	0.0d	0.0b	0.0d	0.0c	0.0d	0.0c	0.0c	0.0c	0.0c	0.0b	0.0c	0.0b	0.0b	0.0b	0.0b	0.0b	0.0b
Natural regeneration	3.4b	1.3c	1.1b	1.8bc	0.4bc	1.6c	0.2c	0.3c	0.1c	4.1ab	0.1b	1.0c	0.0ab	0.2ab	0.1ab	0.3ab	0.0b	0.1ab
Tussocky grass	0.8bc	1.4c	0.6b	0.5cd	0.3bc	0.7cd	0.1c	0.4c	0.3bc	0.1bc	0.1b	0.2c	0.0ab	0.3ab	0.1ab	0.1ab	0.0b	0.1ab
Pollen and nectar	15.7a	13.9a	7.3a	6.0a	1.3ab	8.8a	11.5a	26.0a	12.9a	1.1bc	0.6b	10.4a	0.4a	0.5a	0.4ab	0.1ab	0.0b	0.3a
Wildflower	0.8bc	5.0b	4.4a	4.0a	2.3a	3.3b	2.0b	4.7b	2.5b	4.2a	1.8a	3.0b	0.0b	0.1ab	0.6a	0.4a	0.3a	0.3a
ANOVA F-values																		
Treatment $_{5,25}$	20.62	56.89	24.92	10.16	12.45	43.99	102.89	26.83	15.52	8.58	10.86	46.08	3.20	2.03	3.45	3.93	7.01	7.84
	***	***	***	***	***	***	***	***	***	***	***	***	*	ns	*	**	***	***
Year $_{4,108}$						8.81						8.76						2.51
						***						***						Ns
Year × treatment $_{20,108}$						5.85						8.74						2.18
						***						***						*

ns = no significant difference; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

Table 10. Treatment effects on mean abundance of butterflies per visit between 2002 and 2006. Data are means per visit. Values with the same letter in the same column are not significantly different (*P*> 0.05).

	Total						Immobile species						Mobile species					
	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall
Crop	0.5c	0.4d	0.7c	0.6c	0.8cd	0.6c	0.2c	0.2c	0.1c	0.3d	0.3c	0.2c	0.3d	0.2b	0.6c	0.3	0.5	0.4d
Conservation headland	0.9bc	0.9d	0.9c	0.8c	0.4d	0.8c	0.4bc	0.4c	0.2c	0.5cd	0.2c	0.3c	0.5cd	0.5b	0.6c	0.3	0.3	0.4d
Natural regeneration	1.5b	2.4c	2.6b	2.8ab	1.7bc	2.2b	0.6bc	1.3b	1.5b	1.7bc	1.3b	1.3b	1.0bc	1.2b	1.1bc	1.1	0.5	1.0bc
Tussocky grass	1.8b	2.3c	2.1b	2.0bc	2.0bc	2.0b	1.1b	1.6b	1.4b	1.7bc	1.5b	1.4b	0.7cd	0.7b	0.7c	0.3	0.4	0.6cd
Pollen and nectar	6.4a	13.1a	5.3a	2.9ab	2.7ab	6.1a	2.4a	3.5a	2.8ab	2.0ab	2.1ab	2.6a	3.9a	9.6a	2.5a	0.9	0.6	3.5a
Wildflower	4.1a	6.2b	6.1a	5.3a	4.0a	5.1a	2.5a	4.2a	4.2a	4.3a	3.2a	3.7a	1.6b	2.0b	1.8ab	0.9	0.8	1.4b
ANOVA F-values																		
Treatment $_{5,25}$	48.16	67.15	47.23	11.26	20.23	59.38	23.44	44.12	42.22	12.37	27.54	50.11	33.29	17.29	11.01	3.51	2.45	32.71
	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	*	ns	***
Year $_{4,108}$						6.70						2.77						11.99
						***						*						***
Year × treatment $_{20,108}$						3.23						1.09						3.92
						*						ns						***

ns = no significant difference; * = *P* < 0.05; ** = *P* < 0.01; *** = *P* < 0.001

Table 11. Treatment effects on mean species richness of butterflies per visit between 2002 and 2006. Data are means per visit. Values with the same letter in the same column are not significantly different (*P*> 0.05). Only species with mean abundance of >0.8 per treatment are included.

	Total						Immobile species						Mobile species					
	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall
Crop	0.5d	0.4c	0.5c	0.5c	0.5cd	0.5c	0.2d	0.1c	0.1c	0.2c	0.2cd	0.2c	0.3c	0.2c	0.4b	0.3ab	0.3ab	0.3c
Conservation headland	0.7cd	0.7bc	0.6c	0.4c	0.3d	0.6c	0.3cd	0.3c	0.2c	0.2c	0.1d	0.2c	0.4c	0.4bc	0.4b	0.2b	0.2b	0.3bc
Natural regeneration	1.1c	1.3b	1.3b	1.2ab	1.0bc	1.2b	0.4cd	0.7b	0.7b	0.6b	0.7bc	0.6b	0.7bc	0.5bc	0.6ab	0.6a	0.3ab	0.5b
Tussocky grass	1.1c	1.2b	1.1b	1.0bc	1.0bc	1.1b	0.6bc	0.8b	0.7b	0.7b	0.7bc	0.7b	0.5c	0.4bc	0.4b	0.2ab	0.3ab	0.4bc
Pollen and nectar	1.9b	2.4a	2.3a	1.8a	1.6a	2.0a	1.0ab	1.4a	1.4a	1.2a	1.1a	1.2a	0.9b	0.9b	0.9a	0.6a	0.5a	0.8a
Wildflower	2.6a	2.9a	2.0a	1.1b	1.2ab	2.0a	1.0a	1.2a	1.1ab	0.8b	0.9ab	1.0a	1.6a	1.7a	0.9a	0.4ab	0.3ab	1.0a
ANOVA F-values																		
Treatment $_{5,25}$	43.13	41.53	28.72	14.60	13.75	54.69	18.79	37.92	28.91	18.19	14.42	42.30	25.70	17.06	8.24	4.07	3.75	26.70
	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	**	*	***
Year $_{4,108}$						10.47						3.01						16.90
						***						*						***
Year × treatment $_{20,108}$						3.44						1.33						4.35
						***						ns						***

ns = no significant difference; * = *P* < 0.05; ** = *P* < 0.01; *** = *P* < 0.001

Table 12. Treatment effects on the abundance and diversity of overwintering invertebrates. Values are mean counts from soil cores with a total volume of 5880 cm^3. Means with the same letter in the same column are not significantly different (*P*> 0.05).

Treatment	Prosobranchia	Pulmonata	Nemata	Oligochaeta	Araneae	Isopoda	Chilopoda	Diplopoda	Collembola	Hemiptera	Lepidoptera (larvae)	Diptera	Diptera (larvae)	Hymenoptera (other)	Formicidae	Coleoptera (larvae)	Carabidae	Staphylinidae	Elateridae	Curculionidae	Other larvae	Total	Number of families / groups
Crop	0.17b	0.75ab	2.58ab	11.25b	0.50c	0.25c	0.58	0.42	1.08	0.00b	0.00b	0.00b	0.75c	0.17	0.08	0.67	1.00b	1.50b	0.08	0.25	0.00	22.08b	7.83b
Conservation headland	0.50b	0.42b	3.58ab	9.25b	0.83bc	0.42bc	1.58	1.83	1.17	0.00b	0.00b	0.00b	0.58c	0.00	1.17	1.00	0.83b	1.67ab	0.00	1.08	0.08	26.00b	8.50b
Natural regeneration	1.42b	1.08ab	6.58ab	16.00ab	3.25ab	2.17abc	0.83	1.00	2.00	0.00b	0.58ab	0.00b	2.58bc	0.25	5.50	2.58	2.00ab	3.75abc	0.25	0.50	0.25	52.67a	14.00a
Tussocky grass	2.08ab	1.17ab	2.42ab	19.50a	4.42a	13.42a	0.42	0.58	4.67	0.83a	0.75a	0.83a	2.58abc	0.33	17.67	1.67	4.33a	6.00a	0.17	1.33	0.17	86.00a	17.00a
Pollen and nectar	1.83ab	1.33ab	5.92a	21.83a	2.42abc	3.00abc	1.75	1.33	2.08	0.08b	0.33ab	0.33ab	4.92ab	0.08	0.25	2.25	2.00ab	4.33ab	0.17	0.33	0.25	56.92a	14.67a
Wildflower	6.58a	2.92a	8.00ab	22.67a	3.25ab	4.58ab	0.58	1.50	4.17	0.17b	0.58ab	0.17ab	9.58a	0.00	1.33	2.83	2.33ab	4.92ab	0.00	1.08	0.42	78.08a	15.17a
ANOVA $F_{5, 25}$	7.87	2.68	2.36	9.85	5.39	5.62	0.47	0.65	1.13	5.76	4.46	3.70	9.66	1.24	1.56	2.65	3.41	4.09	1.04	1.07	0.64	13.14	13.09
P	***	*	ns	***	**	***	ns	ns	ns	***	**	*	***	ns	ns	*	*	**	ns	ns	ns	***	***

ns = no significant difference; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

Table 13. Treatment effects on (a) species richness and (b) abundance of invertebrate functional groups based on **spring** pitfall trapping between 2002 and 2006. Data are means per treatment. Values with the same letter in the same column are not significantly different ($P > 0.05$).

a) Species richness

	Decomposers						Seed predators						Predators					
	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall
Crop	7.8	7.1	5.8b	7.0b	7.3b	7.0b	3.5b	3.0ab	3.8ab	3.7	4.1bc	3.6abc	31.3b	32.5	31.7a	28.3	28.8a	30.5ab
Conservation headland	8.5	6.9	5.5b	6.4b	7.1b	6.9b	5.1ab	3.5ab	4.5a	3.2	4.5a	4.2ab	32.8b	30.6	31.3a	28.1	27.5ab	30.1ab
Natural regeneration	9.1	8.1	6.8ab	8.3ab	8.9ab	8.2ab	6.5a	4.3a	3.8a	3.3	4.3a	4.5a	39.8a	34.9	27.7ab	28.7	29.3a	32.1a
Tussocky grass	8.3	8.6	9.1a	8.8ab	9.6a	8.9ab	5.3ab	1.9b	2.1b	1.8	1.8d	2.6c	35.3ab	29.6	22.3b	25.4	22.3b	27.0b
Pollen and nectar	8.9	8.8	8.5a	8.5ab	9.0ab	8.8ab	5.3ab	1.9b	3.3ab	2.8	2.4cd	3.1bc	35.3ab	30.5	27.0ab	27.3	24.1ab	28.8ab
Wildflower	8.8	9.4	8.3a	9.6a	10.2a	9.3a	4.9ab	2.0b	3.3ab	3.3	3.5abc	3.4abc	34.6ab	29.5	25.5ab	25.9	25.8ab	28.3ab
ANOVA F-values																		
Treatment $_{5,25}$	0.78	1.41	7.26	4.24	6.47	4.01	3.09	7.05	4.02	2.35	6.78	7.82	5.09	2.18	3.21	1.04	3.75	2.73
	ns	ns	***	**	***	***	*	***	*	ns	***	***	**	ns	*	ns	*	*
Year $_{4,108}$						3.50						24.19						29.36
						*						***						***
Year × treatment $_{20,108}$						0.72						2.46						2.97
						ns						**						***

b) Abundance

	Decomposers						Seed predators						Predators					
	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall	2002	2003	2004	2005	2006	Overall
Crop	109.8	157.1ab	45.8c	71.1c	77.6d	92.3c	14.2c	17.5ab	12.3	13.3a	36.0ab	18.7c	484.1b	526.6	306.7	384.2	334.8	407.3
Conservation headland	198.5	101.3b	66.2c	109.8bc	140.4cd	123.2bc	58.2b	26.9ab	16.8	17.8a	51.4a	34.2ab	597.1ab	385.8	329.2	413.5	383.6	421.8
Natural regeneration	199.5	156.9ab	208.3ab	214.2ab	290.6bc	213.9ab	145.3a	32.6a	26.3	20.1a	57.7a	56.4a	774.2a	568.6	458.6	567.0	464.8	566.6
Tussocky grass	198.8	177.5ab	376.2a	285.1a	470.1a	301.5a	48.3b	8.7b	24.2	5.3b	18.0b	20.9bc	603.6ab	560.3	416.0	419.0	279.3	455.6
Pollen and nectar	178.9	153.0ab	270.4ab	256.8a	449.4ab	261.7a	72.8ab	8.0b	22.0	18.8a	71.0a	38.5bc	561.0ab	379.0	384.8	386.7	311.6	404.6
Wildflower	143.7	230.7a	269.9ab	301.3a	407.7ab	270.7a	58.5ab	12.5b	25.1	17.6a	101.1a	43.0abc	579.3ab	571.1	415.5	481.0	334.6	476.3
ANOVA F-values																		
Treatment $_{5,25}$	2.15	2.88	39.86	9.45	23.52	16.27	15.20	6.04	1.41	7.77	6.18	7.63	2.80	3.10	3.31	1.37	1.17	2.37
	ns	*	***	***	***	***	***	***	ns	***	***	***	*	*	*	ns	ns	ns
Year $_{4,108}$						12.75						16.02						6.95
						***						***						***
Year × treatment $_{20,108}$						1.68						1.51						0.99
						*						ns						ns

ns = no significant difference; * = *P* < 0.05; ** = *P* < 0.01; *** = *P* < 0.001

Table 14. Treatment effects on (a) species richness and (b) abundance of invertebrate functional groups based on **autumn** pitfall trapping between 2003 and 2006. Data are means per treatment. Values with the same letter in the same column are not significantly different ($P > 0.05$).

