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Crop flower visitation by honeybees, bumblebees and solitary bees: behavioural differences and diversity responses to landscape.

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Abstract

In Europe, oilseed rape is the principal crop used in the production of edible and renewable fuel oil products. Insect pollinators, in particular bees, have been shown to have a positive effect on the seed set of this crop. We undertook experiments looking at behavioural differences between honeybees, bumblebees and solitary bees visiting oilseed rape flowers, and related this to landscape scale responses in visitation rates. We found that behavioural differences between honeybees, bumblebees and solitary bees alter the likelihood of pollen transfer from their bodies to the plant stigma. Solitary bees and bumblebees tend to have greater rates of stigmal contact than honeybees. The interactions between the likelihood of free pollen on bodies and the probability of stigmal contact suggest that only 34.0 % of visitations by honeybees were likely to result in pollen transfer to the stigma, relative to 35.1 % for the bumblebees and 71.3 % for solitary bees. Visitation rates were higher for honeybees in high quality landscapes with relatively large areas of alternative foraging habitat. Visitation rates of honeybees were also more frequent in the vicinity of managed hives. For solitary bees and bumblebees visitation rates did not respond to landscape structure, although more species of solitary bees were found in landscapes with a high cover of semi-natural grassland. While honeybees may be less efficient in pollen transfer per unit visit, where they numerically outweigh other types of bees in a crop (e.g. around managed hives) this may not be important. For this reason the relative ease with which hives can be moved across landscape means that honeybees are perhaps the most suitable taxa for use as a pro-active mitigation measure against pollinator deficits. However, the greater efficiency of solitary bees compensates for the effort required to implement longer term management (i.e. the establishment of flower rich field margins and open soil nesting sites) to support their populations.

Keywords: Oilseed rape; Pollination; honeybees; bumblebees; solitary bees; behaviour; visitation rates; landscape; semi-natural grassland; ecosystem service.

1. Introduction

In Europe, oilseed rape (*Brassica napus* L.: Brasicaceae) is the principal crop used in the production of refined edible and renewable fuel oils (Wittkop *et al.*, 2009). In the UK, it is grown on 15.8 % of available arable land producing 2.8 million tonnes of seed (Defra, 2012). Areas currently cropped by oilseed rape are likely to continue to increase shuold current trends in both the demand and price of this crop rise (Wittkop *et al.*, 2009; Defra, 2012). While yield increases have been seen over the last ten years (currently at 3.9 tonnes hectare^{-1}) this has principally been achieved through improved line varieties and effective agronomy (Defra, 2012). One potential mechanism to further increase yield is to promote improved pollination by insects (Hayter and Cresswell, 2006; Bommarco *et al.*, 2012; Jauker *et al.*, 2012). Although oilseed rape is predominantly wind pollinated (Chifflet *et al.*, 2011), the role of domesticated and wild insect pollinators in promoting pollination is potentially economically significant (Breeze *et al.*, 2011; Chifflet *et al.*, 2011; Bommarco *et al.*, 2012; Jauker *et al.*, 2012; Ollerton *et al.*, 2012). For example, increased insect pollination rates have been shown to raise oilseed rape yields, reduced chlorophyll content and positively impact on oil content and seed weight (Bommarco *et al.*, 2012). However, different breeding lines and cultivars may respond differently to insect pollinators. This was shown by Steffan-Dewenter (2003) who demonstrated that high densities of pollinators could increase mean seed weight per plant for male sterile lines, but not male fertile lines. While insect pollinators may increase oilseed rape yields, wide-scale population declines in Europe and other parts of the world have limited their contribution to this process (Potts *et al.*, 2010).

