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Utilisation of pollen resources by bumblebees in an enhanced arable landscape

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Summary

- Pollen is an essential resource for bumblebees, yet this is often overlooked in studies of their foraging requirements. The decline of bumblebees across the UK and rest of Europe has prompted conservation measures to consider the provision of pollen as well as nectar resources, particularly in intensive agricultural landscapes where the pollination service bumblebees provide is so important.

- This report details a study carried out in July 2003 to investigate the utilisation of pollen from different forage plant species by two bumblebee species with contrasting ecologies (*Bombus pascuorum* and *Bombus terrestris/lucorum*) across an enhanced arable landscape.

- An area of 1.96 km^2, centred on Manor Farm, near Malton in North Yorkshire, was divided into grid squares of 100m x 100m. Pollen loads were sampled from foraging bumblebees in eight random squares within the centre of this grid, and every square was surveyed in detail to map the distribution and abundance of all plant species in flower. Each pollen load was analysed to identify the pollen genera and/or species present, and to estimate the percentage species composition of the load.

- The two bumblebee species showed specialization towards pollen from contrasting species. *B. pascuorum* visited flowers of 23 different species to collect pollen, and although 76% of pollen loads were mixed, many were dominated by species from the Fabaceae, especially *Trifolium pratense. B. terrestris/lucorum* loads contained pollen from 17 species, only 32% of these were mixed, and *Borago officinalis* was the dominant pollen type. The majority of pollen loads of both bee species were dominated by species which had been sown in mixtures under the Countryside Stewardship Scheme. Although several unsown species were visited for pollen, they were only present in a few loads and at low proportions.

- The composition of a bumblebees' pollen load did not always relate to the forage plant species on which that bee had been caught. Calculation of a pollination probability index (PPI) showed that bumblebees tended to collect large amounts of conspecific pollen from their preferred pollen forage plants (ie. *Trifolium pratense*, *Borago officinalis*). This suggested that in our study area, bumblebees may be more efficient pollinators of certain forage plant species than others.

- Maps of flower abundance and distribution showed that the study landscape contained many diverse patches of flowering plants, particularly of the Fabaceae, which are encouraged under agri-environment schemes such as Countryside Stewardship. The area was therefore of higher quality in terms of pollen resources for *B. pascuorum* than *B. terrestris/lucorum. B. pascuorum* was the more abundant species, probably able to undertake relatively short foraging flights with guaranteed rewards, thus enhancing colony success.

- In conclusion, restoration measures, such as those within the agri-environment schemes, must consider the pollen requirements of all bumblebee species in order to conserve populations and retain their important pollination service in agricultural landscapes.

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1. Introduction

Bumblebees depend heavily on nectar and pollen resources from flowers in order to develop and maintain their colonies. Nectar provides a source of carbohydrates for energy, and pollen is the colony's only source of protein and is particularly essential for the development of larvae. The foraging behaviour of bumblebees has been extensively studied, in relation to the energetics of flight (Heinrich, 1979), their choice of flower species (Free, 1970; Heinrich, 1976; Ranta and Lundberg, 1980; Fussell and Corbet, 1992a) and exploitation of patchy resources in the landscape (Osborne and Williams, 2001; Goulson, 2003). However, the majority of foraging studies, particularly in recent years, have tended to focus on the flower visits of individuals observed on localised transect walks. These are likely to reflect the often wide range of plant species visited for nectar, but may not identify those species which are particularly important as pollen sources (Ranta and Lundberg, 1981; Carvell et al., 2003; Goulson and Darvill, 2003).

Analysis of the pollen loads carried by foraging bees can give us useful information about the flowers from which they are obtaining pollen, and about their relative importance based on the proportion of species in each sample (Brian, 1951; Westrich and Schmidt, 1986). The pollen loads collected by bees are particularly good indicators of flower constancy, the tendency to restrict their visits to flowers of a single species (Waser, 1986; Ne'eman et al., 1999). They also provide a useful means of comparing the foraging specializations of different bee species, which are apparent at most foraging sites due to factors such as differences in tongue length and flower handling ability (Ranta and Lundberg, 1980).

The loss of nectar and pollen sources from the countryside is likely to have been a major factor causing the declines suffered by many bumblebee species in the UK (Williams, 1982; Corbet et al., 1991). A recent analysis of change in abundance of selected bumblebee forage plants between 1978 and 1998 using the nationwide Countryside Survey dataset found that more than 70% of forage plants declined in frequency of occupied sample squares, and nearly 30% had shown significant declines (Carvell et al., 2001). These included species such as *Trifolium pratense* which is often cited as a major pollen source for the rarer species (Edwards, 2001). As bumblebees are key pollinators of many entomophilous crops and native plant species, their decline has serious implications for the yields and conservation of these (Corbet et al., 1991; Free, 1993). It is therefore critical that habitat restoration measures such as those now available in Europe within the agri-environment schemes (Defra, 2002) offer options to restore both nectar *and pollen* resources in order to maintain and enhance bumblebee populations in the agricultural landscape.

Arable field margins sown with wildflower seed mixtures have been shown to significantly enhance the local abundance and diversity of nectar and pollen-feeding insects, especially bumblebees (eg. Meek et al., 2002; Carvell et al., in press). A preliminary analysis of pollen loads from bees foraging at such margins suggests that each *Bombus* species has strong preferences for certain flower species in terms of the pollen types it collects (Carvell et al., 2003). Plant species in the sown mixtures also constituted a high proportion of most pollen loads, suggesting that newly created habitats can have an important functional role in providing pollen as well as nectar for bumblebees on farmland. However, the relative value of these, compared to other newly created or existing semi-natural habitats on the farm, in terms of providing pollen resources, has not been tested. Furthermore, bumblebees are known to forage over wide areas which are likely to extend beyond field and even farm boundaries (Osborne et al., 1999; Goulson and Stout, 2001). With this in mind, foraging studies still rarely seek to map the abundance of every species in flower within the foraging range of the bumblebees under study. Sampling pollen loads from bumblebees foraging at known locations, together with knowledge of pollen availability in the local landscape, allows us to assess spatial foraging patterns in such a way that cannot be achieved by field observations alone.

The aims of this study are as follows:

1. To investigate the utilisation of pollen from different forage plant species by two bumblebee species with contrasting ecologies (*Bombus pascuorum* and *Bombus terrestris/lucorum*) across an enhanced arable landscape;
2. To record the distribution and abundance of flowering plants in the landscape as a means of mapping availability of pollen resources, and
3. To use pollen load analysis to assess spatial foraging patterns of *B. pascuorum* and *B. terrestris/lucorum* across the farmed landscape.

2. Methods

2.1 Study area

This study was conducted on Manor Farm and surrounding farmland, Eddlethorpe, near Malton in North Yorkshire (Lat. 54°05'N, Long. 0°49'W), over a total area of 1.96km2 (196ha). Manor Farm is a modern, intensively managed arable enterprise of 164ha where the 'Manor Farm Project' was established in 1998 to demonstrate that practical wildlife conservation and profitable farming can be effectively integrated. Many areas of the farm have been enhanced with newly planted field margins, blocks or corners either as part of the Countryside Stewardship Scheme or ongoing experiments. These provide a variety of flower-rich foraging habitats for bumblebees, together with existing semi-natural habitats at field and woodland edges, and a species rich meadow to the west of the farm.

2.2 Experimental design and sampling

The study area of 1.96km^2 was divided into 196 grid squares, each 100m x 100m (Figure 1). The sampling of bumblebee pollen loads and mapping of pollen availability were carried out during the week of 14th – 18th July 2003.

2.2.1 Mapping pollen availability

In order to create a detailed map of pollen availability within the study area, each grid square was surveyed to identify and score all plant species in flower. Flowers were scored according to their coverage of the entire square (the 'widespread' score) and then according to their local abundance in patches where they occurred in that square (the 'local' score, based on the DAFOR system) as follows:

Widespread flower scores	Local flower scores
1 1-6 % coverage	1 Rare
2 7-12% coverage	2 Occasional
3 13-25% coverage	3 Frequent
4 26-50% coverage	4 Abundant
5 51-100% coverage	5 Dominant

Of the 196 grid squares, 154 contained plant species in flower at the time of the survey. These data on flower abundance within each square were spatially referenced onto the OS map and sampled grid using ArcView GIS 3.2 software, to give a distribution and abundance map for each species in flower within the study area.

2.2.2 Sampling pollen loads

Pollen loads were sampled from bumblebees within a central area of the larger grid, measuring 0.36 km^2. This left a minimum distance of 400m from any 'pollen-sampled' square to the limit of the pollen availability map. A systematic random sample of eight grid squares which contained adequate forage resources to attract pollen-collecting bumblebees (either *Bombus pascuorum* (Scopoli) or *B. terrestris/lucorum* (L.)) was selected (Figure 1). *B. terrestris* and *B. lucorum* are treated as a species pair as workers cannot be reliably distinguished in the field. Within each of the eight squares, the first 15 workers of either species encountered with full pollen baskets was caught. A single complete pollen load was removed from each bee using a cocktail stick, whilst the bee was restrained using a marking cage with soft plunger. The species of bee, plant species on which the bee was foraging when caught and grid square location were recorded on a label which was placed with the pollen load in a small sample tube, and this was cooled for preservation prior to analysis. For squares in which a full sample of 15 workers could not be seen, the observer continued searching for up to 60 minutes until no further pollen-collecting bumblebees were encountered, and then moved on to the next square.

Pollen sampling was undertaken between 10.00hrs and 18.00hrs during dry, sunny weather (weather conditions were noted during sampling).

2.3 Analysis and interpretation of pollen samples

Each pollen sample was processed by embedding as a thin layer in glycerine jelly and mounting on a microslide (Westrich and Schmidt, 1986). Samples were analysed using a light microscope to identify a) the pollen genera and where possible the most likely plant species from which they were collected according to exine morphology and grain size, and b) an estimate of the percentage species composition of each pollen load based on a count of 200 grains per sample. Species present in trace amounts comprising less than 1% of a load were regarded as contamination and were excluded from the subsequent data. For each load, any pollen species occupying a proportion greater than 50% was defined as dominant. Pollen identifications were made with the aid of reference collections and a full list of plant species in flower at the study site during the period of pollen collection. Where the determination of pollen types to species level was not possible, they were identified to plant family level.