a) Species richness

	Decomposers					Seed predators					Predators				
	2003	2004	2005	2006	Overall	2003	2004	2005	2006	Overall	2003	2004	2005	2006	Overall
Crop	3.4	5.7	6.8	6.7	5.6	0.9ab	0.9ab	0.6ab	0.9ab	0.8bc	13.4ab	16.4ab	16.9a	17.0ab	15.9a
Conservation headland	3.9	5.3	6.0	7.4	5.7	1.3ab	1.3ab	0.8ab	0.9ab	1.1ab	14.5ab	16.8ab	16.8a	17.9a	16.5a
Natural regeneration	5.4	7.8	7.8	6.5	6.9	2.1a	1.7a	1.3a	1.2a	1.6a	16.2ab	16.7ab	18.7a	11.8cd	15.8a
Tussocky grass	4.9	7.2	8.4	7.8	7.1	0.1b	0.3b	0.2b	0.2b	0.2c	9.7b	10.4b	11.3b	9.4d	10.2b
Pollen and nectar	5.6	7.2	9.6	7.9	7.6	0.8ab	0.7ab	0.5b	1.1ab	0.8bc	18.9a	14.7ab	16.0a	13.6bcd	15.8a
Wildflower	5.0	8.0	9.3	7.5	7.4	1.7a	1.8a	0.9ab	0.6ab	1.3ab	15.1ab	19.2a	17.3a	13.8abc	16.4a
ANOVA F-values															
Treatment $_{5,25}$	2.16	2.57	2.40	0.91	3.34	5.84	3.86	4.70	2.78	9.73	4.08	3.91	7.85	10.94	9.99
	ns	ns	ns	ns	*	***	*	**	*	***	**	***	***	***	***
Year $_{3,90}$					22.04					1.96					3.54
					***					ns					*
Year × treatment $_{15,90}$					0.82					0.59					2.17
					ns					ns					*

b) Abundance

	Decomposers					Seed predators					Predators				
	2003	2004	2005	2006	Overall	2003	2004	2005	2006	Overall	2003	2004	2005	2006	Overall
Crop	40.4ab	27.2c	41.0b	52.9	40.4b	1.9ab	1.9ab	1.1abc	3.6	2.1ab	109.8ab	183.8	210.8ab	278.9a	195.8ab
Conservation headland	49.6ab	62.1ab	62.8ab	84.8	64.8ab	4.8a	4.5ab	1.2abc	2.3	3.2ab	138.9ab	147.0	268.0ab	285.2a	209.8a
Natural regeneration	132.4a	82.8a	159.0a	102.8	119.2a	3.6a	3.2ab	2.1a	3.2	3.0a	222.1a	132.3	304.5a	84.8b	185.9ab
Tussocky grass	24.1b	56.5ab	140.5a	94.5	78.9a	0.1b	0.3b	0.2c	0.5	0.3c	55.8b	55.7	54.3d	57.6b	55.8c
Pollen and nectar	38.6ab	91.4a	145.5a	105.3	95.2a	1.1ab	1.0ab	0.6bc	1.3	1.0bc	124.3ab	71.1	115.8c	98.1b	102.3b
Wildflower	33.8ab	103.5a	127.3a	87.8	88.1a	2.8a	6.8a	1.5ab	1.2	3.1ab	122.0ab	103.2	129.4bc	93.8b	112.1ab
ANOVA F-values															
Treatment $_{5,25}$	2.74	4.74	6.11	2.14	6.55	4.79	3.82	4.68	2.51	8.86	4.31	1.95	18.17	12.86	11.38
	*	**	***	ns	***	**	*	**	ns	***	**	ns	***	***	***
Year $_{3,90}$					10.85					1.36					1.99
					***					ns					ns
Year × treatment $_{15,90}$					1.01					0.58					1.74
					ns					ns					ns

ns = no significant difference; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

Table 15. Treatment effects on (a) species richness and (b) abundance of invertebrate functional groups based on summer vacuum and sweep net sampling each year between 2003 and 2006. Values with the same letter in the same column are not significantly different (*P*> 0.05).

a) Species richness

	Decomposers					Herbivores					Pollinators					Predators					Parasitoids				
	2003	2004	2005	2006	Overall	2003	2004	2005	2006	Overall	2003	2004	2005	2006	Overall	2003	2004	2005	2006	Overall	2003	2004	2005	2006	Overall
Crop	4.8c	7.7c	7.2b	4.3d	6.0c	18.8c	24.2d	16.0c	17.8c	19.2d	4.3d	6.2b	4.8c	4.4c	4.9e	13.1c	15.5b	8.9c	11.1bc	12.2b	3.4	1.5b	3.3	5.5b	3.4c
Conservation headland	7.6bc	7.8c	8.8b	5.7cd	7.5bc	21.1c	25.3d	20.0c	16.8c	20.8d	6.0cd	8.5b	4.3c	3.8c	5.6de	13.6c	15.2b	10.3bc	9.1c	12.0b	3.4	2.2ab	3.3	6.4ab	3.8bc
Natural regeneration	6.5bc	7.6ab	11.6ab	10.4bc	9.0b	37.2b	39.8bc	39.3ab	37.8ab	38.5bc	12.3a	9.7ab	10.8ab	10.1ab	10.7ab	16.7ab	13.8ab	12.1abc	16.6ab	14.8ab	5.0	3.2ab	4.4	6.8ab	4.9ab
Tussocky grass	5.3c	8.5ab	9.2b	9.1bc	8.0bc	28.7c	39.2c	32.1b	36.5b	34.1c	8.0bcd	7.5b	8.3b	7.7bc	7.9cd	12.3c	14.8ab	13.0ab	17.0ab	14.3ab	3.6	3.8a	4.7	8.9a	5.3ab
Pollen and nectar	14.6a	12.3a	11.0b	10.6b	12.1a	42.4ab	50.6ab	40.0ab	37.8ab	42.7ab	9.6abc	9.2ab	8.3b	7.3bc	8.6bc	18.2a	14.8ab	9.6bc	12.5bc	13.8b	5.3	3.3a	5.4	7.5ab	5.4a
Wildflower	10.8ab	12.4a	16.1a	16.3a	13.9a	48.6a	51.8a	48.0a	50.3a	49.7a	11.5ab	13.3a	12.6a	13.8a	12.8a	18.2a	17.5a	14.5a	19.5a	17.4a	3.9	3.2ab	5.5	8.5ab	5.3a
ANOVA F-values																									
Treatment $_{5,25}$	10.00	4.53	8.03	16.50	23.81	35.04	30.52	30.27	17.34	51.19	11.12	6.83	24.11	15.39	28.43	7.36	3.48	6.26	6.59	8.06	1.33	5.05	3.48	3.46	6.67
	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	*	***	***	***	ns	**	*	*	***
Year $_{3,78}$					2.85					8.31					2.60					9.41					38.74
					*					***					ns					***					***
Year × treatment $_{15,78}$					2.07					1.19					1.92					2.26					0.80
					*					ns					*					*					ns

b) Abundance

	Decomposers					Herbivores					Pollinators					Predators					Parasitoids				
	2003	2004	2005	2006	Overall	2003	2004	2005	2006	Overall	2003	2004	2005	2006	Overall	2003	2004	2005	2006	Overall	2003	2004	2005	2006	Overall
Crop	12c	20c	18b	10c	15e	311b	384b	374	192bc	315d	16b	18c	20c	67ab	30c	45d	53c	35b	30bc	41d	136	107	138	200	145
Conservation headland	24c	19bc	18b	15c	19de	406ab	1374ab	770	139c	672d	90b	29c	49bc	16b	46c	56cd	54c	32b	27c	42cd	240	137	190	351	229
Natural regeneration	23bc	26abc	31b	29b	27cd	642a	574ab	508	645a	592bc	224a	226ab	95a	286a	208ab	54bc	63bc	42ab	61ab	55b	275	203	172	244	224
Tussocky grass	16c	33abc	28b	31b	27c	196b	494ab	254	341abc	321cd	63a	139bc	59ab	24ab	71b	60bc	74ab	41ab	69a	61ab	97	71	124	143	109
Pollen and nectar	55a	37ab	27b	29b	37b	739a	1195a	982	365ab	820a	236a	418ab	39abc	25ab	179ab	75ab	60bc	30b	50abc	54bc	96	166	126	161	137
Wildflower	50ab	45a	60a	72a	57a	746a	773ab	577	593a	672a	177a	250a	148a	119a	174a	92a	104a	53a	83a	83a	104	148	110	172	133
ANOVA F-values																									
Treatment $_{5,25}$	11.00	5.74	10.77	17.51	45.54	8.51	3.38	2.07	6.81	11.44	18.10	12.64	8.05	5.17	24.97	14.32	8.74	3.96	6.86	19.27	2.94	2.35	0.41	0.26	1.41
	***	**	***	***	***	***	*	ns	***	***	***	***	***	**	***	***	***	**	***	***	*	ns	ns	ns	ns
Year $_{3,78}$					0.49					4.98					3.80					14.47					2.45
					ns					**					*					***					ns
Year × treatment $_{15,78}$					1.65					1.10					1.30					1.32					0.80
					ns					ns					ns					ns					ns

ns = no significant difference; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

Table 16. Treatment differences in species richness and abundance of farmland birds between a) visits within year and b) between years. Data are means per 0.3 ha treatment plot. Values with the same letter in the same column are not significantly different (*P*> 0.05).

a) Visits

	Species richness					Abundance					Granivorous passerines					Skylark					Farmland Bird Index species				
	Dec	Jan	Feb	Mar	Overall	Dec	Jan	Feb	Mar	Overall	Dec	Jan	Feb	Mar	Overall	Dec	Jan	Feb	Mar	Overall	Dec	Jan	Feb	Mar	Overall
Crop	0.3	0.5	0.2	0.5	0.4	0.9	2.7	1.2	0.6	1.4	0.0	0.2	0.0	0.0	0.1	0.5	0.6	0.1	0.5	0.4	0.6	1.6	0.8	0.5	0.9
Wild Bird Seed Mixture	2.9	2.5	2.2	1.4	2.3	40.9	44.8	18.7	7.9	28.1	37.0	37.0	14.6	4.8	23.4	1.3	1.3	1.7	2.3	1.7	34.1	39.1	16.9	7.2	24.3
ANOVA F-values																									
Treatment $_{1,5}$	123.89	68.18	35.62	9.08	154.77	225.43	44.89	19.37	13.70	113.77	1107.79	90.68	27.90	6.60	91.04	7.28	3.32	7.74	4.41	19.84	107.11	14.73	13.67	13.81	32.74
	***	***	***	*	***	***	***	**	*	***	***	***	**	*	***	*	ns	*	ns	**	***	*	*	*	***
Year $_{3,30}$					5.48					10.40					15.26					0.50					5.82
					**					***					***					ns					**
Year × treatment $_{3,30}$					6.28					4.29					13.26					0.62					4.74
					**					*					***					ns					*

b) Years

	Species richness						Abundance						Granivorous passerines						Skylark						Farmland Bird Index species				
	2002/3	2003/4	2004/5	2005/6	2006/7	Overall	2002/3	2003/4	2004/5	2005/6	2006/7	Overall	2002/3	2003/4	2004/5	2005/6	2006/7	Overall	2002/3	2003/4	2004/5	2005/6	2006/7	Overall	2002/3	2003/4	2004/5	2005/6	2006/7
Crop	0.7	2.2	1.2	0.8	0.7	1.1	1.6	2.1	2.6	0.7	0.4	1.5	0.0	0.2	0.0	0.0	0.0	0.0	0.3	0.3	1.4	0.3	0.1	0.5	1.4	1.6	1.5	0.3	0.1
Wild Bird Seed Mixture	5.3	5.8	3.5	5.2	3.3	4.6	64.4	40.0	37.8	9.9	5.9	31.6	60.2	31.9	32.9	3.8	3.5	26.5	0.8	1.8	1.3	3.1	1.6	1.7	54.0	35.7	36.8	8.9	4.8
ANOVA F-values																													
Treatment $_{1,5}$	49.00	23.27	14.41	35.18	12.31	163.19	54.10	33.70	30.10	16.96	18.04	199.13	178.19	38.39	95.77	20.57	7.37	181.97	1.00	0.93	4.35	0.71	11.19	14.08	45.46	15.03	26.41	31.98	10.40
	***	**	*	**	*	***	***	**	**	*	**	***	***	**	***	*	*	***	ns	ns	ns	ns	*	*	***	*	**	**	*
Year $_{4,36}$						4.07						9.45						12.36						0.81					
						*						***						***						ns					
Year × treatment $_{4,36}$						1.70						3.28						11.68						2.21					
						ns						*						***						ns					

ns = no significant difference; * = *P* < 0.05; ** = *P* < 0.01; *** = *P* < 0.001

Fig. 1. Map of the UK showing the locations of the six experimental sites.

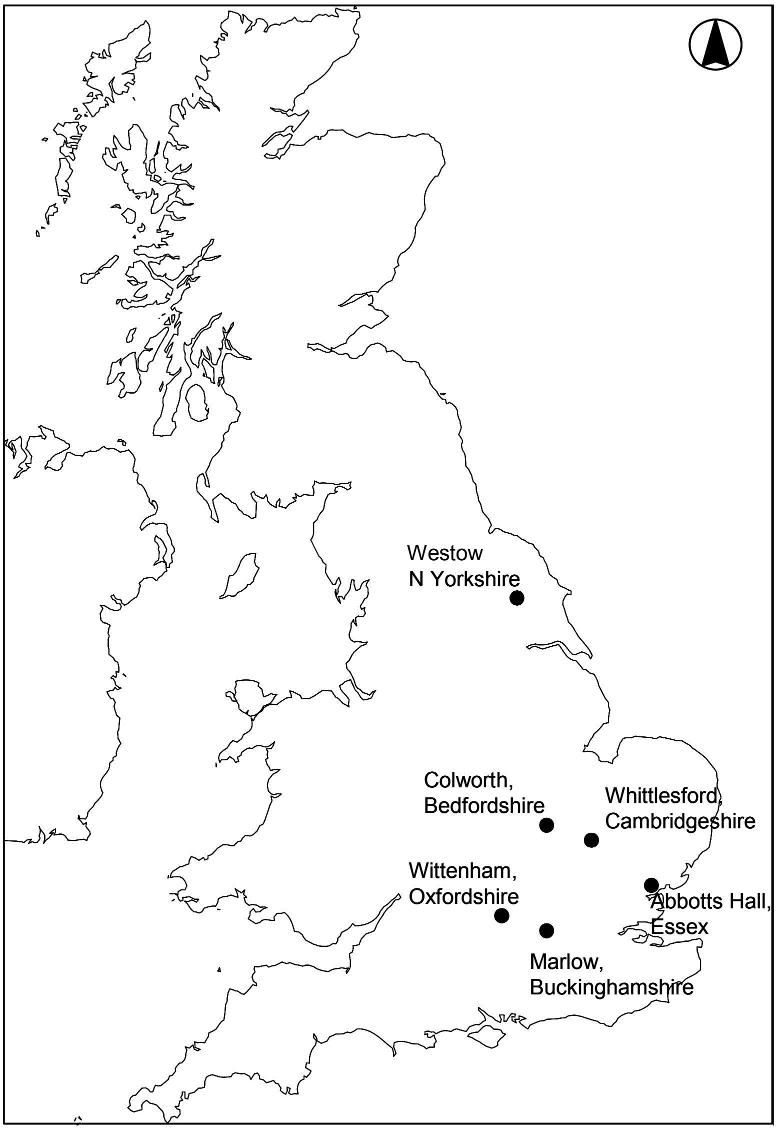


Fig. 2. Summary of all 1186 ANOVA tests showing: a) percentage of significant tests (P<0.05) for each field margin treatment (dotted line represents 5% of significant tests expected by chance alone), and b) percentage of treatments with highest ranked value for each variable.