Considerable debate has arisen as to the roles played by different pollinator taxonomic groups in improving crop yields (e.g. Breeze *et al.*, 2011; Aebi *et al.*, 2012; Ollerton *et al.*, 2012). In particular, the relative role played by actively 'farmed' domesticated honeybees (*Apis mellifera* L.: Apoidea) that are bred and moved around landscapes in artificial hives, and wild bees that are manipulated indirectly through management to improve nesting and foraging resource (Steffan-Dewenter *et al.*, 2002; Pywell *et al.*, 2005; Öckinger and Smith, 2007; Breeze *et al.*, 2011; Aebi *et al.*, 2012; Ollerton *et al.*, 2012). Increasing global food requirements linked with the high economic value of pollination (estimated to be as high as €135 billion worldwide (Potts *et al.*, 2010)) mean that elucidation of roles played by different pollinator taxa is crucial. This is in part because management that benefits different pollinator taxa will not necessarily be identical (e.g. Steffan-Dewenter *et al.*, 2002; Jauker *et al.*, 2009). For example, many solitary bees depend on the availability of bare ground as a nesting habitat (Potts *et al.*, 2005), something that is of little importance to honeybees located in artificial hives. Independent of the relative importance of different taxa, the delivery of crop pollination services is likely to be greatest where diverse pollinator assemblages exist (Hoehn *et al.*, 2008; Breeze *et al.*, 2011; Ollerton *et al.*, 2012).

Visitation rates are typically a reflection of the local density of individual pollinator species, and are likely to be an important indicator of the effectiveness of bees in promoting increased crop yields (Richards *et al.*, 2009; Garibaldi *et al.*, 2011). This follows on from the assumption that the more flowers visited by an individual bee so the greater the likelihood of pollen transfer (Vazquez *et al.*, 2005; Richards *et al.*, 2009). Certainly, the ability to manipulate visitation rate in honeybees, by directly moving hives to the location of flowering crops, gives them the greatest appeal from a crop management perspective (Breeze *et al.*, 2011). While visitation rates of honeybees are likely to be greater than that seen for wild pollinators in the vicinity of hives, Garibaldi *et al.* (2011) suggests that honeybees tend to represent less than 25% of all visitations to crops. However, visitation rates alone will not represent the whole picture, as the effectiveness of bees in pollinating crops will depend on species specific behaviour on arriving at a flower (Wallace *et al.*, 2002). Specifically, the likelihood that individuals will have pollen accessible on their body (i.e. not stored only in a pollen basket), and that this pollen then comes in contact with the stigmas of the plant, will influence pollination success (Bosch and Blas, 1994; Wallace *et al.*, 2002). It is the interaction between visitation rates and the likelihood of con-specific pollen transfer to the stigma that will influence overall pollination success within crops. Note, we are not suggesting that these are the only limiting factors to pollination success, rather that they represent an important base line to the likelihood of pollen transfer.

In this study we look at how differences in small scale behaviour between honeybees, bumblebees and solitary bees (*Andrena*, *Osmia* and *Lassioglossum* spp.; Apoidea) affects the likelihood of pollen transfer for oilseed rape, and then relate this to landscape scale patterns in both visitation rates and species richness. We predict that: 1) The probability of pollen transfer will be lower per unit visit for honeybees than wild bees as a result of behavioural differences in how they interact with flowers (Bosch and Blas, 1994; Wallace *et al.*, 2002); 2) Visitation rates of bees will be higher at field edges than interior as bees spill-over from semi-natural habitats; 3) The impacts of landscape structure (alternative foraging and nesting habitats) will be more pronounced for bumblebees and solitary bees, as their populations are more likely to have reached an equilibrium with local conditions. In contrast, the yearly relocation of honeybee hives by professional apiarists will result in less pronounced responses to landscape structure.

2. Methods

We undertook three complementary experiments to identify links between small scale behavioural differences in honeybees, bumblebees and solitary bees in how they visit oilseed rape flowers, and their responses to landscape structure in terms of visitation rates and overall species richness. All studies were undertaken in Wiltshire, UK and focused specifically on bees (Apoidea).