2.4 Data Analysis

The data were analysed in four stages; firstly, the overall pollen load characteristics of *B. pascuorum* and *B. terrestris/lucorum* were compared by looking at both the number of loads in which different plant species were present, and the mean proportion of each pollen species per load across all loads. Secondly, the relationship between the forage plant species on which a bumblebee was caught and the composition of its' pollen load and was examined (2.4.2). Thirdly, differences between the sample squares in terms of the diversity of pollen loads collected by bumblebees, and the relationship between flowering plant diversity and pollen load diversity per square were examined (2.4.3). Finally, we examined the distribution and abundance of different flowering plant species across the study landscape, and spatial relationships between these and the pollen loads collected by bumblebees (2.4.4). Several of these analyses involved assessments of species diversity which were represented by calculating Simpson's diversity index, taking into account both the number and relative proportion of every plant species in a sample, as explained below (2.4.1).

2.4.1 Simpson's diversity index
The species diversity of each pollen load was represented by calculating Simpson's diversity index (Begon et al., 1990):

$$\text{Simpson's index} = \frac{1}{\sum_{i=1}^{S} Pi^2}$$

where S is the total number of species in the pollen load, and P*i* is the proportion of the load occupied by the *i*th species. Larger values indicate higher diversity.

For each of the *Bombus* species studied, the mean proportion of each pollen type per load across all loads was calculated. In order to compare the breadth of the pollen diets of *B. pascuorum* and *B. terrestris/lucorum*, Simpson's index was calculated from these means to represent the diversity of pollen types collected overall.

Simpson's index was also calculated for the diversity of plant species in flower in each sample square, with S equal to the total number of flowering species in the square, and P*i* as the proportion of the summed 'local' abundance scores occupied by the *i*th species.

The diversity (Simpson's index) of pollen loads collected by bumblebees from each forage plant species on which those bees were caught was also calculated. These values were compared using a one-way ANOVA. Tukey's honest significant difference test was also performed to assess differences between species.

2.4.2 Differences between forage plant species
To examine the relationship between the forage plant species on which bumblebees was caught and the composition of their pollen loads, we calculated the Pollination Probability Index (PPI) as proposed by Ne'eman et al. (1999). This index for pollen load analysis aims to reflect flower constancy at the pollinator population level, and

may also serve as an estimation for pollination probability. For each forage plant species on which bumblebees were caught during sampling, the mean proportion of conspecific pollen per load was calculated (PCP). The proportion of bees (out of the total number observed) carrying conspecific pollen was also calculated for each forage plant species (PBP). The pollination probability index was then calculated as follows: PPI = PCP x PBP. The PPI varies from 0 in cases where bees did not collect any conspecific pollen, to 1 in cases where all bees collected only conspecific pollen from that particular forage species.

2.4.3 Differences between sampled squares

Differences in the mean diversity of pollen loads of each *Bombus* species sampled from each of the eight grid squares were tested using a one-way ANOVA, with Tukey's honest significant difference test. The effect of flowering plant diversity on pollen load diversity was examined by simple linear regressions, with both diversity of all plant species per square and diversity of bumblebee pollen forage species per square as explanatory variables.

2.4.4 Spatial relationships between bumblebee pollen loads and plant species in flower

To assign a single flower abundance score for further analysis, the relationship between the mean 'local' and 'widespread' flower scores per square for each species (described above, 2.2.1) was examined. Simple linear regression showed these two variables to be highly correlated ($F_{1,163}$= 1953.52, P<0.001, r^2 = 0.92), with perhaps a tendency for local scores to be higher where species had been sown in field margins or corners. The bcal scores were applied for subsequent analysis as we considered these to be a more biologically relevant unit of forage availability to a bumblebee.

The test whether the proportion of a pollen species collected by each *Bombus* species was related to flower abundance of that plant species across the whole study area (1.96 km^2) simple linear regression was used. For further analyses, we attempted to relate the proportion of each pollen type in the 'average' bees' load with flower abundance within a radius of 0m (ie. the sample square), 100m, 200m, and so on, from where that load was sampled, using regressions. However, problems were encountered in the interpretation of these data due to the heterogeneity of the local landscape in terms of flowering plant distribution, and small sample sizes for several pollen types. Furthermore, the majority of pollen loads contained species flowering in the sample square, so the regression models were most significant at a radius of zero metres.

Further analyses therefore focused on the two preferred major pollen sources for *B. pascuorum* and *B. terrestris/lucorum* in our study area: *Trifolium pratense* and *Borago officinalis* respectively. A Chi-squared test was used to test for significant differences between the proportion of bumblebees carrying each pollen species at different distances from the nearest known flowering patch of that plant species. Distances between sampled squares were calculated as centre-to-centre distance to the nearest 100m, using Pythagoras calculations for diagonals.

All statistical analyses were performed using Minitab 13 statistical software (Ryan et al., 2000).

3. Results

In total, 107 pollen samples were analysed, with a few missing data points due to a lack of pollen-collecting bumblebees at certain forage patches. Workers of *Bombus pascuorum* were more numerous than *Bombus terrestris/lucorum* at the study site, probably as a result of the plant species composition of the relevant forage patches being more preferable to the former species. Hence, 79 pollen samples were collected from *B. pascuorum* and 28 from *B. terrestris/lucorum*.

3.1 Pollen load characteristics of B. pascuorum *and* B. terrestris/lucorum

Pollen load analysis showed that *B. pascuorum* had visited flowers of at least 23 different species, assuming that pollen grains only classified to genus level or of 'unknown' identity were from single species (Table 1a). Seventy-six per cent of *B. pascuorum* pollen loads were mixed, but many of these mixed loads were dominated by one species. Species from the Fabaceae were present in 95% of all loads, notably *Trifolium pratense*, *Lotus corniculatus*, *Lathyrus pratensis* and *Trifolium repens/hybridum*, and where present, these occupied on average between 46% and 70% of the load. *T. pratense* was present in 14 loads at over 90%, and is referred to from here as the preferred pollen species for *B. pascuorum*. Other pollen sources were members of the Scrophulariaceae, Lamiaceae and Asteraceae, each present in 17% of loads (Table 1a), but only on average at between 5% and 30%. Overall, the Simpson's diversity index for the pollen diet of *B. pascuorum* in this study was 6.1.

Pollen loads from *B. terrestris/lucorum* were from 17 species overall, with a Simpson's index of 4.5 indicating a narrower diet breadth than for *B. pascuorum*. Thirty-two per cent of the 28 loads were of mixed species. *Borago officinalis* was the dominant pollen source (Table 1b), present in 46% of loads occupying an average of 87% per load (referred to as the preferred pollen species of *B. terrestris/lucorum*). Other notable pollen sources were from the Fabaceae (mainly *T. repens/hybridum*), Asteraceae and Dipsacaceae (*Dipsacus fullonum*) present in 36%, 18% and 11% of all loads respectively. Of the pollen species only present in single loads, *Ononis spinosa*, *Filipendula ulmaria* and *Rubus fruticosus* constituted over 50%, and *Mentha* spp. was the only pollen type in one particularly large load. Others, such as *T. pratense*, *Chamerion angustifolium* and *Arctium minus* were present at less than 20% of the load.

In terms of whether pollen sources had been sown on or around the farm in mixtures as part of the Countryside Stewardship Scheme or other habitat enhancement, the data show that both bumblebee species visited a similar number of unsown and sown species to collect pollen (Tables 1a and b). However, the unsown species tended to be present in only a few loads and at low proportions.

3.2 Differences between forage plant species

The forage plant species on which a bumblebee was caught during sampling did not necessarily relate to the composition of the pollen load carried by that bee (Figure 3). There were significant differences between the number of *B. pascuorum* workers caught on a plant species and the number of pollen loads in which that plant species was dominant at over 50% (Chi-squared value = 35.68, df = 6, $P<0.001$; excluding species with counts less than 5). This difference was not significant for *B. terrestris/ lucorum* (Chi-squared value = 2.53, df = 2, ns).

Pollen loads sampled from bees foraging at their preferred pollen species tended to contain a lower diversity of pollen types than less preferred species, such as *B. pascuorum* on *Trifolium pratense* and *B. terrestris/lucorum* on *Borago officinalis* (Table 2). This tendency was just not significant for *B. pascuorum* (ANOVA on mean Simpson's index per load sampled from each forage plant species $F_{10,68} = 1.91$, $P = 0.059$) but was significant for *B. terrestris* ($F_{6,21} = 17.36$, $P<0.001$). Furthermore, the PCP, PBP and PPI values presented in Table 2 were generally highest for the preferred pollen species of each *Bombus* species.

3.3 Differences between sampled squares

There were no significant differences in the diversity of *B. pascuorum* pollen loads collected from the eight sample squares (ANOVA on Simpson's index; $F_{7,71} = 1.37$, ns). *B. terrestris/lucorum* pollen loads were of significantly different diversity between the sampled squares (ANOVA $F_{5,22} = 5.34$, $P<0.01$), but this appeared to relate more to the presence of *Borago officinalis* from which single species loads were collected rather than to the overall diversity of forage plants per square. Linear regressions showed that there was no significant effect of flowering plant diversity per square, either of all plant species or only bumblebee pollen forage species, on the diversity of pollen loads of either bee species.

3.4 The 'pollen landscape' of Manor Farm

The distribution and relative abundance of key bumblebee forage plant species in flower within the study area during sampling are shown in Figure 2. Many species occur along boundary features of the landscape such as field margins, particularly where they have been sown on the farm (eg. *Borago officinalis* and *Lotus corniculatus*). Where they appear to flower in the centre of fields, species have often been sown either as part of a wild bird mix (eg. *Dipsacus fullonum*), a wildflower 'island' disconnected from the margin (eg. *Lathyrus. pratensis*) or as part of an organic grass ley (eg. *T. pratense* to the north-west of the sample grid). In total, 165 plant species were recorded in flower across the study area during the sampling week. A full species list of these, along with their mean flower abundance scores per square, is given in the Appendix.

3.5 Spatial relationships between bumblebee pollen loads and plant species in flower

Overall, there was a significant positive relationship between the mean proportion of pollen species in *B. pascuorum* loads and their flower abundance across the study area ($F_{1,17} = 1953.52$, $P<0.01$, $r^2 = 0.30$). This relationship was not significant for *B. terrestris/lucorum* pollen loads, suggesting that preferred pollen sources of these species were not generally abundant across the landscape.

For each plant species from which bees collected pollen, counts were made of the number of conspecific loads which had been sampled from bees foraging in squares where its flowers were absent (Table 1a and b). All squares within which *B. pascuorum* loads were sampled were within 200m of the nearest flowering *T.*

pratense patch. However, our data show that of the 27 loads containing *T. pratense* pollen, six were sampled from bees at least 100m from the nearest patch and nine were sampled from bees at least 200m from the nearest patch of flowers (Figure 4). There were significant differences between the proportion of *B. pascuorum* carrying *T. pratense* pollen at 0m, 100m and 200m from the nearest known patch of flowers (Chi-squared value = 30.07, df = 2, P<0.001).