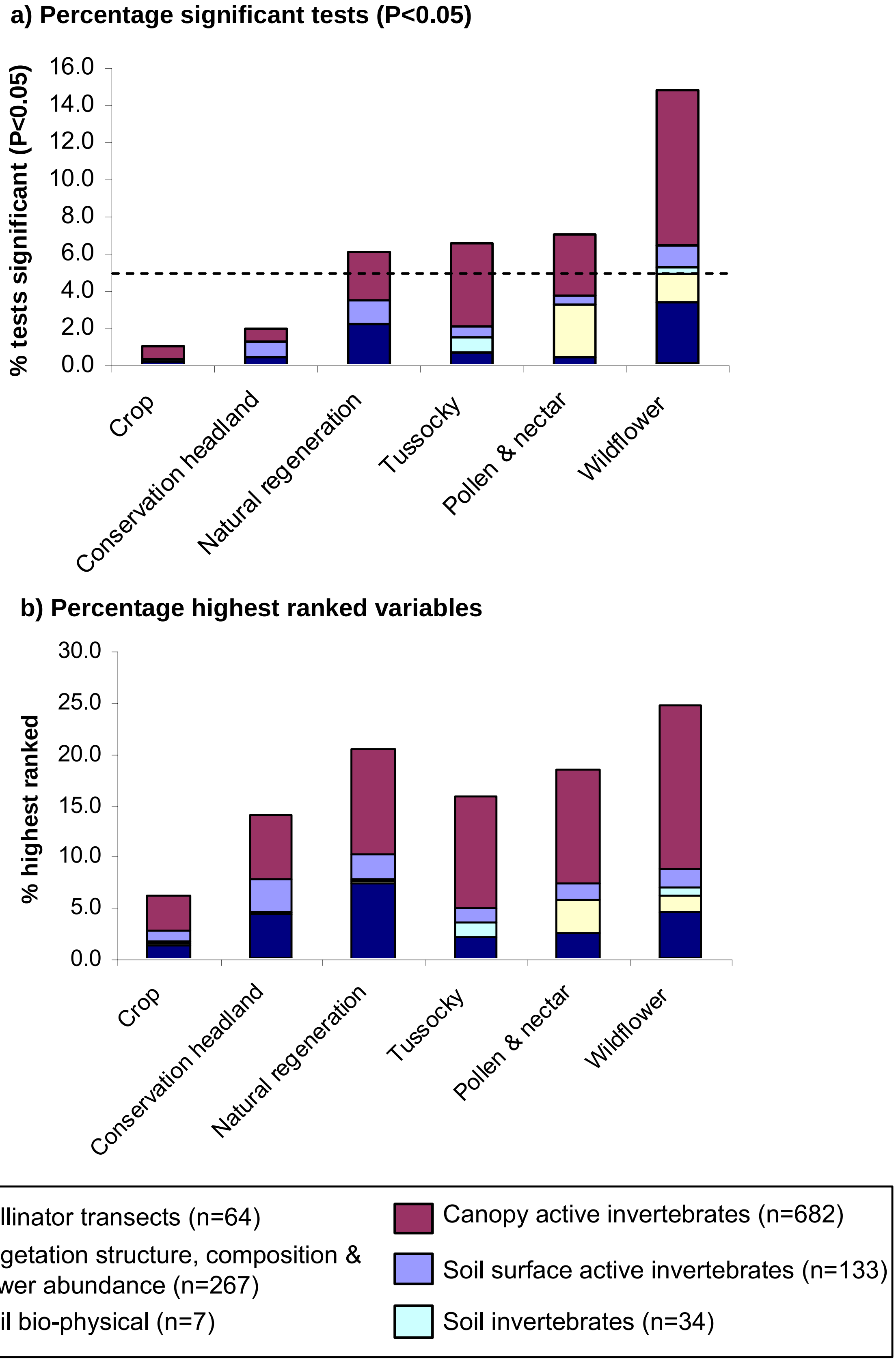


Fig. 3. Treatment effects on carbon sequestration in the 0-5 cm and 6-10 cm soil fractions after 5 years as measured by % loss on ignition.

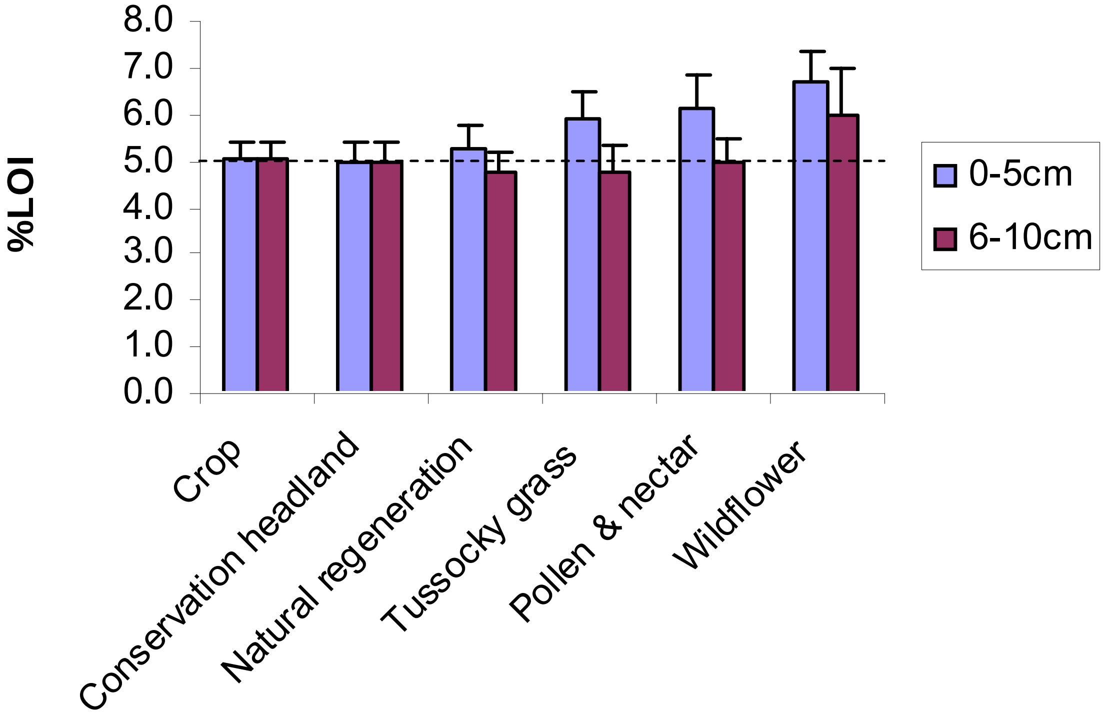


Fig. 4. Treatment effects on mean (± se) biomass production between 2003 and 2006 as estimated from drop disk measurements.

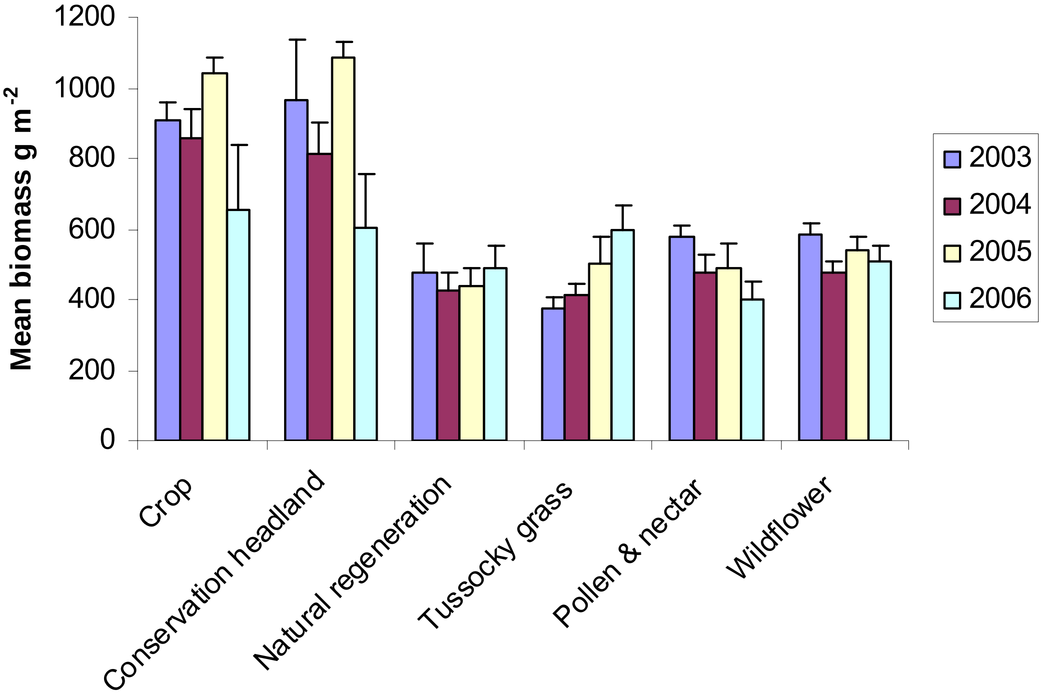
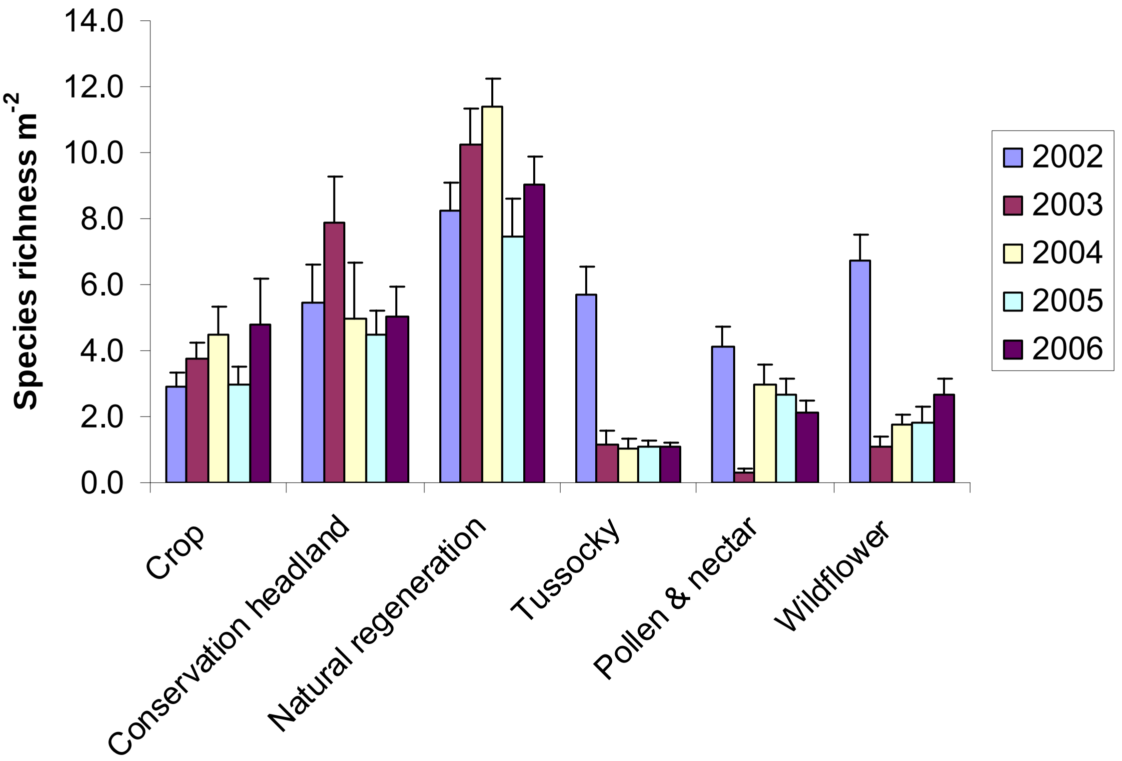


Fig. 5. Treatment effects on mean (± se) species richness m^{-2} of a) annuals and b) perennials between 2003 and 2006.

a) Annuals



a) Perennials

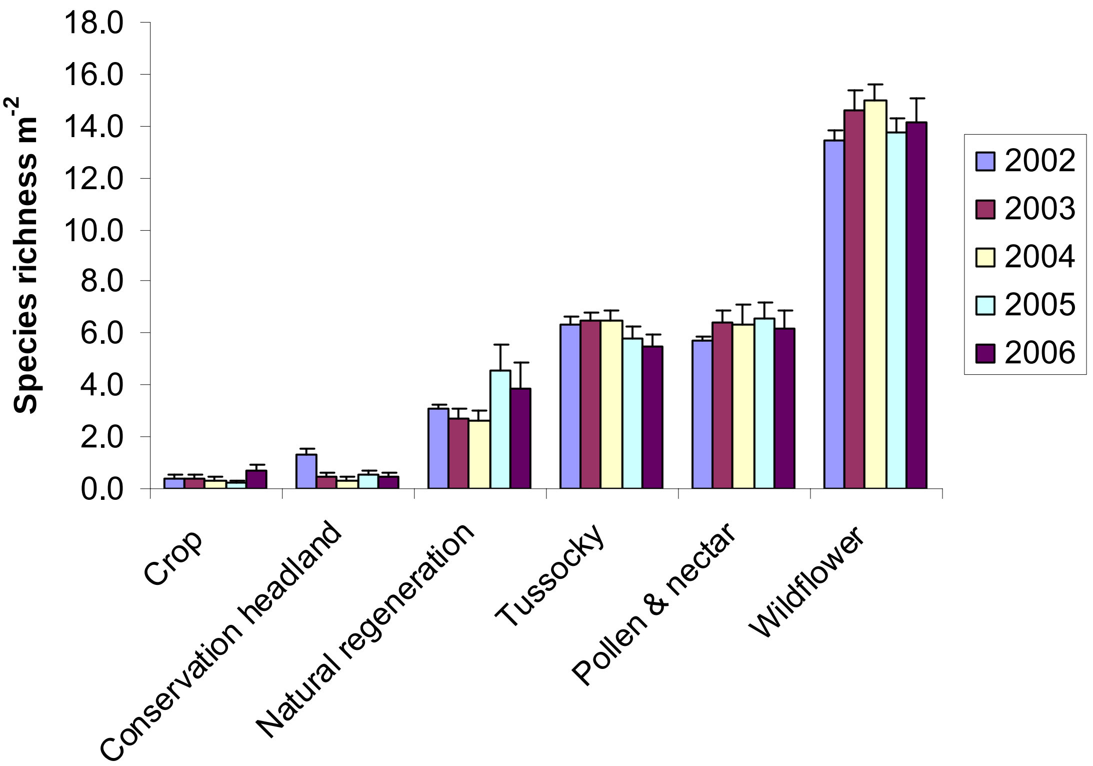


Fig. 6. Changes in the species number (richness) of all vascular plants and sown species in the wildflower field margin treatment between 2002 and 2006.