2.1. Small scale taxonomic differences in behaviour

Three fields of oilseed rape (DK Cabernet variety) were selected on each of two farms in Wiltshire, UK. These were Windwhistle Farm (Lat. N51:03:12; Long. W1:53:30) and Burcombe Manor (Lat. N51:04:42; Long. W1:54:06). Individual farms were separated by *c.* 2.3 km, with fields within a farm separated by at least 300 m. For each of the six fields, two separate 50 m × 2 m fixed transects were established running into the fields from the edge along tram lines (the tyre tracks through crops resulting from farm machinery). Each transect was started at a distance of 25 m from the crop margin, with paired transects within individual fields separated by 22 m (the width of the tram lines). For two month (29/4/2012 to 31/5/2012) covering the flowering period of oilseed rape, individual transect were surveyed for bees on eight separate occasions following standard limits for weather conditions for butterfly surveys given by Pollard and Yates (1993). As the sampling season was relatively early transects were walked between 10.30 - 16.00 hours to ensure high levels of bee activity. Each transect was walked for a period of 30 minutes, so that a single field (the experimental unit) received 8 hours of observations on a 100 × 2 m area (equivalent to 2.4 minutes m^{-2}).

Pollinators were identified to the following taxonomic resolution. Honeybee (*Apis mellifera*); Bumblebees to species *Bombus lapidarius*, *B. terrestris*, *B. lucorum*, *B. pascuorum*, *B. pratroum*, *B. hortorum*, *B. hypnoroum*, *B. vestalis*, *B. rupestris.* Bumblebees were further distinguished between foraging queens and workers as these were both observed in large numbers; Solitary bees, identified to body forms typical of common oilseed rape pollinators. These were *Lasiglossum* spp. (genus level only), *Osmia* (separated to *bicolour* and *rufa*) and *Andrena* (separated to body forms typical of *dorsata*, *carantonica*, *nigroaenea*, *haemorrhoa*, *fulva*, *flavipies*, *nitida*, *cineraria*, *bicolour* and *minuta*). Previous non-quantitative surveys (*unpublished data*) suggest that these are the principal species that locally pollinate oilseed rape in southern Britain. As we were observing behaviour it was often not possible to take specimens and so some cryptic species may have been recorded under these ‘body form’ species categories. Note, this ‘body form’ approach is widely used for bumblebees for field observations (Edwards and Jenner, 2005). After observing a bee during transect walks the following behavioural observations were made: 1) Time spent on flower head in seconds (to provide a measure of mean visitation time for each pollinator); 2) The presence of free dry pollen anywhere on the individual; 3) Whether stigma contact with the oilseed rape flower is made; 4) Whether the pollinator probes for nectar; 5) Whether pollen is actively collected and transferred to pollen baskets. Each bee individual was observed for three separate flower visitations to obtain an average time spent on a flower, or the probability of a particular behaviour occurring. Note, if observed bees left transects before all three observations could be made this record was excluded from subsequent analysis.

The product of the probabilities of free pollen present on bees and stigmal contact provided a basis for estimating the percentage likelihood that an individual visitation by a bee would result in pollen transfer. While this is a simplification and ultimately represents an upper limit to the likelihood of pollination occurring, it provides a useful correction factor when assessing the importance of between taxa visitation rates. This was assessed for honeybees, bumblebees and solitary bees.

2.2 Bee visitation rates

In 2011, a regional study was conducted on 24 farms growing oilseed rape in rotation with winter wheat in Wiltshire, UK (supplementary material appendix A). On each of these farms a single oilseed rape field was randomly chosen as the experimental unit of the study. The farms were chosen so that eight farms each were in areas of low, moderate or high overall habitat quality for bees, based on a 1 km radius immediately surrounding the study fields. This categorical treatment of ‘overall habitat quality’ was based on an aggregate of site characteristics determined from individual site visits and an examination of aerial photographs and topography maps. High overall habitat quality was defined as farms situated in large areas of non-crop flower rich semi-natural grassland (mean percentage area in 1 km radii = 19.2 %, SE ± 6.7), that had an abundance of suitable nesting sites with south facing slopes (14.6 %, SE ± 5.1) and a spatially complex arrangement of habitat types, in part resulting from a lower overall proportion of arable cropping in the area (29.6 %, SE ± 3.7). Medium overall habitat quality was defined as sites with relatively good availability of alternative foraging resources in the form of semi-natural grassland (11.5 %, SE ± 4.1), but little high quality nesting habitat (0.85 %, SE ± 0.4). Sites of medium habitat quality were also far less spatially complex and dominated by arable agriculture (52.3 %, SE ± 3.1); Sites with low overall habitat quality had little non-crop foraging resources (3.7 %, SE ± 1.3) or suitable nesting habitat (1.4 %, SE ± 1.1), and were similarly dominated by arable agriculture (52.0 %, SE ± 10.9). There was no spatial autocorrelation between the study sites and the proportion of flower rich semi-natural grassland (Morrans I: observed = -0.03, expected = -0.04, p>0.05), nesting habitat (Morrans I: observed = -0.06, expected = -0.04, p>0.05) or arable agriculture (Morrans I: observed = 0.02, expected = -0.04, p>0.05) . There was no practical way to block sites given their spatial arrangement.