All squares in which pollen-collecting *B. terrestris/lucorum* were sampled were within 200m of the nearest flowering *Borago officinalis* patch. The majority of loads sampled were from bees within the same square as a patch of *B. officinalis* flowers (ie. at 0m), and two loads were from bees in squares at 100m from the nearest patch. These differences were significant (Chi-squared value = 15.45, df = 2, P<0.001).

Further interesting patterns of forage utilisation are revealed by examining the distribution of flower species only present in a small number of pollen loads. For example, of the four loads of *B. pascuorum* containing *Lamium purpureum*, two were sampled at 400m from the nearest patch of flowers, and two at 500m from the nearest patch. This is the furthest pollen-foraging distance for which we have evidence for *B. pascuorum* from this study, although of course we cannot be certain that the *L. purpureum* pollen was collected from the flower patches mapped within the study area. For *B. terrestris/lucorum*, a single load sampled from a worker foraging at *Dipsacus follonum* contained 100% pollen from *Mentha* spp., the nearest flowering patch of which was 600m away.

4. Discussion

The bumblebees in our study area appear to collect the majority of their pollen from a few plant species ('majors') and much smaller amounts from many others ('minors', as referred to by Heinrich, 1976). This tendency is well recognised in the literature, as is the tendency for the major pollen species to differ between bumblebee species (eg. Brian, 1951; Free, 1970; Heinrich, 1976). *Bombus pascuorum* pollen loads contained an overwhelming amount of pollen from the Fabaceae, particularly *Trifolium pratense*. Brian (1951) found that pollen from *T. pratense* was the major constituent of larval cells in *B. pascuorum* nests in Scotland, and other studies have revealed similar preferences for this and other Fabaceae by the longer-tongued *Bombus* species (Anasiewicz and Warakomska, 1977; Edwards, 2001; Carvell et al., 2003). *Bombus terrestris/lucorum*, both short-tongued species, tended to collect pollen from *Borago officinalis*, and *Trifolium repens/hybridum* could also be considered a major pollen source as it constituted a high proportion of loads where present. Species from the Asteraceae, Dipsacaceae, Rosaceae and an unidentified pollen type were present as minors. These preferences to plant family are similar to those suggested in other studies, although the species may differ according to local abundance (Brian, 1951; Carvell et al., 2003).

Simpson's index for the diversity of pollen types collected was higher for *B. pascuorum* (6.1) than for *B. terrestris/lucorum* (4.5), suggesting that at this site *B. pascuorum* has a broader pollen diet. That the index has low sensitivity to sample size (Magurran, 1988) is important here as the greater abundance of *B. pascuorum* led to a larger sample of pollen loads for this species. However, it is interesting that these findings compare with those of Goulson and Darvill (2003) who examined the flower visits of several bumblebee species across a large area of diverse unimproved grassland and found a relationship between abundance and diet breadth. Even though our results come from a relatively small sample of loads from *B. terrestris/lucorum*, these are likely to represent the behaviour of most individuals. According to Free (1970), bumblebees tend to exhibit day-to-day constancy as well as constancy during a foraging trip. Free (1970) also found that although pollen collecting behaviour of *B. lucorum* workers was fairly similar within one colony, workers of another colony made different use of the surrounding flora, suggesting that the colony may influence an individual's choice of forage. This should be noted when interpreting analysis of pollen loads from bees in the field, rather than from the nest.

The forage plant species on which a bumblebee was caught did not always relate to the composition of the pollen load carried by that bee, highlighting the value of the pollen analysis method in studying bumblebee forage preferences. For example, *B. pascuorum* was often seen foraging at *Dipsacus follonum* and *Prunella vulgaris*, yet these species barely featured in the pollen loads, so must be visited primarily for nectar. Considering this, it is not surprising that pollen loads sampled from the major pollen plants of both *Bombus* species tended to contain a lower diversity of species than those from their minors (although not significant for *B. pascuorum*). Furthermore, the diversity of pollen loads sampled from any one square was not related to flowering plant diversity within that square, indicating that pollen collection at the local scale does not follow the general tendency for bumblebee abundance and diversity to be correlated with plant species richness (eg. Carvell, 2002).

The pollination probability index (PPI) (Ne'eman et al., 1999) allowed us to examine these patterns more closely. The PPI was higher for bumblebees caught foraging at their preferred pollen forage plants, suggesting that in the landscape around Manor Farm they may be more efficient as pollinators of these plant species than other less favoured pollen source species. Care should be taken with the use and interpretation of this index, as bumblebees may not serve as legitimate pollinators of all plant species visited for pollen (Westrich, pers. comm.). However, the implication of this for conservation is that if preferred pollen source species such as *T. pratense* are sown as part of a mixture of either native wildflower species (as in the current UK Countryside Stewardship Arable option R3 with GX supplement) or agricultural legumes (as in Arable option WM2, the pollen and nectar mix; Defra, 2002) they may themselves have a high probability of pollination, but may in turn reduce the chances of other species in the mixture being pollinated by bumblebees. Further research is required in this area. We would expect the average UK farm to support an assemblage of five or six *Bombus* species with a range of flower preferences, along with other insect pollinators, so if chosen carefully then most species in a sown mixture could have equal pollination probability.

The quality of our study landscape for foraging bumblebees, at least during the July sampling period, was evident from the mapped abundance and distribution of preferred forage plant species. The presence of a species-rich meadow and organic farm to the north-west, combined with the network of sown flower-rich habitats on Manor Farm itself make it atypical of the arable landscape of the UK (Meek et al., 2003). This landscape clearly favours *B. pascuorum* to a greater extent than *B. terrestris/lucorum* in terms of available pollen sources, as all four Fabaceae species were sown in several mixtures. It is therefore no surprise that the proportion of pollen species in *B. pascuorum* loads was related to their flower abundance both across the study area, and also, for the majority of loads, in the square from which they were sampled. Most squares in which *T. pratense* flowers were absent contained one of the other favoured Fabaceae species, although several *B. pascuorum* pollen loads in these squares contained *T. pratense* pollen, possibly collected from up to 200 metres away. Together, these results suggest that *B. pascuorum* workers may have been undertaking short foraging flights with guaranteed rewards, thus increasing colony efficiency and fecundity. Our approach could be greatly enhanced with knowledge of the nest locations of the sampled bees, although these are difficult to find (Fussell and Corbet, 1992b). From the limited evidence available, bumblebees colonies do appear to attain larger size and forage closer to the nest in areas with a greater density and diversity of suitable flowers (Brian, 1954; Goulson et al., 2002).

For *B. terrestris/lucorum*, the greater proportion of unsown species collected in pollen loads, and lack of pollen-foraging workers in several sample squares, suggests that apart from *Borago officinalis* sown into a seed-bearing mixture for wild birds, enhancement on this particular farm was less favourable. *B. terrestris/lucorum* and other short-tongued bumblebee species have been less affected than longer-tongued species by the loss of semi-natural habitats in agricultural landscapes (Williams, 1982; Edwards, 2001). This may be partly due to their greater foraging range (Walther-Hellwig and Frankl, 2000) and early emergence in spring, when mass-flowering crops such as oil-seed rape can provide valuable forage resources (Westphal et al., 2003). However, suitable pollen resources must be made available to these species throughout their seasonal development, particularly in areas with few mass-flowering crops or existing semi-natural habitats.

In summary, this study has confirmed that bumblebees have strong preferences for certain pollen types which vary between species. The distribution and abundance of preferred pollen types across a landscape are likely to affect the observed pattern of flower visitation to these and other forage plant species. Further research is required to ascertain how pollen species differ in their quality or nutritional value for bees, which may be related to protein content (Cook et al., 2003). Utilisation and availability of pollen sources early in the season should also be considered, although at present no other study has mapped the local landscape in terms of its pollen resources to this level of detail. We stress the importance of considering the pollen requirements of different bumblebee species in the design of restoration measures to conserve populations and retain their important pollination service across agricultural landscapes.

5. Acknowledgements

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Figure 1. Map of Manor Farm and the surrounding landscape showing the study area within sampled grid squares (n=196) and squares chosen for pollen load sampling (n=8).
OS Grid Reference for the south-western corner of the study area is SE763649.