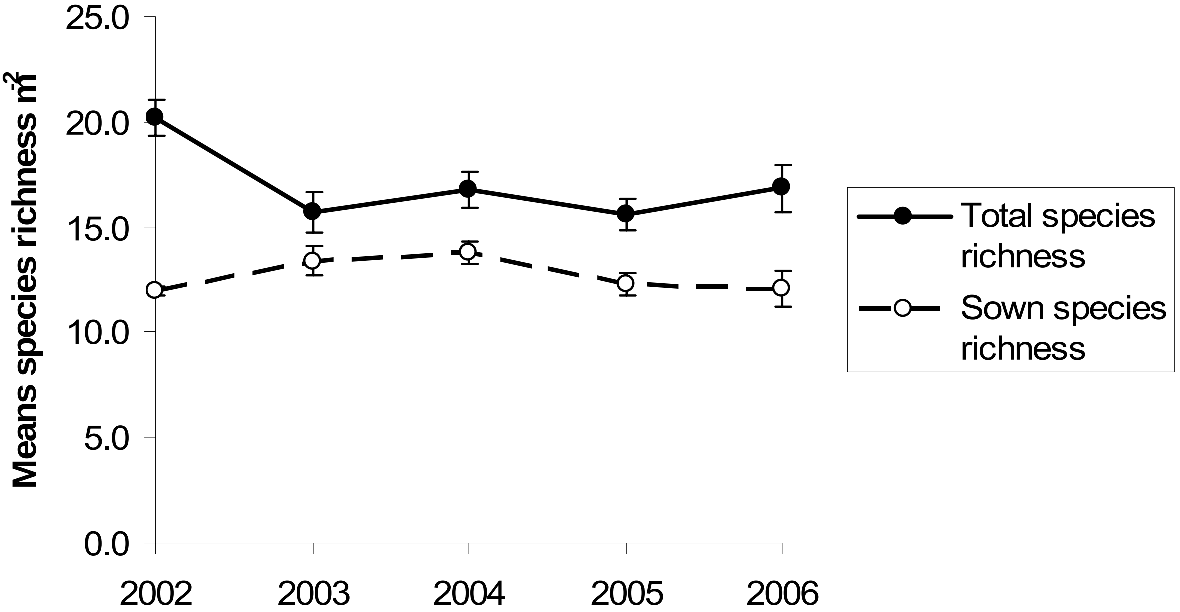


Fig. 7. Treatment effects on mean (± se) species richness per plot of declining arable plants between 2002 and 2006.

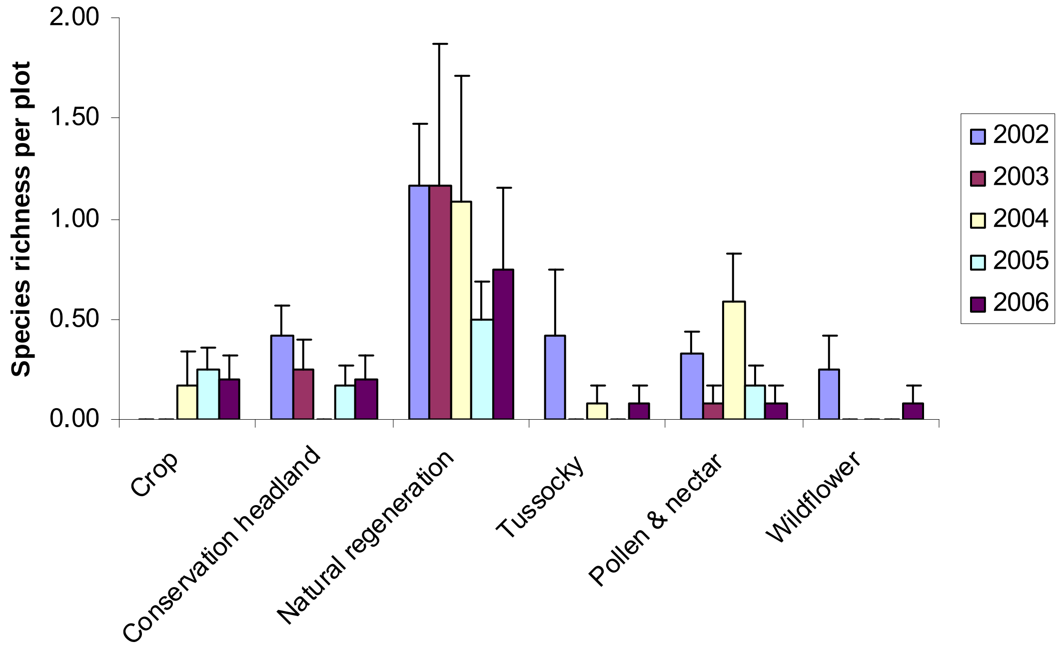


Fig. 8. Changes in the mean (± se) percentage cover of sown forbs and grasses in the pollen and nectar margins between 2002 and 2006.

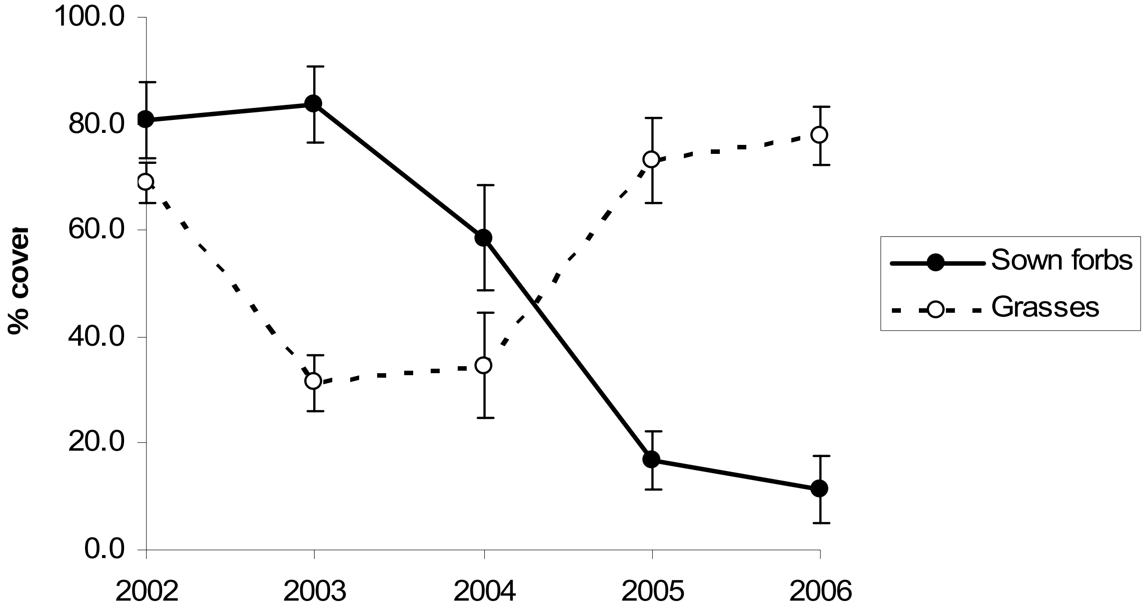


Fig. 9. Treatment effects on mean (± se) abundance of bumblebee forage flowers m^{-2} between 2002 and 2006.

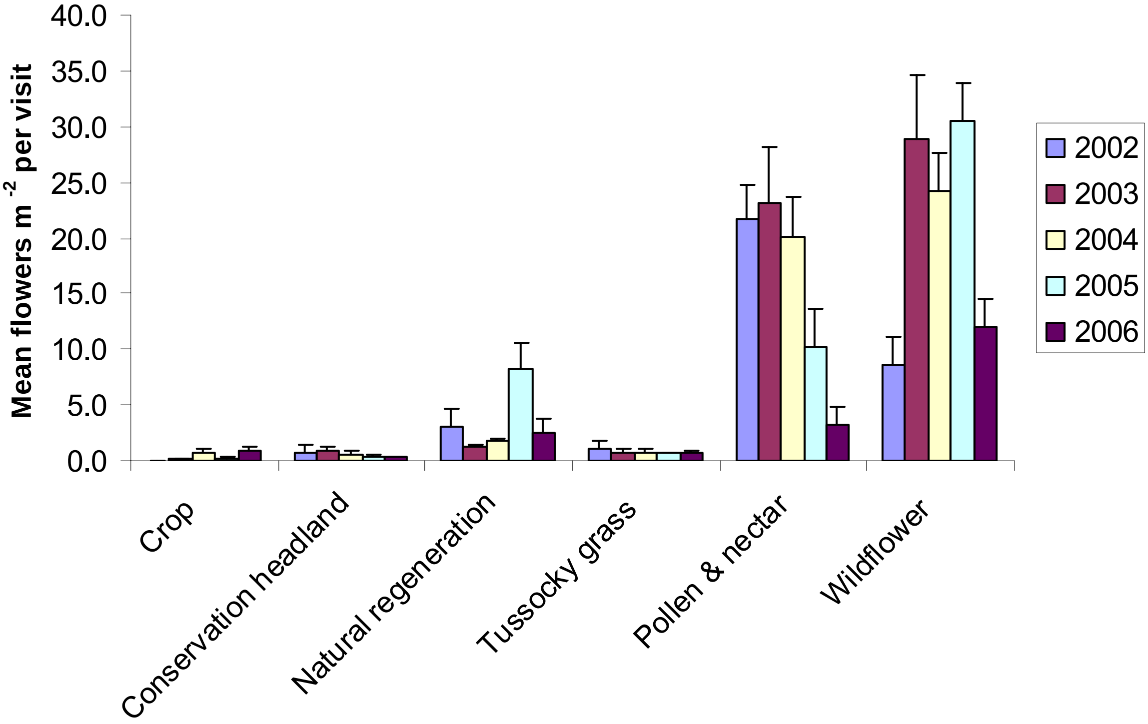
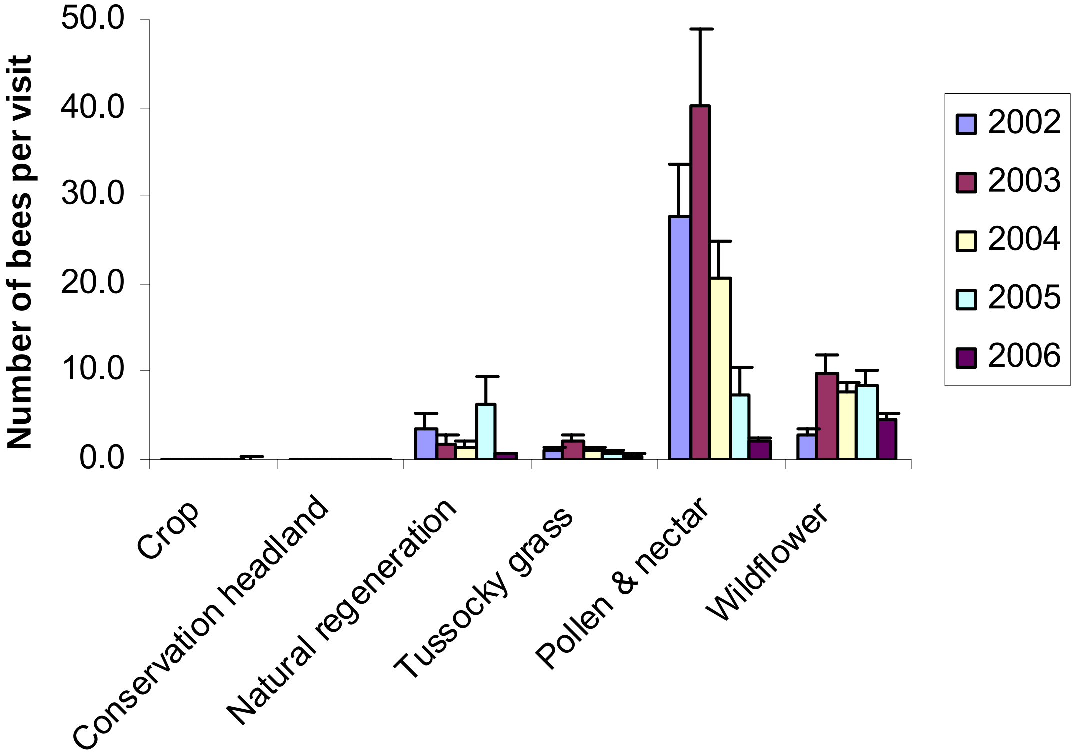


Fig. 10. Treatment effects on mean (± se) a) abundance and b) species richness (number) of bumblebees per visit between 2002 and 2006.

a) Abundance of bees



b) Species richness of bees

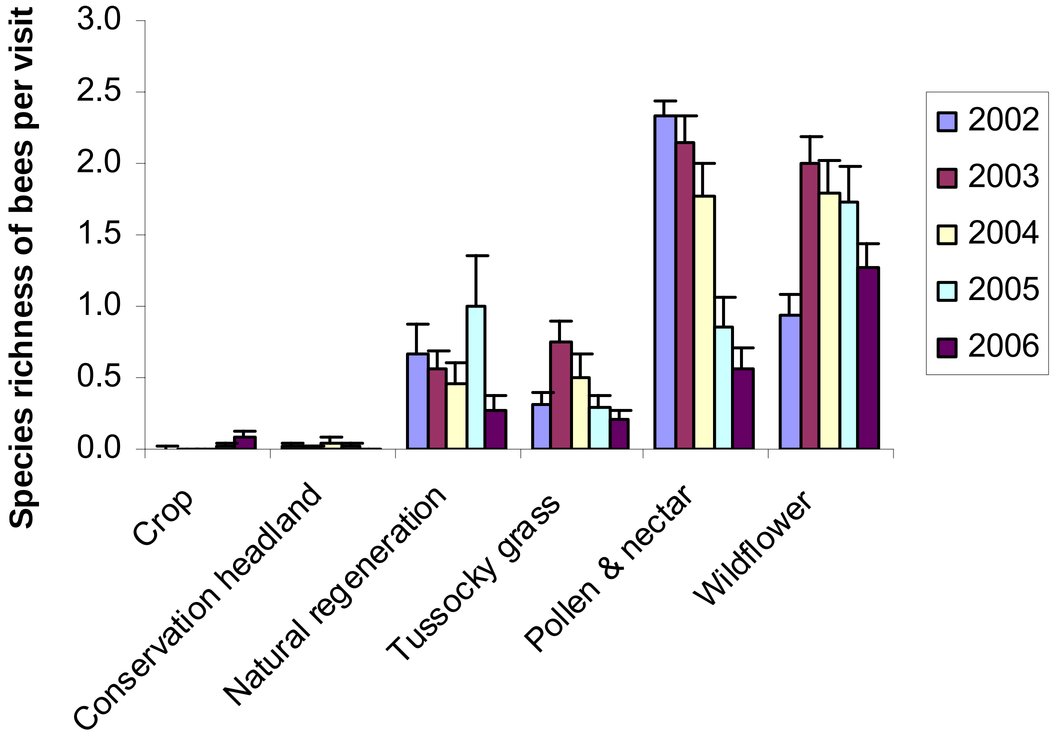


Fig. 11. Relationship between log transformed abundance of bee forage flowers and bees averaged for each site across all five years. Log bee abundance = - 0.0544 + 0.8455 Log bee forage flowers m^{-2}; $F_{1,34}$ = 141.29 ($P<0.001$); R^2 = 80.6%.