For each level of 'overall habitat quality', four of the farms had commercially run honeybee hives in close proximity to the experimental field (<0.25 km), and four were isolated from hives (> 2 km). This categorical effect is referred to as 'Hive'. Finally a split-split plot treatment of 'within field location' was added, whereby sampling in each of the 24 field was established either at the fields edge (30 m from the boundary) or field centre (at least 90 m from boundary). Note, that this design was suitable for identifying differences in visitation rates between the edge and field interiors, but was inadequate for determining how visitation rates decayed with the distance from field edge. Two 1 × 2 m permanent quadrats were established at *c.* 30 m apart for both the edge and interior of each field. These two quadrats were summed in all subsequent analyses. For each quadrat, three separate 7 minute timed observation (taken between 18/4/2011 to the 20/5/2011) were made during the oilseed rape flowering period to count total abundance of honeybees, bumblebees and solitary bees. No distinction was made between species (except, by definition, the honeybees), with the aim of identifying net visitation rates for these three key pollinator groups. Again counts were undertaken only where weather conditions met the criteria given in Pollard and Yates (1993). All visitation rates were expressed in individuals m^2 $hour^{-1}$

2.3. Landscape scale impacts on bee species richness

Coloured water traps on each of the 24 farms were used to determine farm scale bee species richness. This component of the study was not intended to investigate within site variation in species richness, but was to focus on between farm variation resulting from landscape structure, overall habitat quality and the impact of managed honeybee hives. For this reason sampling was undertaken in both crop and non-crop habitats to produce a comprehensive measure of farm scale species richness. Water traps are an effective passive sampling method for assessing bee diversity patterns that are unaffected by collector bias (Westphal *et al.*, 2008). Individual traps were 20 cm in diameter and filled to a depth of 5 cm with water and a small quantity of unscented detergent. UV-bright yellow paint was used to improve the attractiveness of the pan traps to pollinators and collect species likely to pollinate oilseed rape (Sparvar Leuchtfarbe, Spray-Color GmbH, Merzenich, Germany). Sampling was undertaken at each farm for a 48 hour period during the peak of oilseed rape flowering (20/4/2011 and 13/5/2011). At each of the 24 sites two water traps were placed in the centre of the oilseed rape field, separated by *c.* 22 m. Each trap was placed on the top of a wooden stake so that it was level with the top of the crop flowers. An additional two pan traps were located within 100-200m of the edge of the field in non-crop foraging habitat. Each of these pan traps was separated by *c.* 300 m. After 48 hours the contents of all four pan traps within a field were collected and stored in alcohol. All bees collected were identified to species. Species inventories were aggregated across the four pan traps, so that a single species richness value was determined for each of the 24 farms.