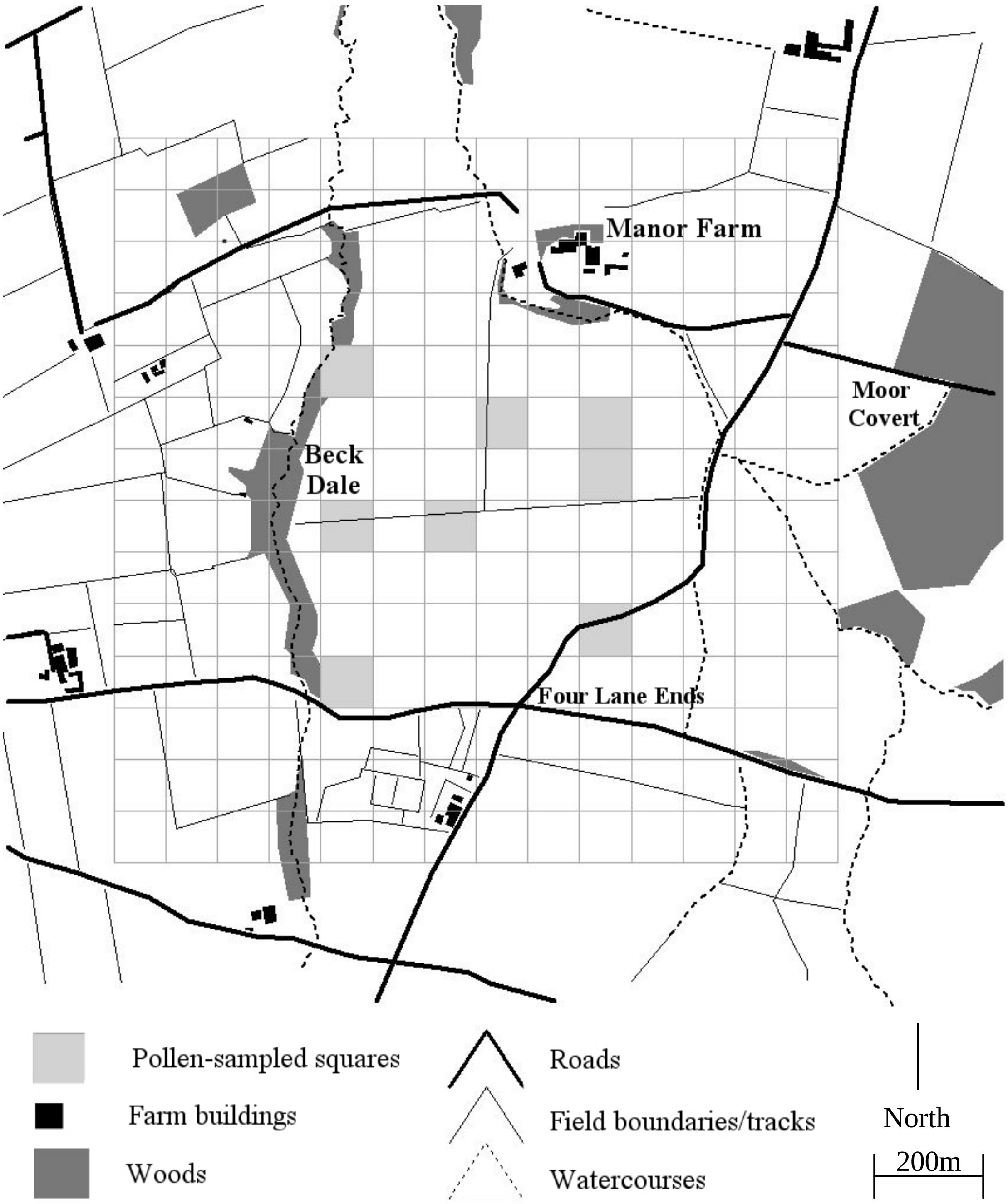
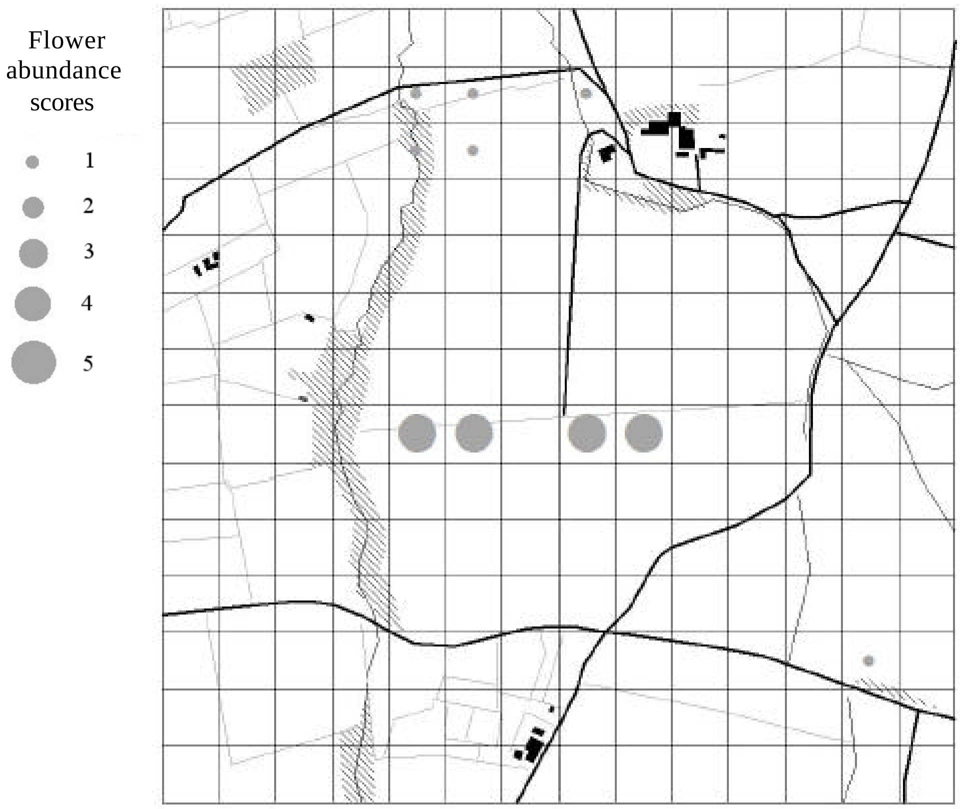
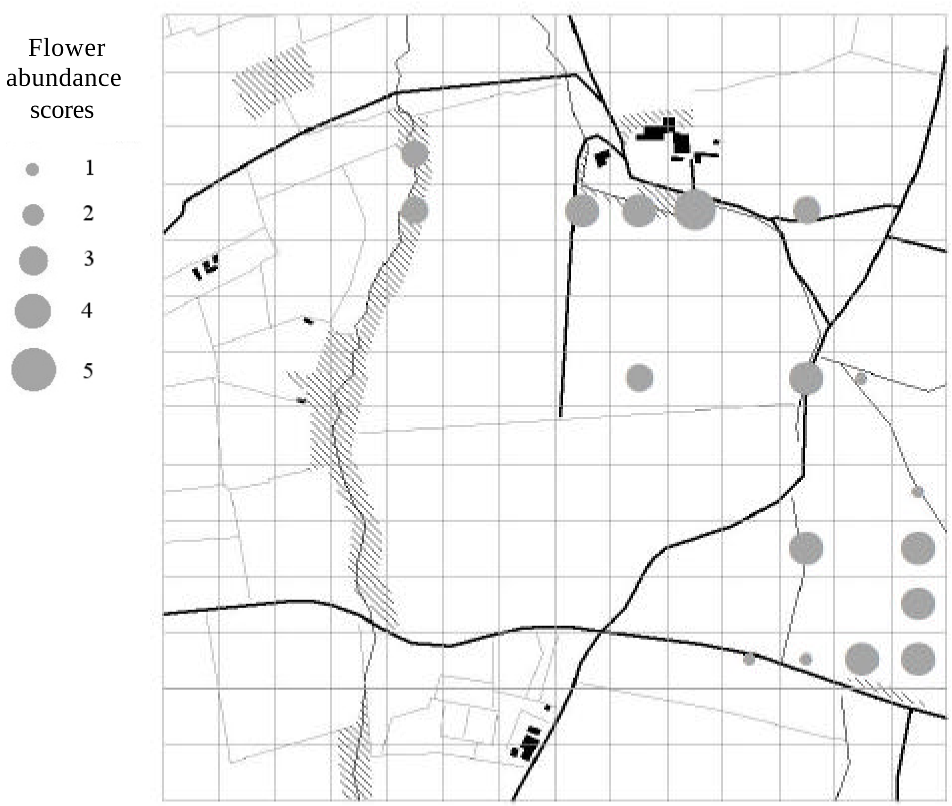


Figure 2 (over page). Maps showing the distribution and relative abundance of plant species in flower within the study area between 14th – 18th July 2003. Scores relating to the 'local' abundance of flowers in patches where they occurred are shown for key bumblebee pollen sources; a) *Borago officinalis,* b) *Centaurea cyanus*, c) *Centaurea nigra*, d) *Dipsacus follonum*, e) *Lathyrus pratensis*, f) *Lotus corniculatus*, g) *Mentha* spp., h) *Rhinanthus minor,* i) *Rubus fruticosus*, j) *Trifolium repens/hybridum*, k) *Trifolium pratense*. (s = species sown on the farm; u = species not sown and naturally occurring; b = both sown and naturally occurring; see methods section 2.2.1 for explanation of flower scores; key to map symbols and scale as in Figure 1)