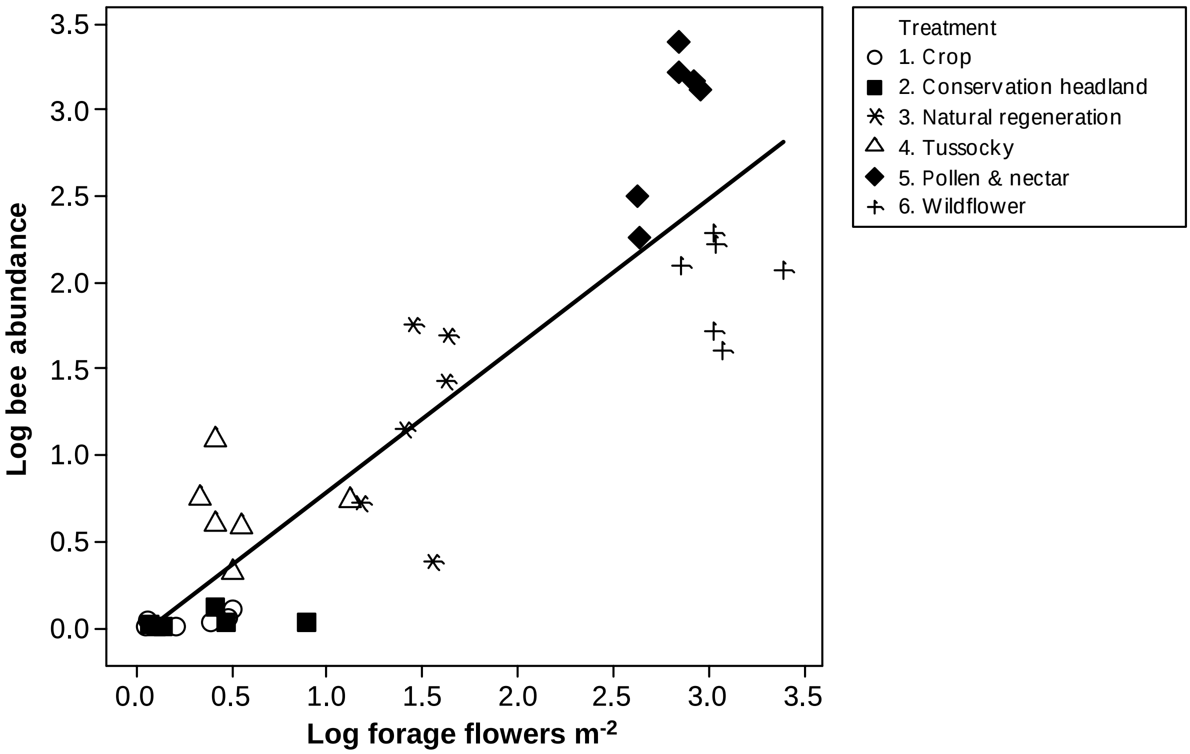


Fig. 12. Flower utilisation by foraging bumblebees in the field margin treatments between 2002 and 2006. UKBAP species in bold.

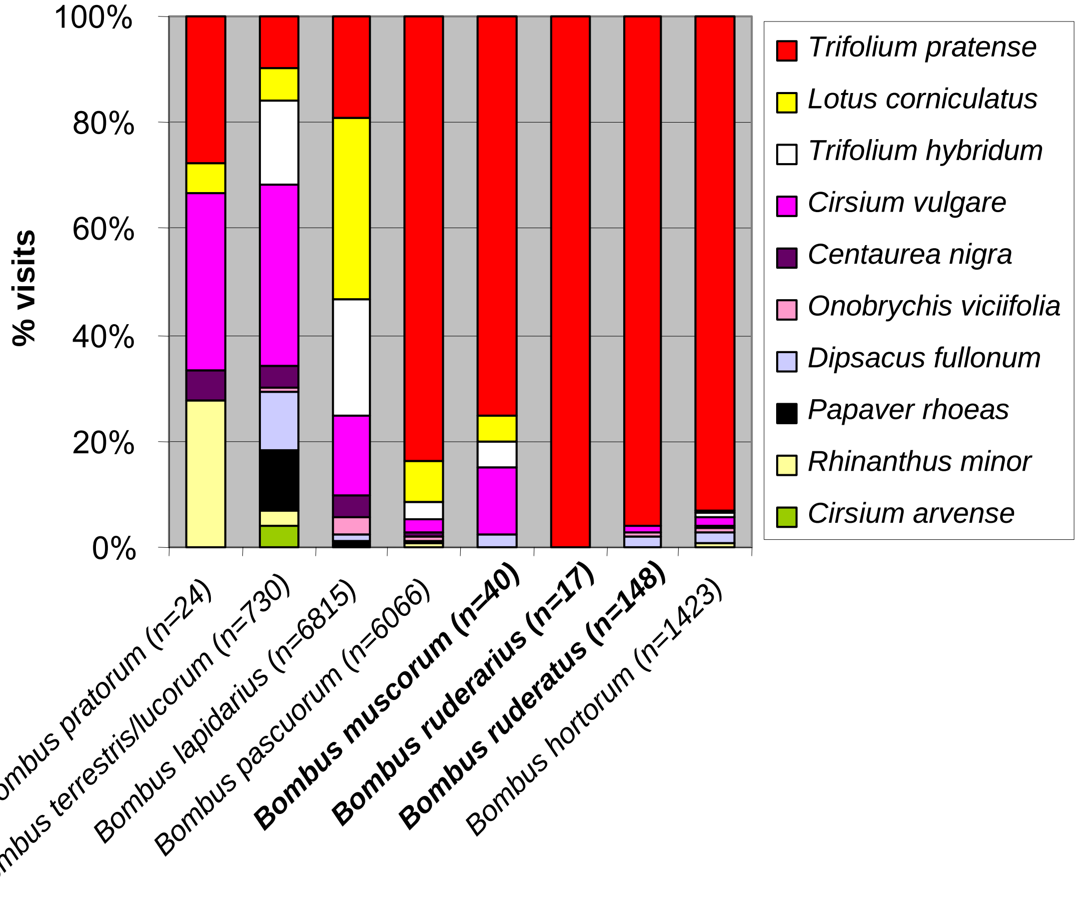
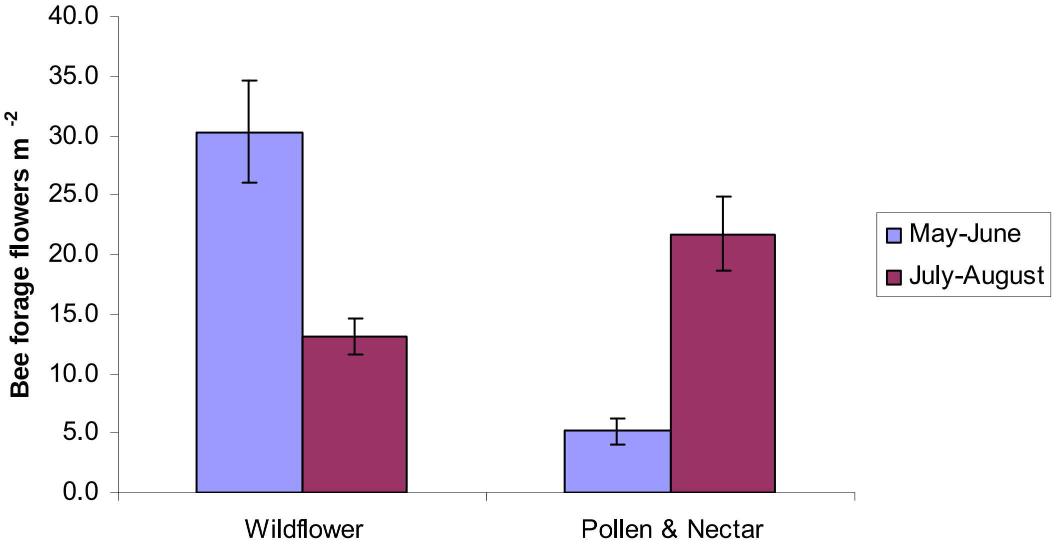


Fig. 13. Seasonal effects of seed mixture composition on abundance of a) bee forage flowers and b) all bumblebees between 2002 and 2006.

a) Abundance of bee forage flowers



b) Abundance of bees

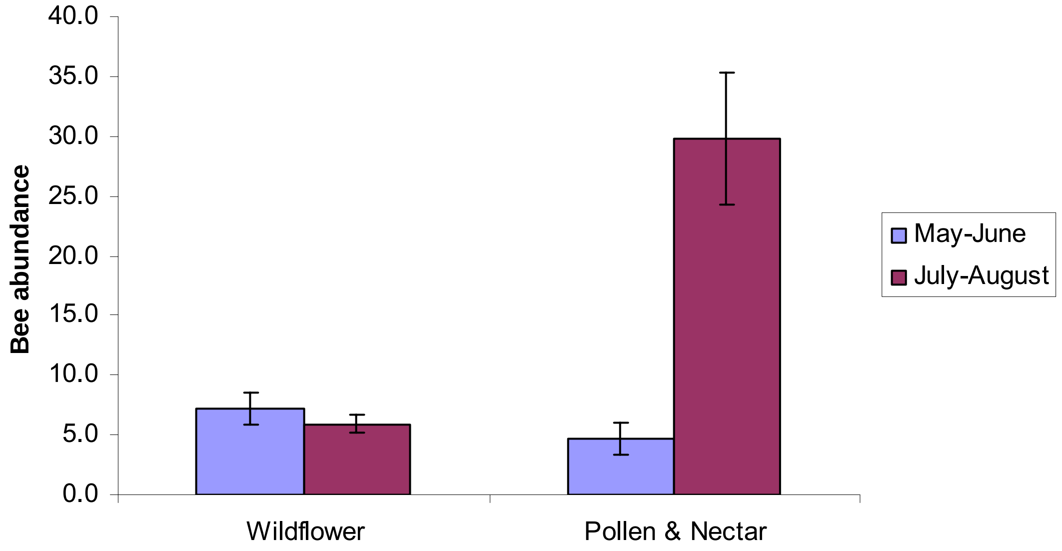
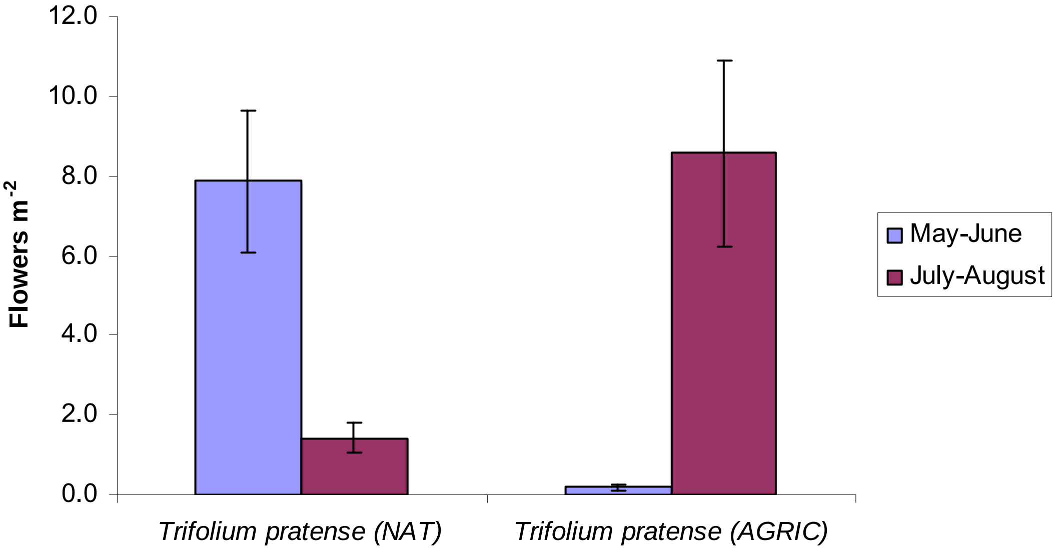


Fig. 14. Seasonal differences in flower abundance of native vs. agricultural varieties of a) *Trifolium pratense* and b) *Lotus corniculatus* in wildflower (NAT) and pollen and nectar (AGRIC) mixtures between 2002 and 2006.

a) *Trifolium pratense*



b) *Lotus corniculatus*

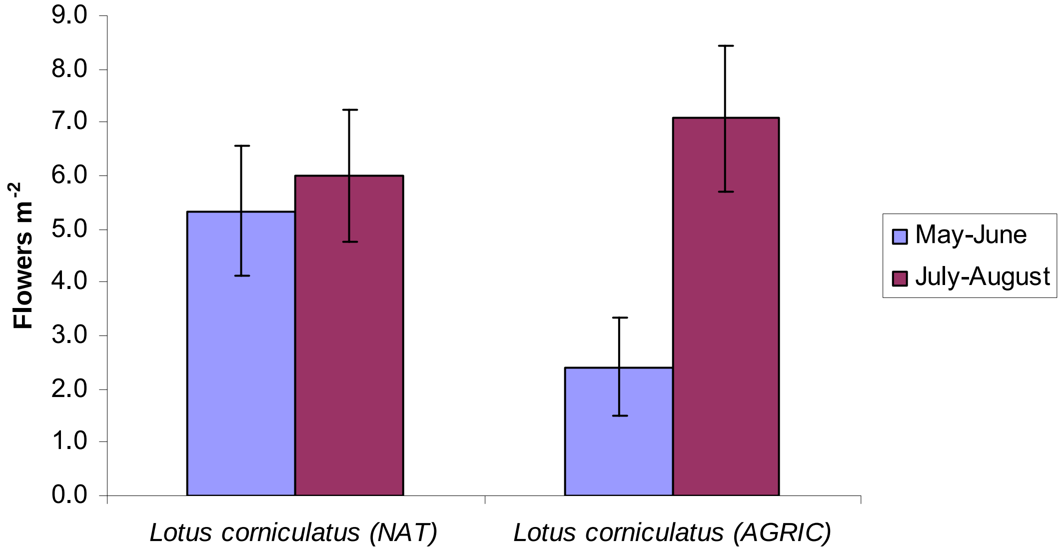
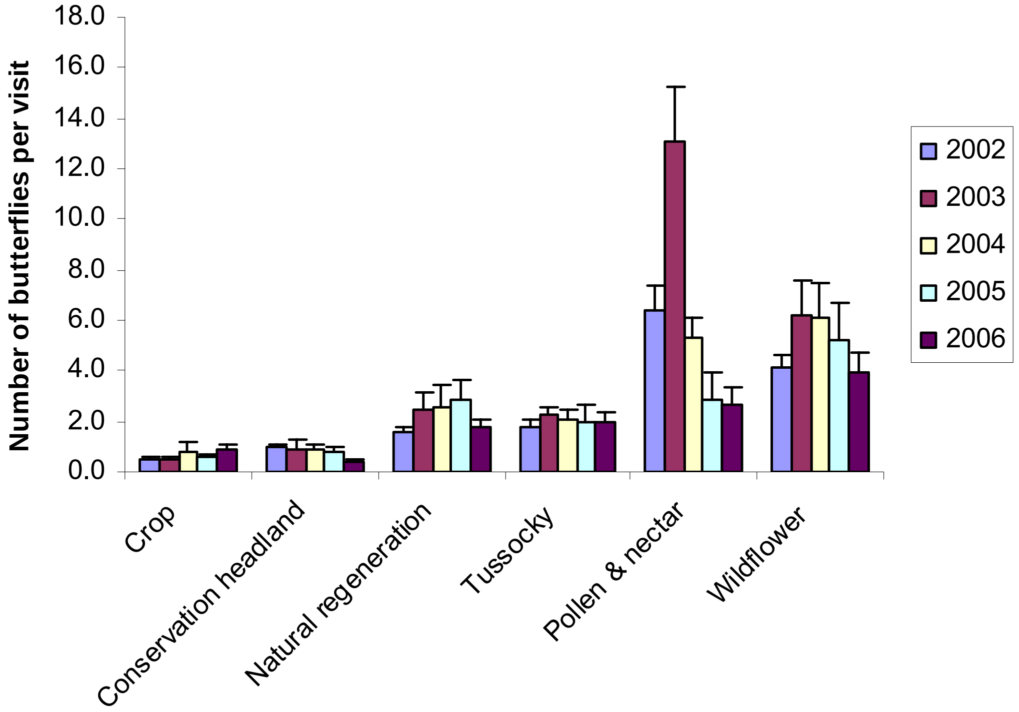


Fig. 15. Treatment effects on mean (± se) a) abundance and b) species richness (number) of butterflies per visit between 2002 and 2006.

a) Abundance of butterflies



b) Species richness of butterflies

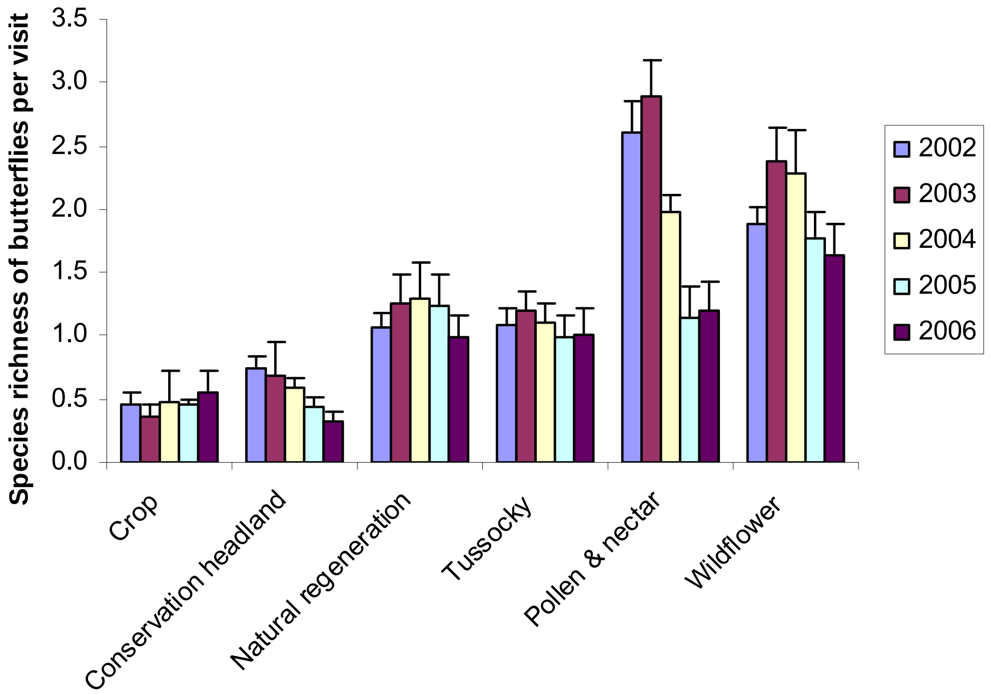


Fig. 16. Treatment effects on mean (± se) abundance of earthworms after 5 years summed from four soil cores (14 (L) × 7 (W) × 15 (D) cm) per plot.

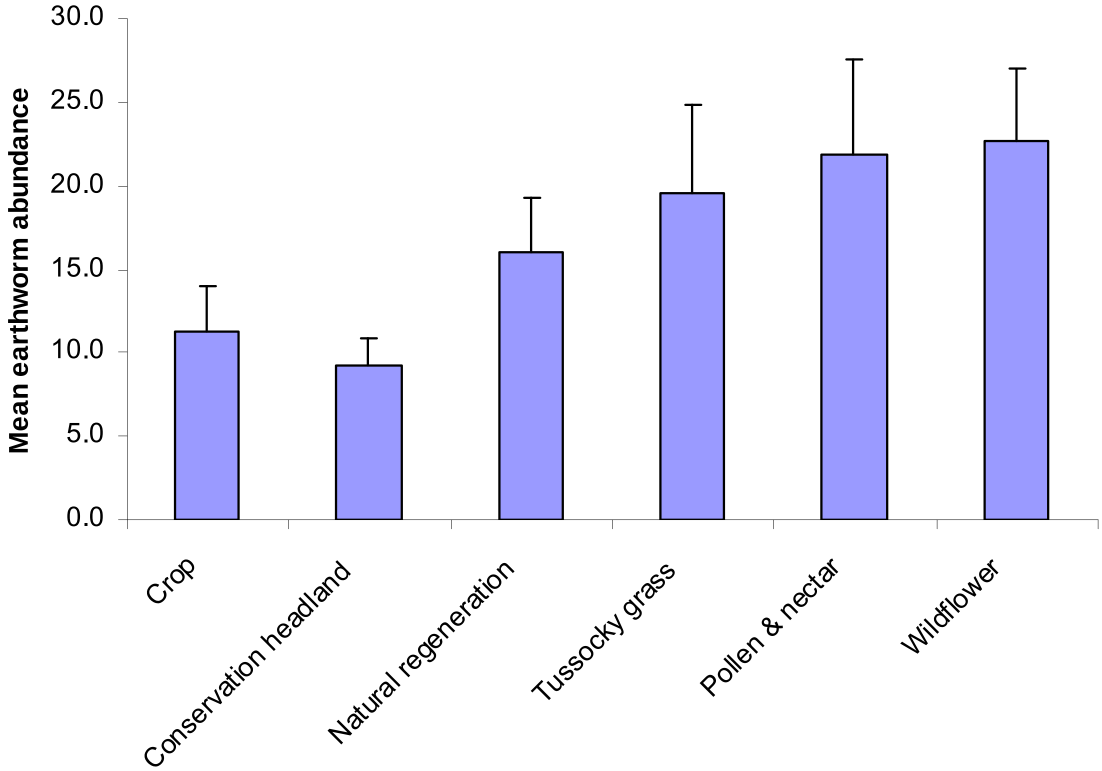
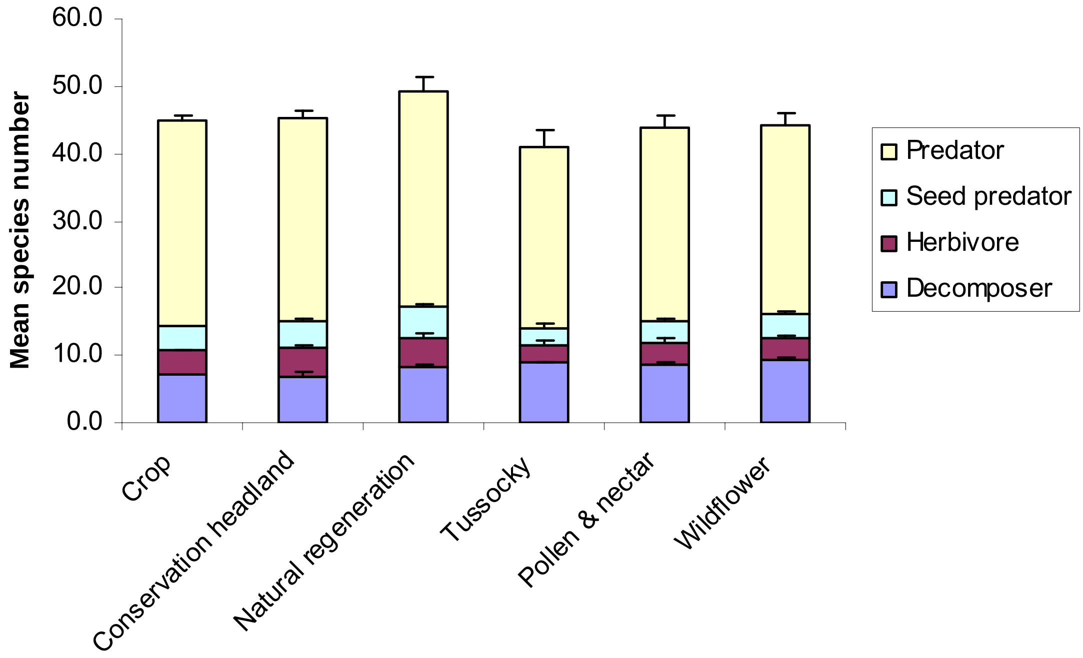


Fig. 17. Treatment effects on a) mean (± se) species richness and b) mean (± se) abundance of invertebrate functional groups based on spring pitfall trapping.

a) Species richness



b) Abundance

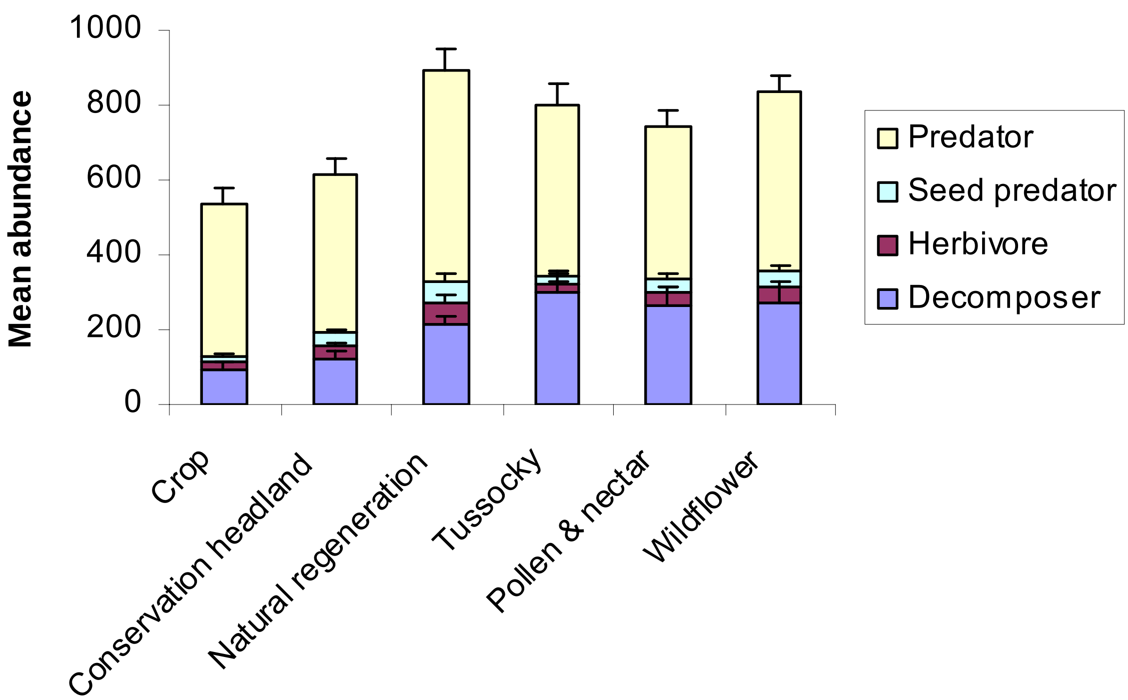
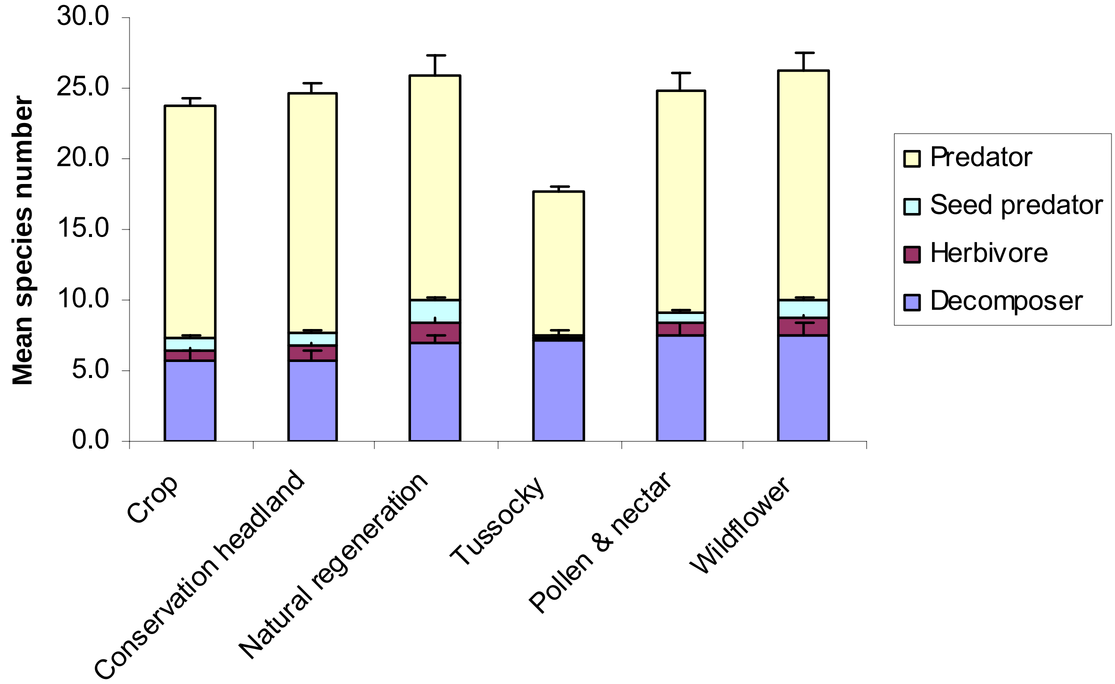


Fig. 18. Treatment effects on a) mean (± se) species richness and b) mean (± se) abundance of invertebrate functional groups based on autumn pitfall trapping.