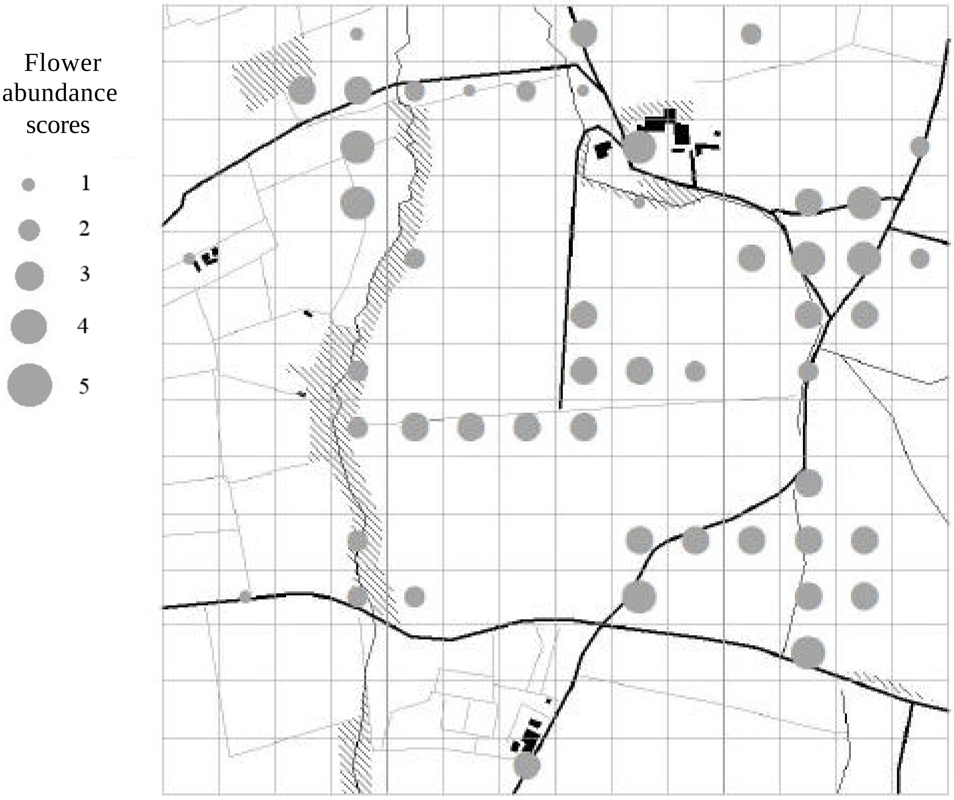
a) ***Borago officinalis* (s)**



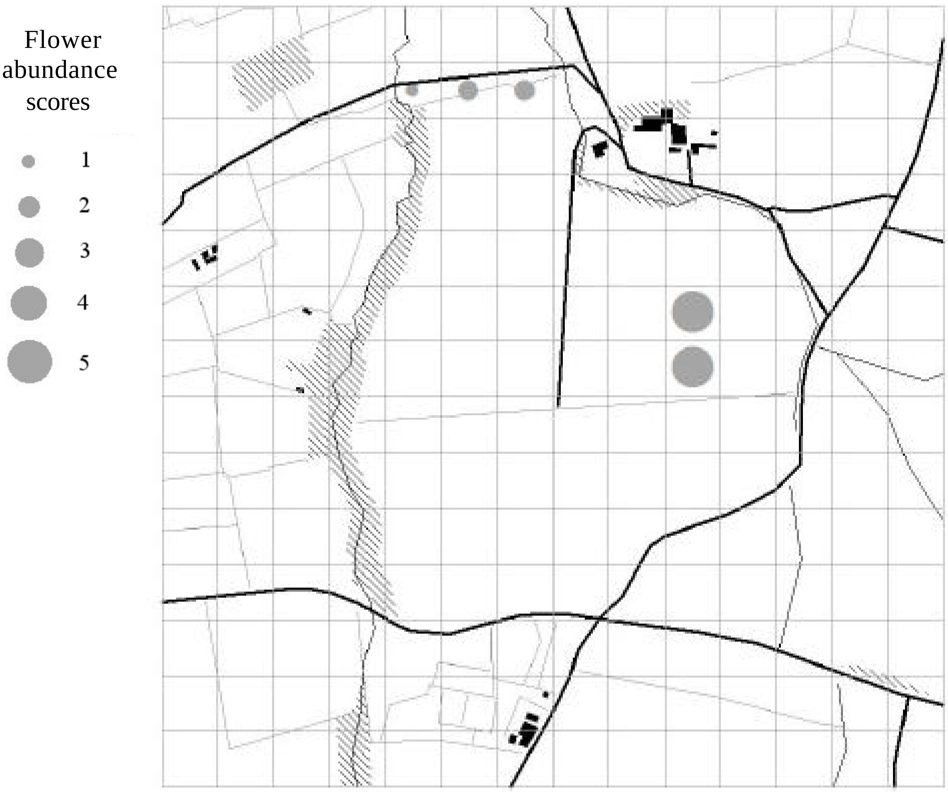
b)*Centaurea cyanus* (s)



c) ***Centaurea nigra*** **(s)**



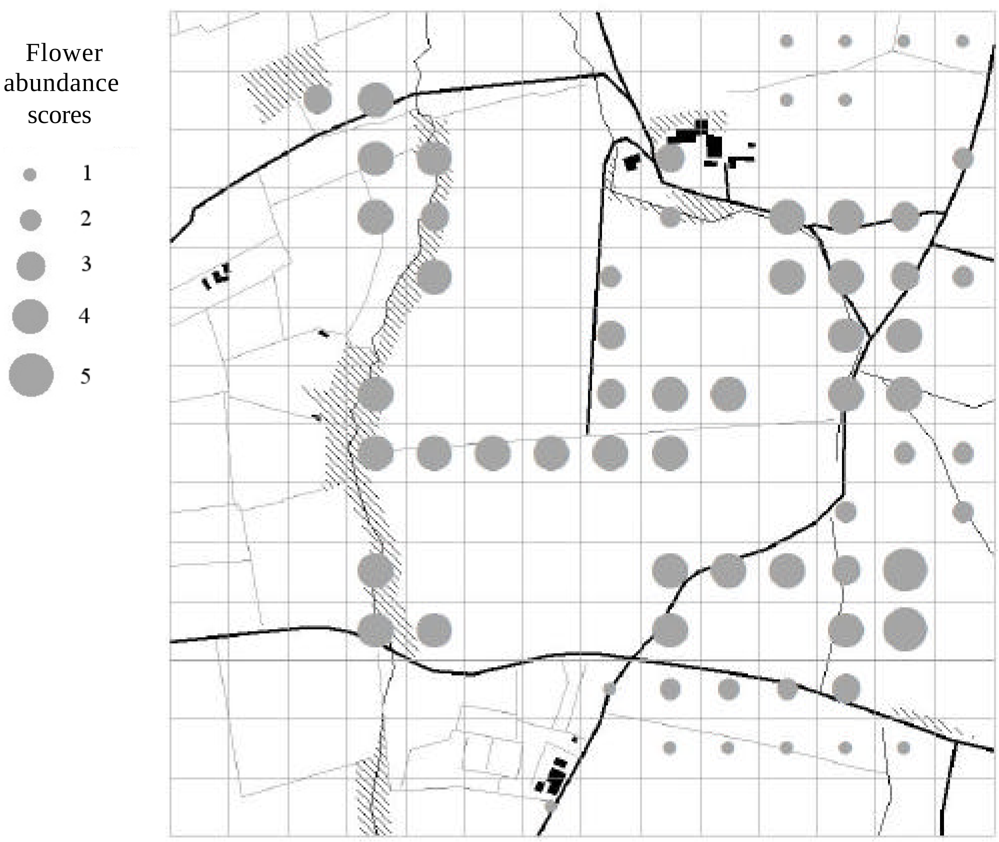
d) ***Dipsacus follonum*** **(s)**



.en 2004

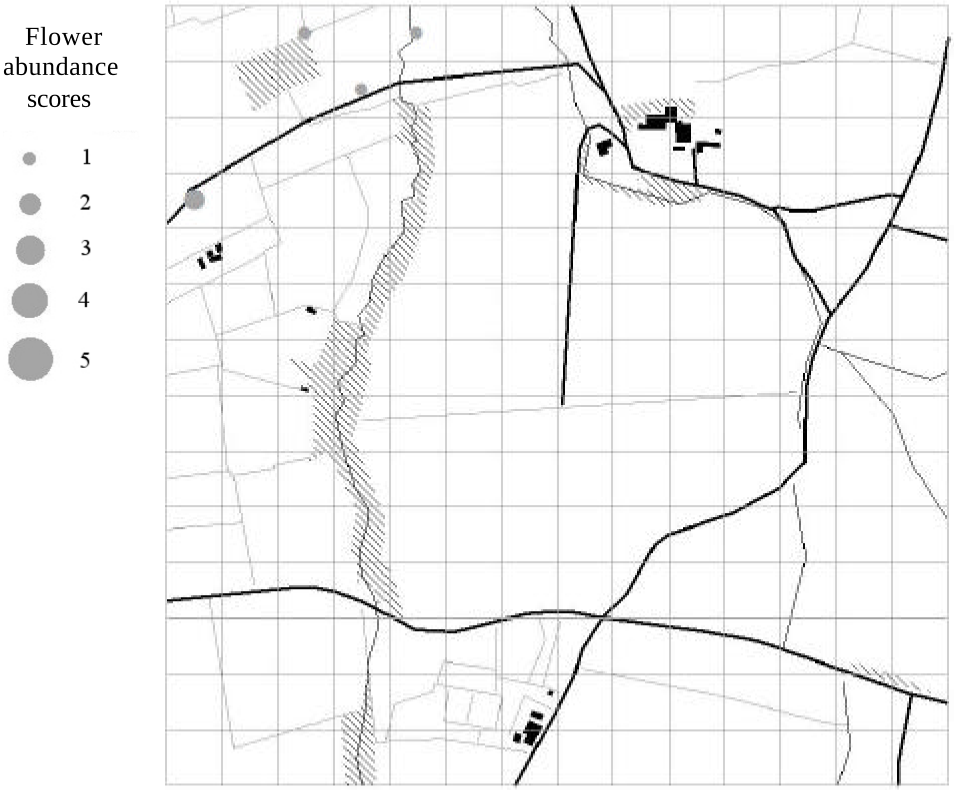
e) *Lathyrus pratensis* (b)

f) *Lotus corniculatus* (b)