a) Species richness



b) Abundance

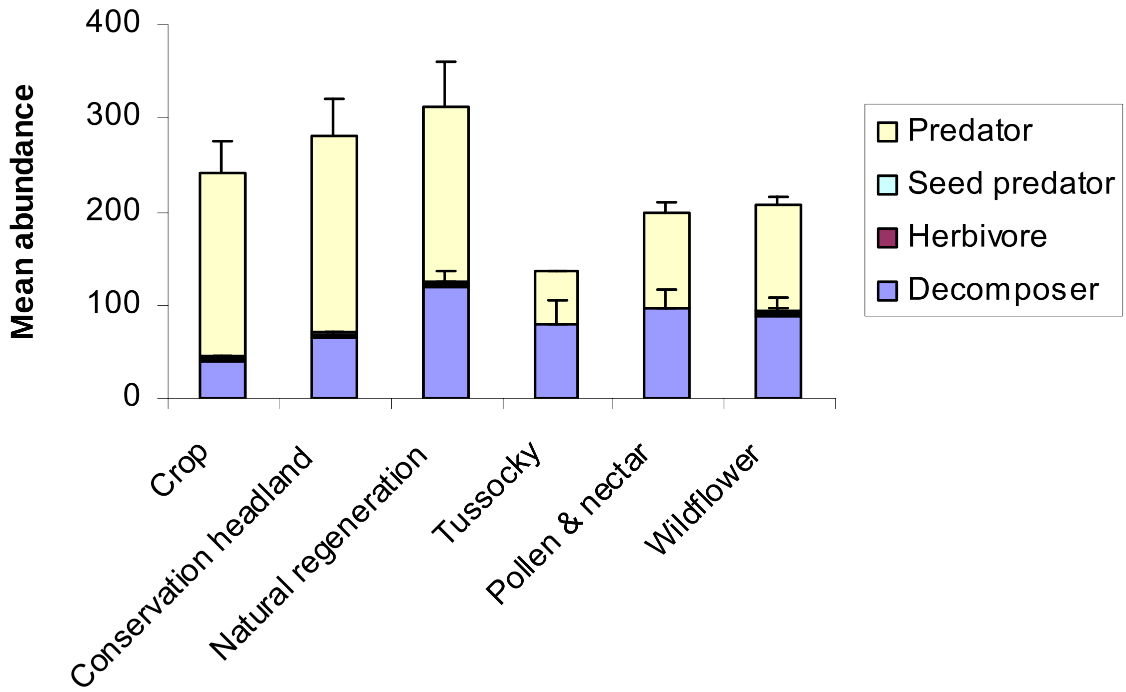
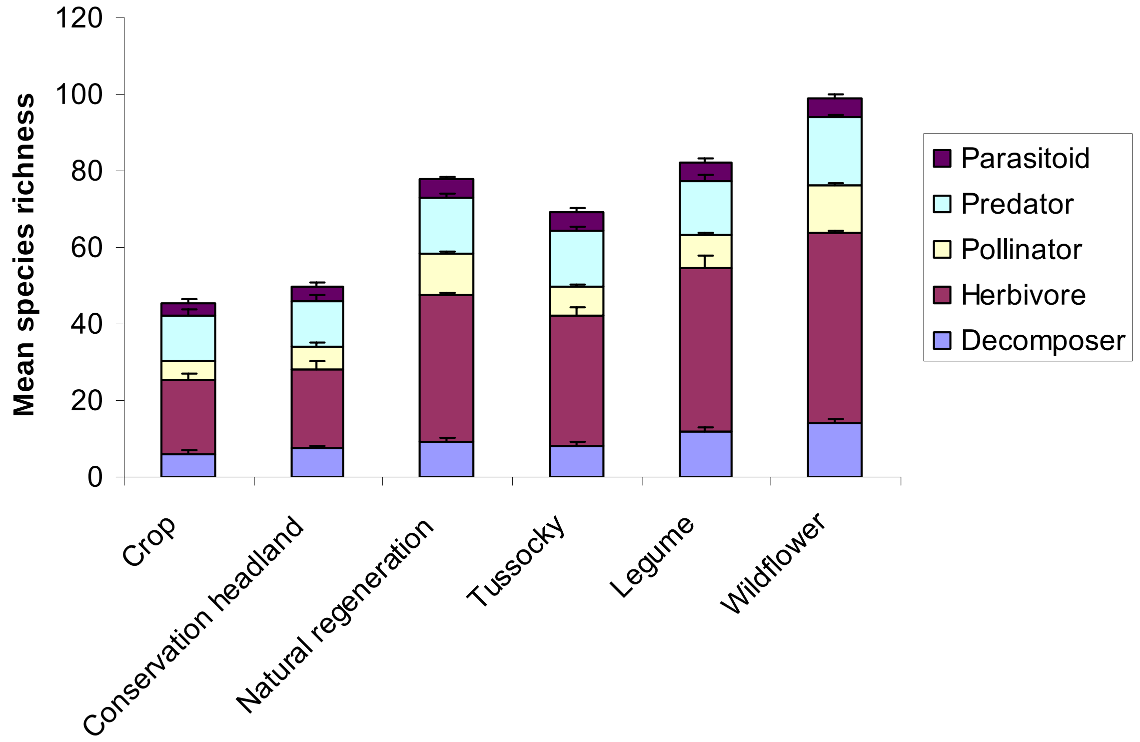


Fig. 19. Treatment effects on a) mean (± se) species richness and b) mean (± se) abundance of invertebrate functional groups based on summer vacuum and sweep net sampling.

a) Species richness



b) Abundance

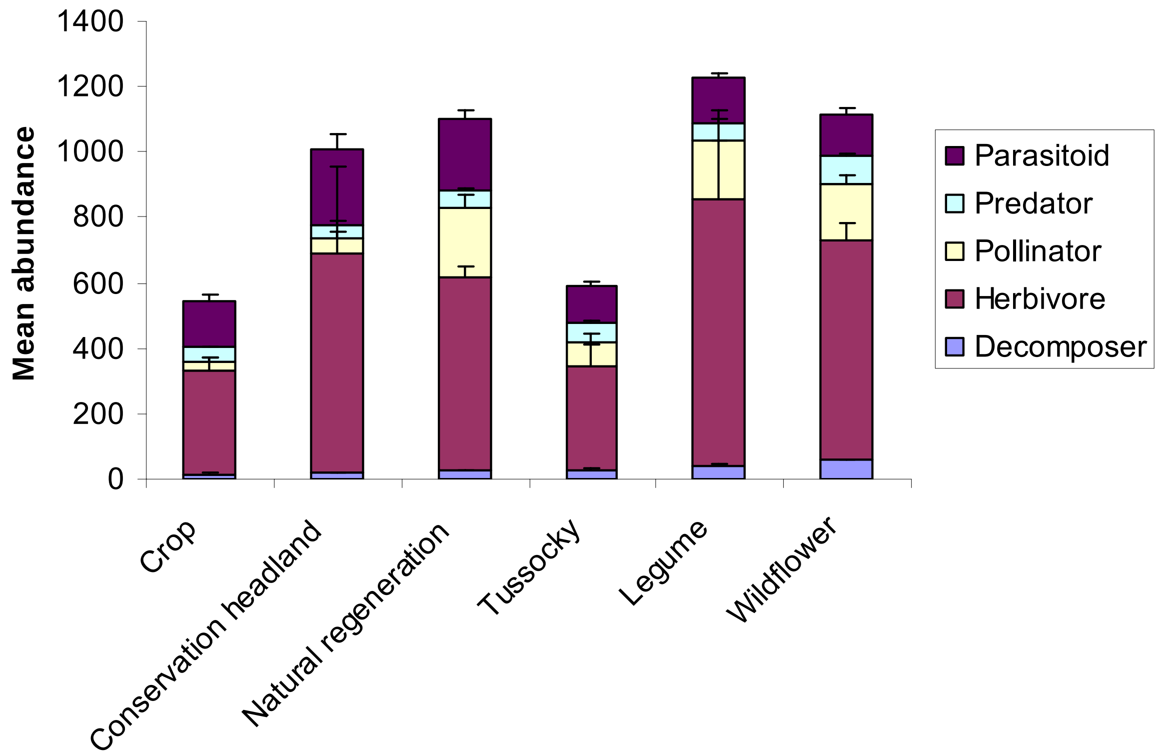
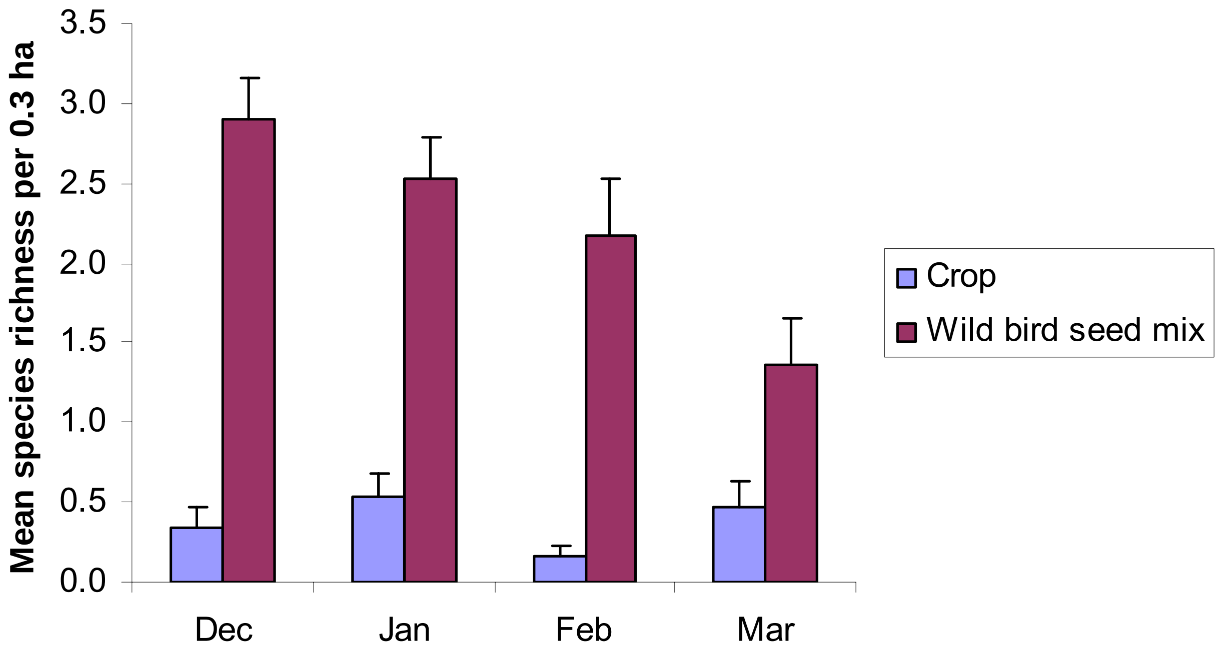


Fig. 20. a) Seasonal and b) Annual changes in mean (± se) species richness of the winter bird assemblage in the crop and wild bird seed mixture patch.

a) Seasonal changes in bird species richness



b) Annual changes in bird species richness

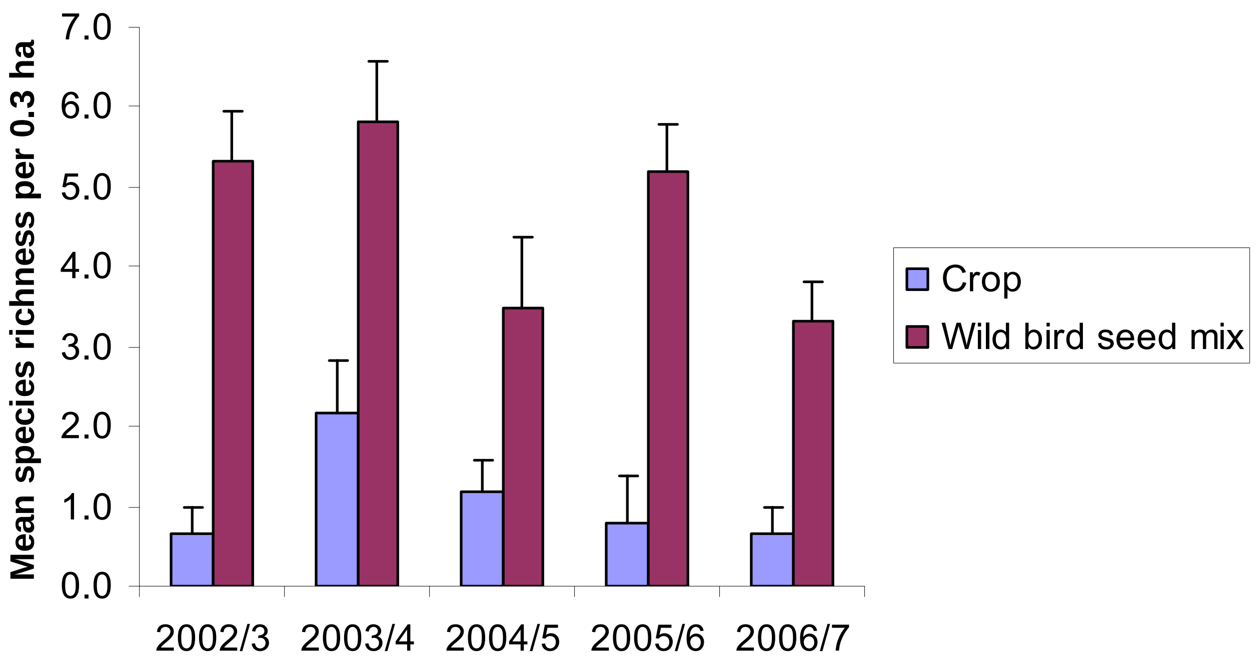
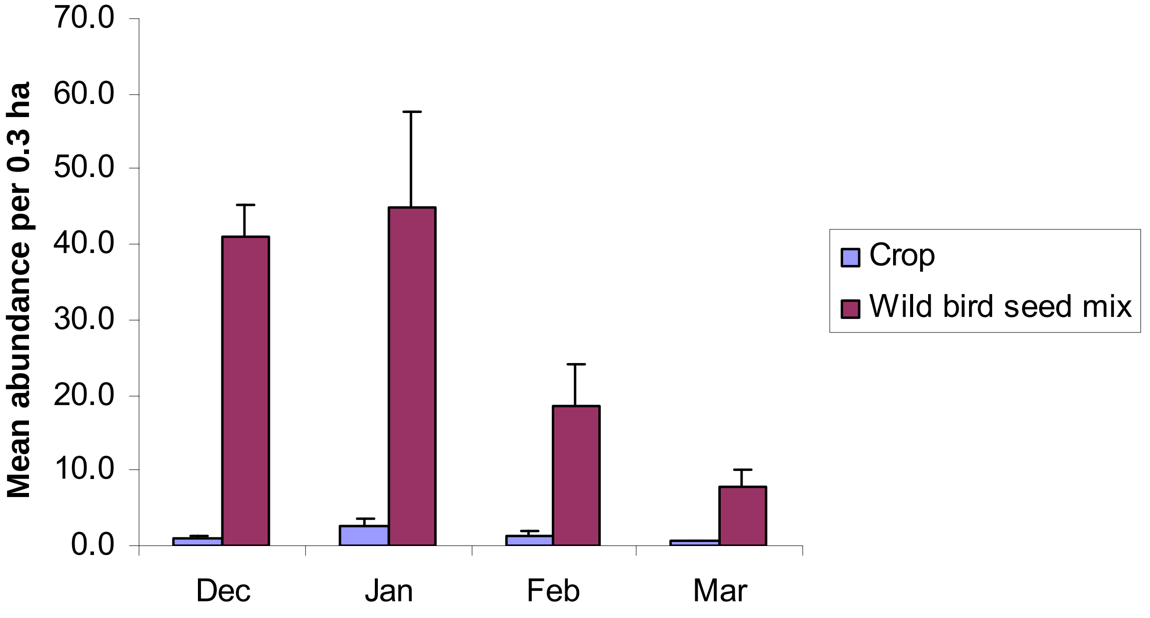


Fig. 21. a) Seasonal and b) Annual changes in mean (± se) abundance of winter birds n the crop and wild bird seed mixture patch.