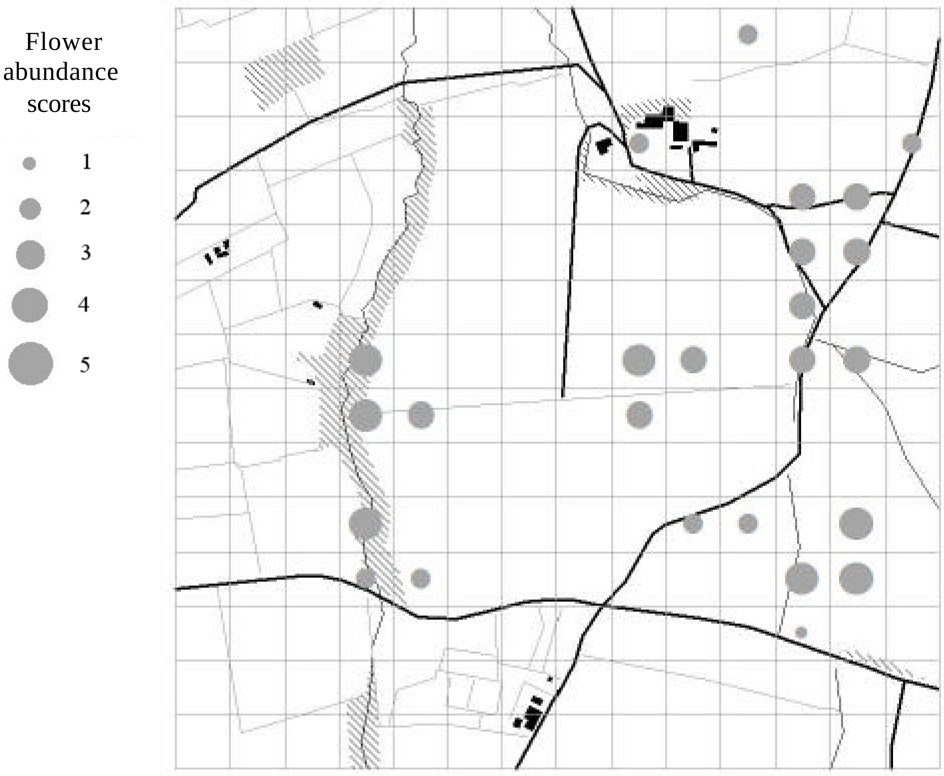


2004

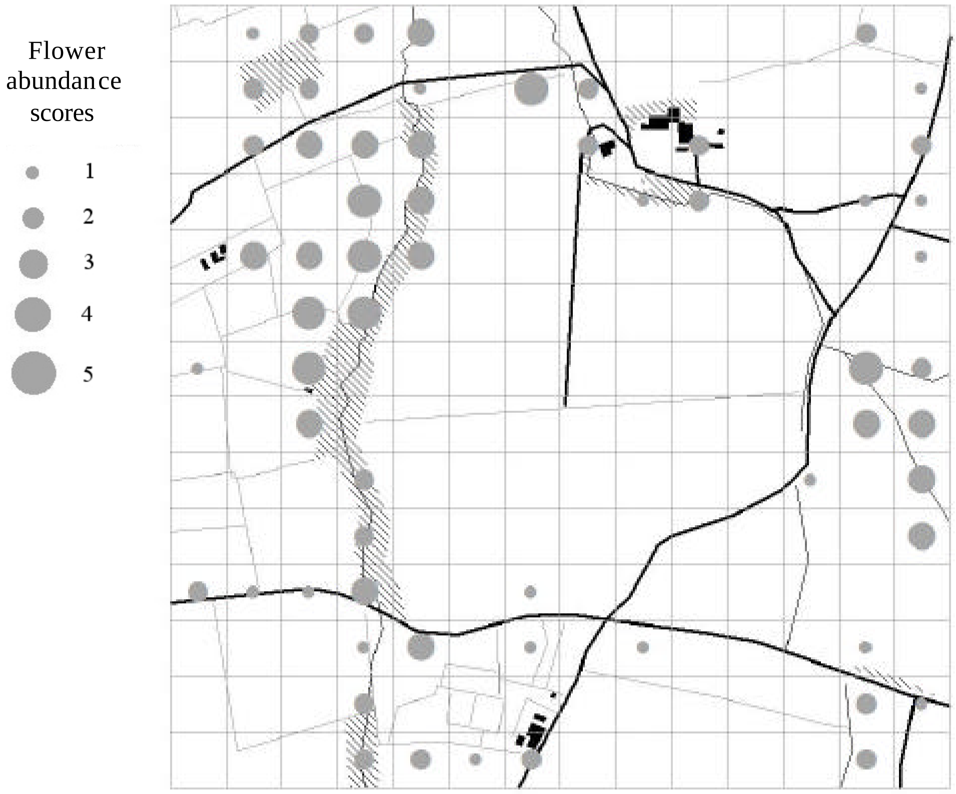
g) *Mentha spp.* (u)



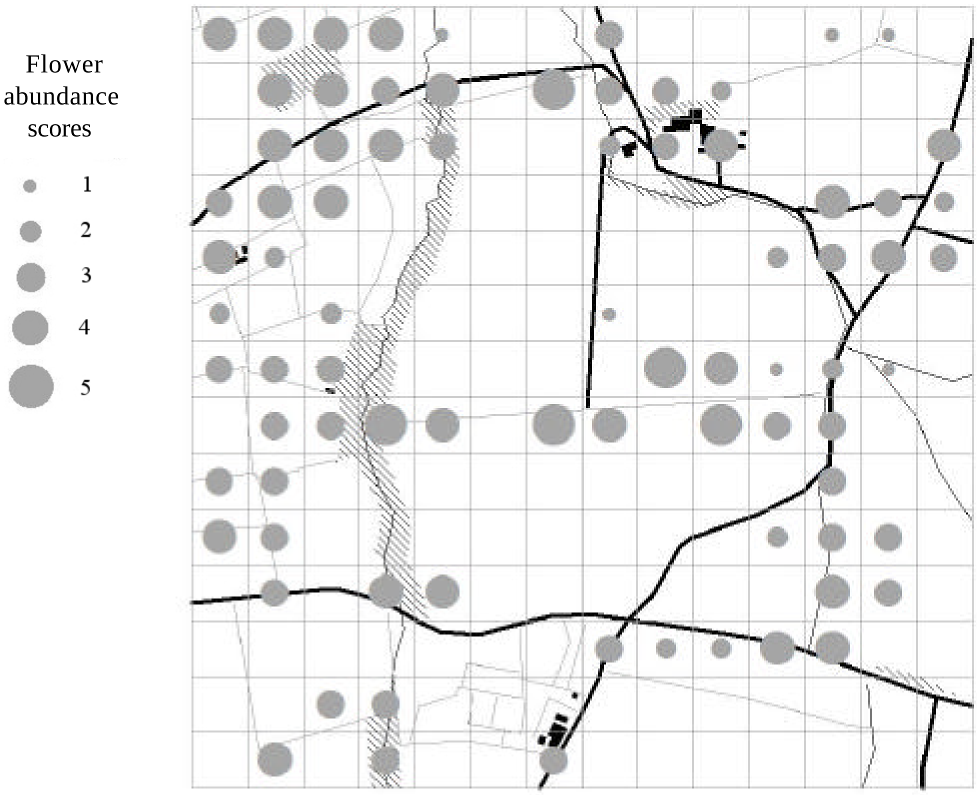
h)*Rhinanthus minor* (s)



i)*Rubus fruticosus* (u)



j) *Trifolium repens/hybridum* (b : not distinguished in pollen analysis so combined here)



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k) *Trifolium pratense* (s)

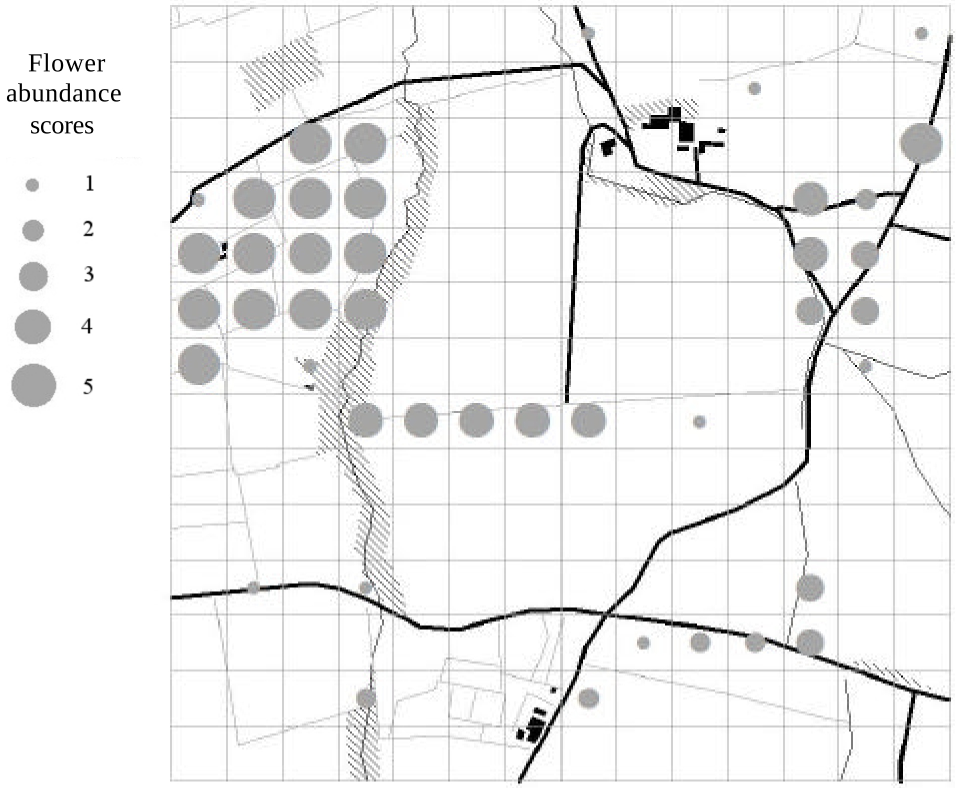
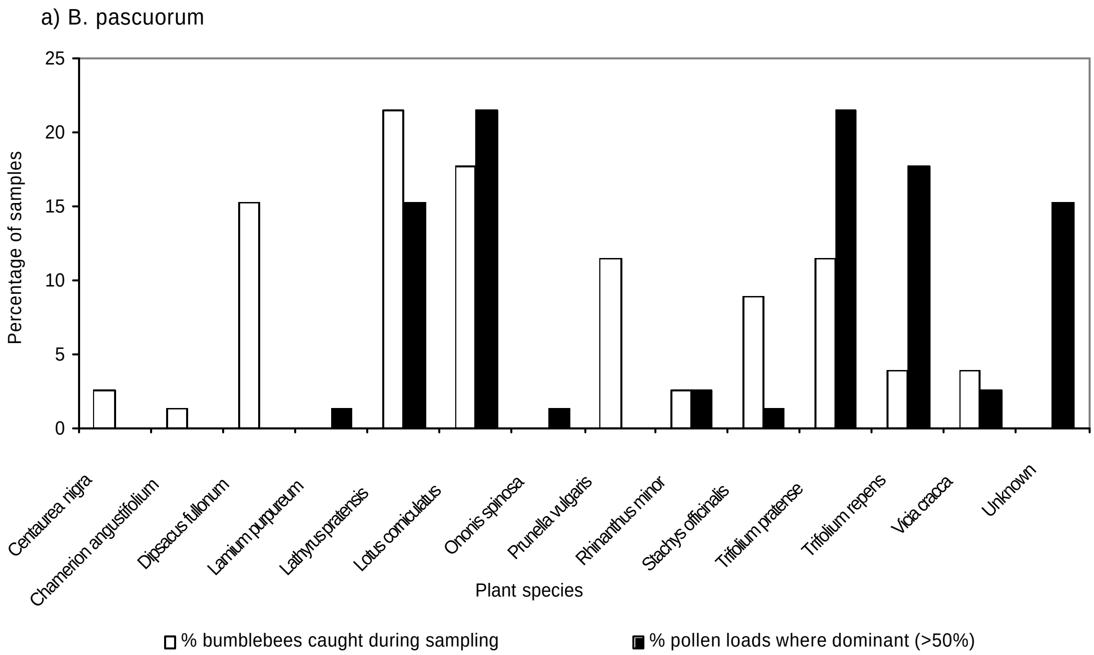


Figure 3. Comparison of forage plant species as observed during sampling with those dominating pollen loads for a) *B. pascuorum* and b) *B. terrestris/lucorum*.
(the unknown category refers to pollen loads which contained no dominant species (>50%) or in one case which was dominated by an unknown pollen species)



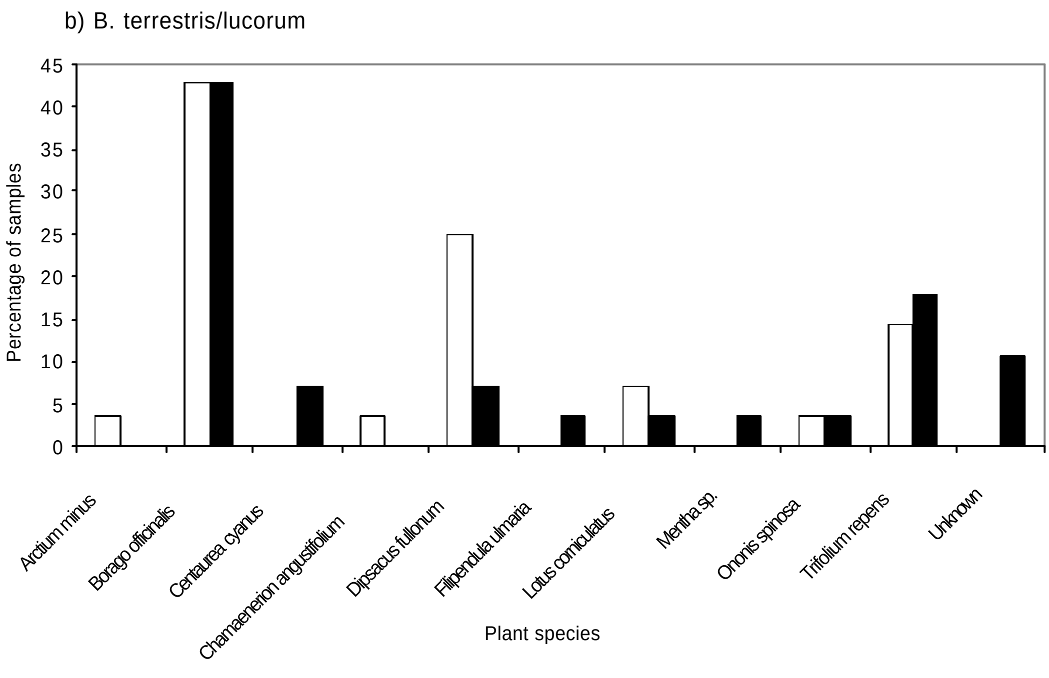


Figure 4. Relationship between the percentage of *Trifolium pratense* pollen in pollen loads of *Bombus pascuorum* and distance to the nearest patch of flowering *T. pratense* (each point represents the mean % per pollen load sampled from one grid square, ± stand errors).

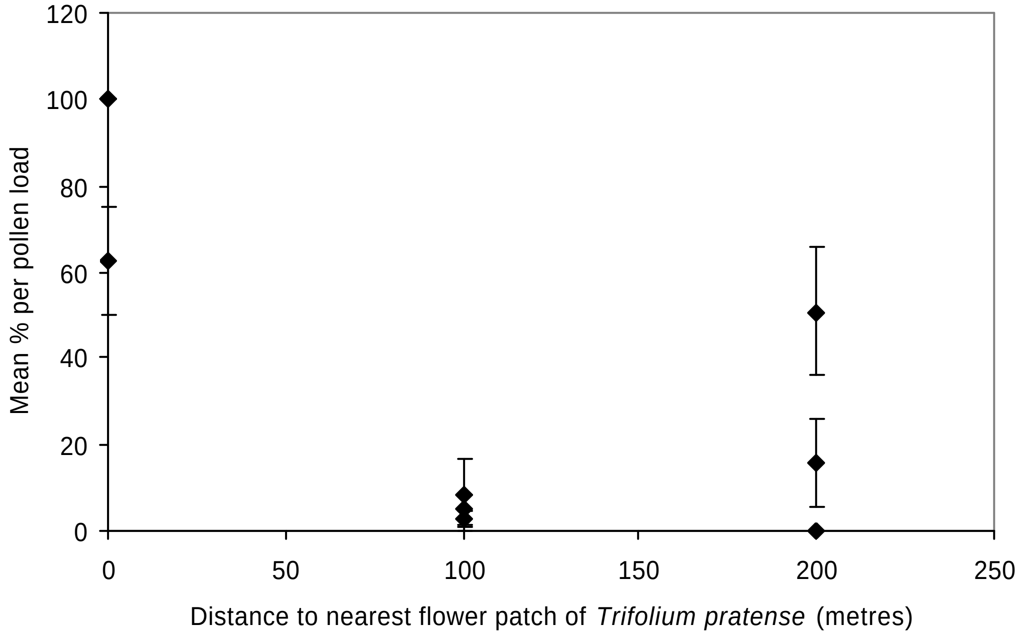


Table 1a. Composition of pollen loads collected by *Bombus pascuorum* (n=79), ranked in descending order by the mean percentage of each pollen type per load.

(s = species sown on the farm; u = species not sown and naturally occurring; b = both sown and naturally occurring; note that *Trifolium repens* and *T. hybridum* pollen types could not be distinguised during analysis)

Pollen species or type	Family	Sown on Manor Farm?	Mean % pollen per load	±SE mean	Number of loads containing pollen species	Number of loads from squares where pollen absent
Trifolium pratense	Fabaceae	s	22.18	4.28	27	15
Lotus corniculatus	Fabaceae	b	21.58	4.23	27	0
Lathyrus pratensis	Fabaceae	b	18.78	3.48	32	2
Trifolium repens/ hybridum	Fabaceae	b	16.65	3.58	25	4
Rhinanthus minor	Scrophulariaceae	s	4.44	1.59	13	0
Unknown	Unknown	u	2.97	1.71	3	-
Vicia cracca	Fabaceae	b	2.59	1.78	3	0
Ononis spinosa	Fabaceae	s	1.77	1.30	2	1
Stachys officinalis	Lamiaceae	u	1.65	1.28	9	1
Centaurea nigra	Asteraceae	s	1.50	0.71	10	0
Lamium purpureum	Lamiaceae	u	1.46	1.15	4	4
Dipsacus follonum	Dipsacaceae	s	0.70	0.52	3	1
Chamaenerion angustifolium	Onagraceae	u	0.63	0.63	1	0
Rubus fruticosus	Rosaceae	u	0.63	0.45	2	2
Rosaceae type	Rosaceae	u	0.51	0.51	1	-
Fabaceae type	Fabaceae	s	0.51	0.51	1	-
Centaurea cyanus	Asteraceae	s	0.25	0.25	1	1
Geranium spp.	Geraniaceae	u	0.25	0.25	1	1
Hypericum spp.	Hypericaceae	u	0.25	0.25	1	1
Lathyrus pratensis/ Vicia cracca	Fabaceae	b	0.25	0.25	1	1
Prunella vulgaris	Lamiaceae	s	0.25	0.25	1	0
Cirsium vulgare	Asteraceae	u	0.17	0.13	3	1
Impatiens glandulifera	Balsaminaceae	u	0.01	0.01	1	1

Table 1b. Composition of pollen loads collected by *Bombus terrestris/lucorum* (n=28), ranked in descending order by the mean percentage of each pollen type per load.

(s = species sown on the farm; u = species not sown and naturally occurring; b = both sown and naturally occurring)

Pollen species or type	Family	Sown on Manor Farm?	Mean % pollen per load	±SE mean	Number of loads containing pollen species	Number of loads from squares where pollen absent
Borago officinalis	Boraginaceae	s	40.57	9.28	13	2
Trifolium repens/ hybridum	Fabaceae	b	17.50	7.23	5	1
Unknown	Unknown	u	9.32	4.98	5	-
Dipsacus follonum	Dipsacaceae	s	8.93	5.18	3	0
Centaurea cyanus	Asteraceae	s	6.43	4.49	2	2
Mentha spp.	Lamiaceae	u	3.57	3.57	1	1
Lotus corniculatus	Fabaceae	b	3.32	2.41	2	0
Ononis spinosa	Fabaceae	s	2.86	2.86	1	0
Cirsium vulgare	Asteraceae	u	1.96	1.79	2	0
Filipendula ulmaria	Rosaceae	u	1.79	1.79	1	0
Rubus fruticosus	Rosaceae	u	1.61	1.61	1	0
Melilotus altissima	Fabaceae	u	0.71	0.71	1	1
Trifolium pratense	Fabaceae	s	0.64	0.64	1	0
Impatiens glandulifera	Balsaminaceae	u	0.36	0.36	1	1
Chamaenerion angustifolium	Onagraceae	u	0.18	0.18	1	0
Ericaceae type	Ericaceae	u	0.18	0.18	1	1
Arctium minus	Asteraceae	u	0.07	0.07	1	0

Table 2 Simpson's diversity index and calculation of the Pollination Probability Index for each forage plant species on which bumblebees were caught.

PCP = the mean proportion of conspecific pollen in each pollen load
PBP = the proportion of bumblebees (out of N caught) carrying conspecific pollen
PPI = the calculated pollination probability index (see section 2.4.2)

B. pascuorum

Forage plant species	N caught	Simpsons mean	± SE	PCP	PBP	PPI
Centaurea nigra	2	2.11	0.89	0.17	0.50	0.083
Chamaenerion angustifolium	1	2.00	*	0.50	1.00	0.500
Dipsacus fullonum	12	1.32	0.11	0.04	0.17	0.006
Lathyrus pratensis	17	1.81	0.27	0.41	0.82	0.335
Lotus corniculatus	14	1.25	0.09	0.62	0.64	0.396
Prunella vulgaris	9	2.33	0.38	0.02	0.11	0.002
Rhinanthus minor	2	1.94	0.84	0.23	1.00	0.225
Stachys officinalis	7	1.38	0.27	0.17	0.86	0.146
Trifolium pratense	9	1.19	0.11	0.76	0.89	0.680
Trifolium repens	3	1.53	0.43	0.80	1.00	0.800
Vicia cracca	3	1.03	0.03	0.68	1.00	0.683

B. terrestris/lucorum

Forage plant species	N caught	Simpsons mean	± SE	PCP	PBP	PPI
Arctium minus	1	1.04 a	*	0.02	1.00	0.020
Borago officinalis	12	1.01 a	0.01	0.92	0.92	0.840
Chamaenerion angustifolium	1	2.20 b	*	0.05	1.00	0.050
Dipsacus fullonum	7	1.16 a	0.14	0.36	0.43	0.153
Lotus corniculatus	2	2.69 b	0.31	0.47	1.00	0.465
Ononis spinosa	1	1.49 a	*	0.80	1.00	0.800
Trifolium repens	4	1.12 a	0.12	0.75	0.75	0.563

ANOVA on mean Simpsons index per load from each forage plant species; $F_{10,68} = 1.91$, $P = 0.059$ for *B. pascuorum* and $F_{6,21} = 17.36$, $P<0.001$ for *B. terrestris/lucorum*. Means with different letters are significantly different (Tukey's test $P<0.05$).

APPENDIX.

Species list of plant species in flower within the study area, 14th – 18th July 2003.

Values represent mean 'local' and 'widespread' scores per square, with standard deviations to indicate variability across the site; garden varieties and crops are shown with common names.