a) Seasonal changes in bird abundance



b) Annual changes in bird abundance

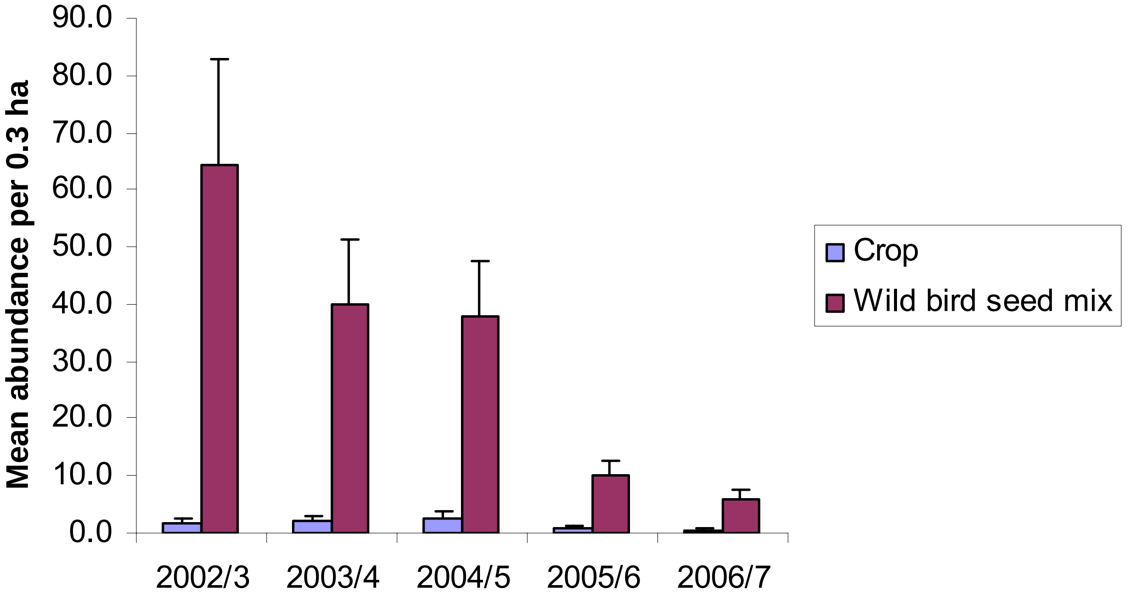


Fig. 22. Changes in the mean (± se) percentage cover of seed-bearing crop species sown in the wild bird seed mixtures patches between 2003/4 and 2006/7.

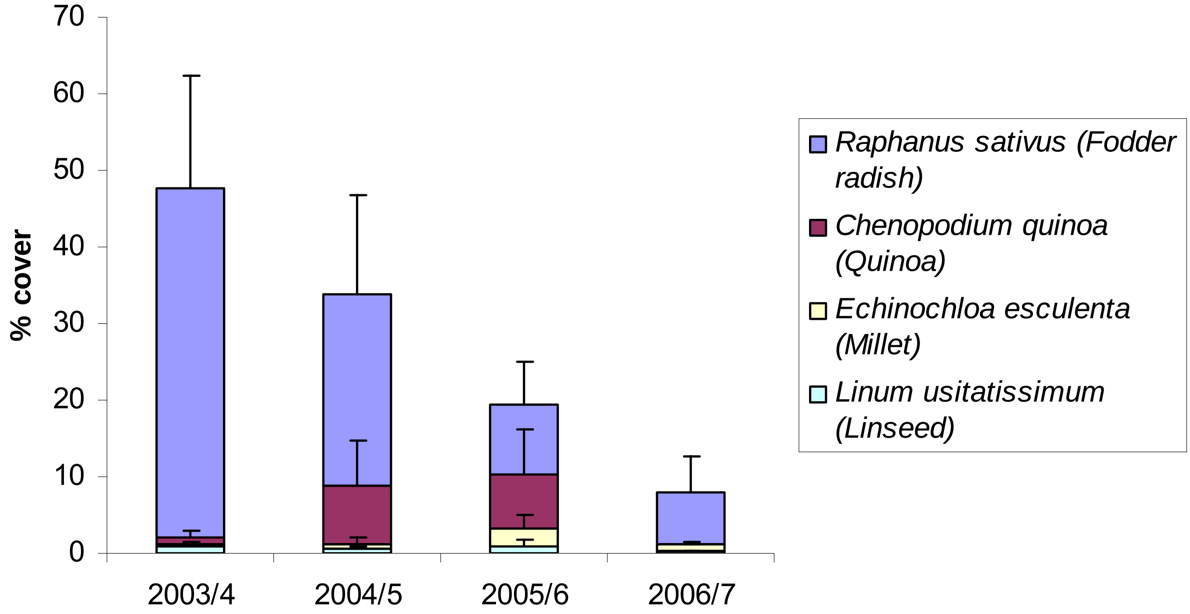
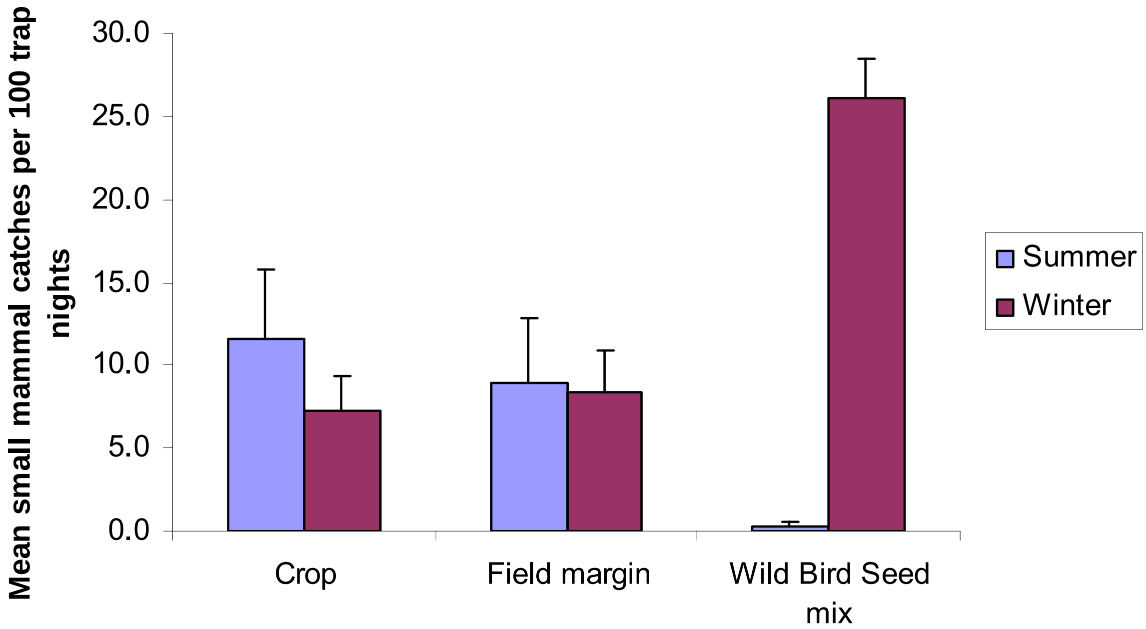


Fig. 23. Treatment effects on mean (± se) abundance of small mammals based on winter and summer trapping.



Appendix 2. Details of the crop rotation at each site

Site	County	Year	Crop
Abbotts Hall	Essex	2001	Wheat
Abbotts Hall	Essex	2002	Wheat
Abbotts Hall	Essex	2003	Oats
Abbotts Hall	Essex	2004	Barley
Abbotts Hall	Essex	2005	Wheat
Abbotts Hall	Essex	2006	Oats
Colworth	Bedfordshire	2001	Wheat
Colworth	Bedfordshire	2002	Wheat
Colworth	Bedfordshire	2003	Wheat
Colworth	Bedfordshire	2004	Oilseed rape
Colworth	Bedfordshire	2005	Wheat
Colworth	Bedfordshire	2006	Wheat
Little Wittenham	Oxfordshire	2001	Wheat
Little Wittenham	Oxfordshire	2002	Wheat
Little Wittenham	Oxfordshire	2003	Barley
Little Wittenham	Oxfordshire	2004	Oilseed rape
Little Wittenham	Oxfordshire	2005	Wheat
Little Wittenham	Oxfordshire	2006	Peas
Marlow	Buckinghamshire	2001	Barley
Marlow	Buckinghamshire	2002	Wheat
Marlow	Buckinghamshire	2003	Oilseed rape
Marlow	Buckinghamshire	2004	Wheat
Marlow	Buckinghamshire	2005	Wheat
Marlow	Buckinghamshire	2006	Wheat
Westow	Yorkshire	2001	Wheat
Westow	Yorkshire	2002	Wheat
Westow	Yorkshire	2003	Oats
Westow	Yorkshire	2004	Wheat
Westow	Yorkshire	2005	Oats
Westow	Yorkshire	2006	Wheat
Whittlesford	Cambridgeshire	2001	Wheat
Whittlesford	Cambridgeshire	2002	Wheat
Whittlesford	Cambridgeshire	2003	Sugar beet
Whittlesford	Cambridgeshire	2004	Peas
Whittlesford	Cambridgeshire	2005	Wheat
Whittlesford	Cambridgeshire	2006	Barley

Appendix 3. Details of the seed mixtures sown in the field margin treatments

Tussocky Grass mix			
Grasses	**%**	**Kg ha^{-1}**	**Cost £ ha^{-1} (€ ha^{-1})**
Cynosurus cristatus	20.0	4.00	
Dactylis glomerata	10.0	2.00	
Festuca pratensis	30.0	6.00	
Festuca rubra ssp. commutata	30.0	6.00	
Poa pratensis	10.0	2.00	
Total	**100.0**	**20.00**	**£60 (74€)**

Pollen & Nectar mix			
Grasses	**%**	**Kg ha^{-1}**	
Cynosurus cristatus	24.0	4.80	
Festuca rubra ssp. commutata	28.0	5.60	
Festuca rubra ssp. juncea	16.0	3.20	
Poa pratensis	12.0	2.40	
Forbs			
Lotus corniculatus (var. Leo)	5.0	1.00	
Onobrychis viciifolia	6.0	1.20	
Trifolium hybridum	3.0	0.60	
Trifolium pratense (var. Britta)	6.0	1.20	
Total	**100.0**	**20.0**	**£90 (111€)**

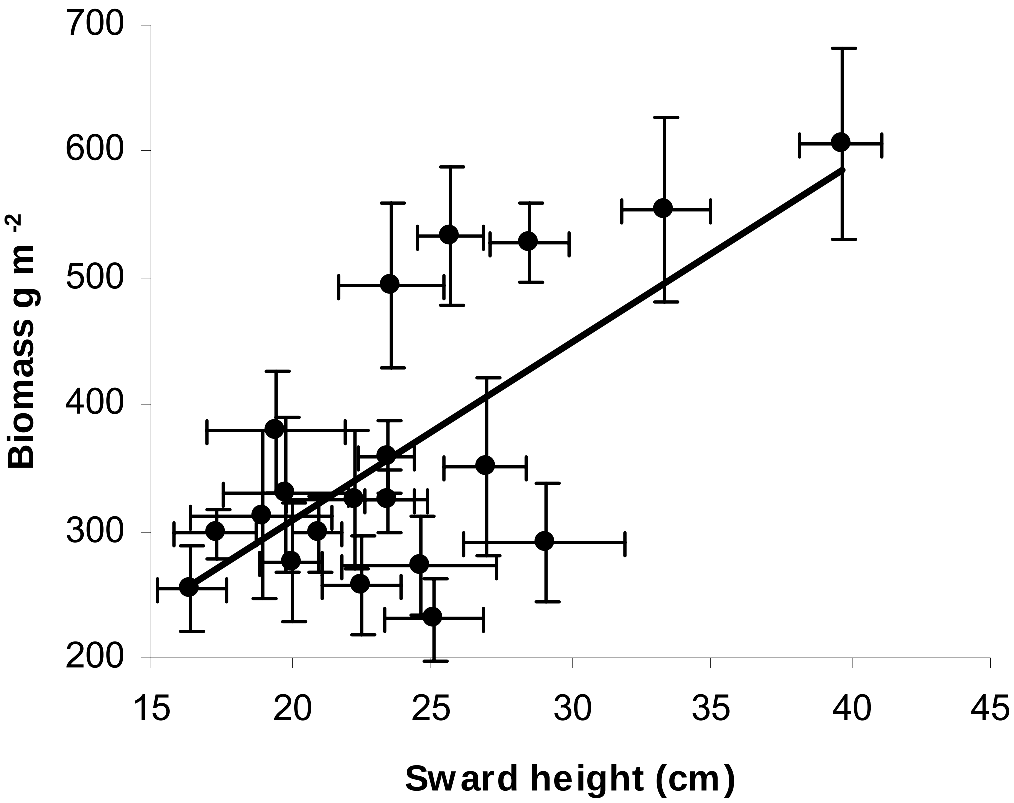
Wildflower mix			
Grasses	**%**	**Kg ha^{-1}**	
Cynosurus cristatus	23.8	8.88	
Festuca rubra ssp. commutata	27.8	10.36	
Festuca rubra ssp. juncea	15.9	5.92	
Poa pratensis	11.9	4.44	
Forbs			
Achillea millefolium	0.5	0.19	
Centaurea nigra	1.0	0.37	
Centaurea scabiosa	0.5	0.19	
Daucus carota	1.0	0.37	
Galium verum	1.0	0.37	
Knautia arvensis	1.5	0.56	
Leontodon hispidus	0.5	0.19	
Leucanthemum vulgare	1.5	0.56	
Lotus corniculatus	0.5	0.19	
Lychnis flos-cuculi	0.5	0.19	
Malva moschata	1.0	0.37	
Plantago lanceolata	1.0	0.37	
Plantago media	1.0	0.37	
Primula veris	1.0	0.37	
Prunella vulgaris	0.5	0.19	
Ranunculus acris	2.0	0.74	
Rhinanthus minor	1.0	0.37	
Rumex acetosa	0.5	0.19	
Sanguisorba minor	2.0	0.74	
Silene dioica	1.5	0.56	
Trifolium pratense	0.7	0.25	
Total	**100.0**	**37.25**	**£891 (1098€)**

Wild Bird Seed mix	**%**	**Kg ha^{-1}**	
Echinochloa esculenta	35.0	2.63	
Linum usitatissimum	35.0	2.63	
Raphanus sativus	15.0	1.13	
Chenopodium quinoa	15.0	1.13	
Total	**100.0**	**7.50**	**£50 (62€)**

Appendix 4. Biomass estimation for restored species-rich grasslands based on drop disk measurement of sward height

Each point represents the mean oven-dried biomass measurements from five 40 × 40 cm quadrats clipped to ground level and the mean sward height based on 20 drop disk (300 mm diameter, 200 g) measurements from each plot (R.F.Pywell, unpublished data).

Biomass m^{-2} = 23.53 + 14.14 Sward ht (cm)
$F_{1,19}$ = 16.56; P<0.001; R-sq = 48%



References to published material

9. This section should be used to record links (hypertext links where possible) or references to other published material generated by, or relating to this project.