	Local Score		Widespread Score	
Flowering plant species	Mean	St Dev	Mean	St Dev
Achillea millefolium	0.58	1.12	0.34	0.78
Aegopodium podagraria	0.01	0.14	0.01	0.07
Aethusa cynapium	0.01	0.10	0.01	0.10
Agrostemma githago	0.01	0.14	0.01	0.07
Alchemilla mollis	0.01	0.07	0.01	0.07
Alliaria petiolata	0.01	0.07	0.01	0.07
Anagallis arvensis	0.02	0.21	0.01	0.07
Anchusa arvensis	0.03	0.21	0.04	0.33
Anthriscus sylvestris	0.01	0.07	0.01	0.07
Arctium minus	0.13	0.51	0.08	0.27
Ballota nigra	0.01	0.07	0.01	0.07
Barbarea intermedia	0.01	0.14	0.01	0.07
Barbarea vulgaris	0.01	0.07	0.01	0.07
Bellis perennis	0.02	0.23	0.02	0.16
Borago officinalis	0.13	0.73	0.05	0.22
Brassica napus	0.03	0.17	0.04	0.26
Buddleija davidi	0.01	0.07	0.01	0.07
Calystegia sepium	0.02	0.12	0.02	0.12
Calystegia silvatica	0.19	0.73	0.07	0.25
Campanula rotundifolia	0.04	0.28	0.06	0.46
Capsella bursa-pastoris	0.33	1.02	0.17	0.61
Carduus nutans	0.04	0.36	0.03	0.30
Centaurea cyanus	0.27	0.96	0.13	0.50
Centaurea nigra	0.68	1.25	0.45	1.01
Chaerophyllum temulentum	0.01	0.14	0.01	0.07
Chamerion angustifolium	0.79	1.48	0.41	0.89
Chenopodium album	0.10	0.48	0.04	0.20
Chrysanthemum segetum	0.02	0.16	0.01	0.10
Circaea lutetiana	0.08	0.47	0.07	0.38
Cirsium arvense	1.43	1.63	0.81	1.17
Cirsium palustre	0.17	0.67	0.14	0.55
Cirsium vulgare	0.84	1.27	0.72	1.25
Conium maculatum	0.04	0.28	0.03	0.19
Convolvulus arvensis	0.01	0.14	0.01	0.07
Conyza canadensis	0.04	0.30	0.05	0.34
Crepis capillaris	0.17	0.65	0.15	0.61
Dactylorhiza fuchsii	0.06	0.32	0.10	0.56
Daucus carota	0.34	1.02	0.21	0.75
Dipsacus fullonum	0.08	0.54	0.04	0.28
Echinops sphaerocephalus	0.01	0.07	0.01	0.07
Echium plantagineum	0.01	0.07	0.01	0.07

	Local Score		Widespread Score	
Flowering plant species	Mean	St Dev	Mean	St Dev
Epilobium ciliatum	0.42	1.11	0.45	1.26
Epilobium hirsutum	0.52	1.13	0.28	0.64
Epilobium obscurum	0.15	0.59	0.16	0.62
Epilobium palustre	0.01	0.14	0.01	0.07
Epilobium parviflorum	0.18	0.54	0.39	1.20
Epilobium tetragonum	0.01	0.07	0.01	0.07
Erodium cicutarium	0.01	0.07	0.02	0.21
Eupatorium cannabinum	0.01	0.14	0.01	0.07
Euphorbia exigua	0.01	0.07	0.01	0.07
Fallopia convolvulus	0.06	0.39	0.03	0.22
Filipendula ulmaria	0.44	1.17	0.23	0.73
Fumaria officinalis	0.02	0.21	0.01	0.07
Galeopsis bifida	0.02	0.14	0.05	0.37
Galeopsis tetrahit	0.06	0.35	0.03	0.17
Galium aparine	0.20	0.78	0.08	0.34
Galium uliginosum	0.03	0.24	0.06	0.46
Galium verum	0.24	0.83	0.15	0.58
Geranium dissectum	0.04	0.28	0.02	0.14
Geranium molle	0.01	0.14	0.01	0.14
Geranium pratense	0.02	0.12	0.02	0.12
Geranium pusillum	0.03	0.30	0.03	0.30
Geranium pyrenaicum	0.02	0.16	0.01	0.10
Geranium robertianum	0.11	0.50	0.09	0.40
Geranium sp.	0.22	0.71	0.17	0.57
Geum urbanum	0.03	0.16	0.03	0.16
Heracleum sphondylium	0.17	0.53	0.17	0.61
Hieracium sp.	0.01	0.07	0.01	0.07
Hypericum pulchrum	0.02	0.20	0.03	0.32
Hypericum tetrapterum	0.02	0.12	0.02	0.12
Hypericum sp.	0.04	0.23	0.05	0.34
Hypochaeris radicata	0.09	0.42	0.16	0.75
Impatiens glandulifera	0.03	0.26	0.01	0.10
Knautia arvensis	0.06	0.23	0.07	0.36
Lam ium album	0.04	0.21	0.03	0.17
Lamium hybridum	0.01	0.14	0.02	0.21
Lamium purpureum	0.05	0.26	0.05	0.23
Lapsana communis	0.15	0.52	0.09	0.28
Lathyrus pratensis	0.48	1.20	0.27	0.75
Leontodon hispidus	0.02	0.12	0.03	0.30
Leucanthemum vulgare	0.55	1.09	0.39	0.95
Ligustrum ovalifolium	0.02	0.29	0.01	0.07
Lonicera periclymenum	0.07	0.35	0.04	0.20
Lotus corniculatus	0.98	1.57	0.55	1.04
Lotus uliginosus	0.25	0.92	0.15	0.65

	Local Score		Widespread Score	
Flowering plant species	Mean	St Dev	Mean	St Dev
Lychnis flos-cuculi	0.01	0.07	0.01	0.07
Lysimachia punctata	0.01	0.10	0.01	0.10
Malva moschata	0.10	0.36	0.17	0.69
Malva sylvestris	0.01	0.14	0.01	0.07
Malva sp. Garden	0.01	0.07	0.01	0.07
Matricaria discoidea	0.58	1.27	0.28	0.69
Matricaria recutita	0.82	1.43	0.36	0.67
Medicago lupulina	0.02	0.21	0.01	0.07
Mentha arvensis	0.02	0.17	0.02	0.12
Mentha aquatica	0.01	0.07	0.02	0.21
Mentha sp.	0.03	0.19	0.03	0.25
Myosotis arvensis	0.72	1.32	0.40	0.84
Odontites verna	0.01	0.07	0.01	0.07
Onobrychis viciifolia	0.02	0.12	0.02	0.12
Ononis spinosa	0.02	0.12	0.02	0.12
Papaver argemone	0.01	0.07	0.01	0.07
Papaver rhoeas	0.63	1.05	0.45	0.82
Persicaria lapathifolia	0.13	0.54	0.08	0.34
Persicaria maculosa	0.54	1.17	0.32	0.76
Pilosella officinalis	0.01	0.07	0.01	0.07
Plantago lanceolata	0.25	0.72	0.24	0.81
Polygonum aviculare	0.44	1.14	0.22	0.67
Potentilla erecta	0.13	0.70	0.11	0.59
Potentilla fruticosa	0.01	0.07	0.01	0.07
Potentilla reptans	0.04	0.26	0.03	0.16
Prunella vulgaris	0.57	1.23	0.32	0.77
Pulicaria dysenterica	0.02	0.23	0.01	0.10
Ranunculus acris	0.22	0.62	0.25	0.87
Ranunculus flammula	0.01	0.07	0.01	0.07
Ranunculus repens	0.57	1.09	0.47	1.05
Raphanus raphanistrum	0.11	0.47	0.07	0.31
Rhinanthus minor	0.37	1.02	0.28	0.91
Rorippa nasturtium-aquaticum	0.03	0.29	0.01	0.10
Rosa sp. (Garden)	0.01	0.07	0.01	0.07
Rubus fruticosus	0.68	1.15	0.42	0.75
Rumex obtusifolius	0.02	0.23	0.01	0.10
Sambucus nigra	0.06	0.24	0.06	0.24
Sanguisorba officinalis	0.01	0.07	0.02	0.21
Scrophularia auriculata	0.16	0.61	0.10	0.39
Senecio jacobaea	0.48	0.89	0.53	1.19
Senecio sylvaticus	0.04	0.30	0.04	0.33
Senecio vulgaris	0.54	1.27	0.47	1.26

	Local Score		Widespread Score	
Flowering plant species	Mean	St Dev	Mean	St Dev
Silene alba	0.01	0.07	0.01	0.07
Silene latifolia	0.06	0.24	0.06	0.24
Silene dioica	0.24	0.66	0.21	0.62
Silene noctiflora	0.02	0.21	0.01	0.07
Sinapis arvensis	0.01	0.07	0.01	0.07
Sisymbrium officinalis	0.05	0.27	0.03	0.17
Solanum dulcamara	0.01	0.07	0.01	0.07
Sonchus arvensis	0.19	0.62	0.16	0.54
Sonchus asper	0.19	0.59	0.14	0.49
Stachys officinalis	0.14	0.70	0.11	0.59
Stachys sylvatica	0.35	0.83	0.24	0.64
Stellaria graminea	0.22	0.87	0.14	0.66
Stellaria media	0.10	0.56	0.04	0.22
Symphytum x uplandicum	0.01	0.07	0.01	0.07
Taraxacum officinale agg.	0.08	0.30	0.10	0.51
Torilis japonica	0.07	0.37	0.05	0.21
Tragopogon pratensis	0.01	0.10	0.01	0.10
Trifolium campestre	0.06	0.34	0.06	0.39
Trifolium dubium	0.40	1.07	0.22	0.66
Trifolium hybridum	0.16	0.57	0.12	0.48
Trifolium pratense	0.70	1.54	0.48	1.18
Trifolium repens	1.32	1.65	0.81	1.29
Trifolium rep/hyb	1.48	1.90	0.93	1.48
Tripleurosp inodorum	0.24	0.75	0.13	0.38
Verbascum thapsus	0.01	0.07	0.01	0.07
Veronica persica	0.13	0.59	0.06	0.24
Vicia cracca	0.58	1.25	0.35	0.89
Vicia sativa	0.02	0.16	0.01	0.10
Vicia sepium	0.01	0.07	0.01	0.07
Vicia tetrasperma	0.14	0.65	0.09	0.49
Viola arvensis	0.34	0.90	0.19	0.57
Viola tricolor	0.01	0.07	0.01	0.07
CANTERBURY BELLS Campanula	0.01	0.07	0.01	0.07
LINSEED	0.03	0.25	0.02	0.14
MUSTARD	0.01	0.07	0.01	0.07
FODDER RADISH	0.03	0.21	0.02	0.12
POTATO	0.01	0.10	0.01	0.10
TREE MALLOW	0.01	0.07	0.01	0.07