2.4. Quantification of landscape structure.

The categorical factor of overall habitat quality (see above) was based on an amalgamation of various aspects of landscape structure. To compliment this categorical overall measure of habitat quality, we also looked at the importance of individual aspects of landscape structure in determining bee species richness. Landscape structure was assessed at 2 km radii surrounding the study fields in each of the 24 farms using a combination of remote sensing and ground observation. This was done using the 2007 UK Land Cover Map (Morton *et al.*, 2011) at a resolution of 25 m pixels, combined with on site confirmation of habitats at scales smaller than this resolution. Steffan-Dewenter *et al.* (2002) suggested that solitary bees respond to landscape structure at scales of less than 1 km radii around sampling points, while bumblebees and honeybees respond at sales above 2 km. However, strong inter-correlation between landscape parameters at 1 and 2 km radii within the current study area meant that such a distinction was largely meaningless. We therefore assessed landscape structure within these single 2 km radii. Three measures of landscape structure were considered: 1) The proportion of species-rich high quality grassland, principally lowland calcareous grassland of the form CG2-CG3 in the UK National Vegetation Classification (Rodwell, 1992). Such grassland has been identified as an important non-crop foraging resource for bees in agricultural landscapes (e.g. Morandin *et al.*, 2007; Jauker *et al.*, 2009); 2) The proportion of arable agriculture, intended to be an indicator of management intensity at a landscape scale (Heard *et al.*, 2007); 3) Bee nesting habitat, represented by the combined proportion of land use parcels containing permanent bare ground that was not regularly disturbed (i.e. not crop within the last 5 years) and that had a South-East to South-West aspect receiving a minimum of 4 hrs sun per day. These areas had a maximum vegetation height of 5 cm at time of survey. All derivation of landscape structure parameters were undertaken in ArcGIS 9.2 (ESRI Inc., California, USA). Note that as the categorical measure of overall habitat quality was based on these individual measures of landscape structure they were never directly compared in the same statistical model.

2.5. Statistical analysis

Each of the behavioural traits (average time on flower and proportion of individuals covered with dry pollen, collecting pollen, collecting nectar or making stigma contact) were analysed separately using generalised linear mixed models in SAS version 9.1. The individual unit of observation was the mean likelihood of the expression of a trait (given as a proportion) for an individual species at a site. For each model, the single fixed effect was taxa, i.e. whether the species were honeybees, bumblebees or solitary bees. Random effects were site, genera nested with site and species nested within genera nested within site. The ‘species’ random effect accounted for differences in castes recorded for the bumblebees. To account for the fact that different numbers of individuals of each species were observed this was included as a random effect. All models considering proportion data used a binomial error structure and logit link function reflecting the fact that probabilities were bounded between 0 and 1. Note, that for the response variable average time spent on flowers a normal error structure and identify link function were used.

The visitation rates of honeybees (individuals m^2 $hour^{-1}$), bumblebees and solitary bees in fixed quadrats were assessed using mixed models in response to the fixed effects of ‘overall habitat quality’, honeybee ‘hive’ presence and ‘location’ in the oilseed rape field. All interactions of these three explanatory variables were tested. To account for the split-plot structure of the experimental design (within site location of traps at field edges and interior), random effects classifying individual sites were included in the model. Model simplification was by deletion of the least significant terms. A normal error structure and identity link function was used for all analyses of visitation rates. Where single fixed effects were part of significant interaction terms they were always retained.

The final set of models used yellow water trap data to determine the responses of bumblebee and solitary bee species richness to overall habitat quality and then separately to continuous measures of landscape structure using two separate models. The first set of models investigated the response of species richness to the designed component of this study (as described above) so that all interactions of the fixed effects of ‘overall habitat quality’ and ‘hive’ were investigated. Note, that ‘location’ was not considered as species richness was determined using water traps at a farm scale, and did not consider within oilseed rape field differences. The second set of models focused on correlating general descriptors of landscape structure with bee species richness. These were the proportion of arable agriculture, semi-natural grassland and nesting habitat. No interaction terms were considered. Model simplification was by deletion of the least significant effects. All models assessing the response of species richness used a Poisson error structure and log link function. The explanatory power of these two separate models was finally compared using Akaike Information Criterion (*AICc*) to assess whether overall responses of bee species richness were better predicted by an overall measure of habitat quality or by individual measures of landscape structure such as the availability of semi-natural grassland.

3. Results

3.1 Small scale taxonomic differences in behaviour

A total of 1,181 individual observations from 20 species (*Apis* = 1; *Bombus* = 8; *Andrena* = 8; *Osmia* = 2; *Lassioglossum* was treated as an aggregate species) were made from the transect walks. There were strong differences in behaviour between honeybees, bumblebees and solitary bees in all but one of the observed behavioural traits. Overall, the average time spent by an individual on an oilseed rape flower was highest for the solitary bees ($F_{2,15}$=28.8, $p<0.001$; Fig. 1), which tended to spend more than double the time on individual flowers than either honeybees or bumblebees. Both honeybees and bumblebees spent a comparable, but shorter, time foraging on individual flowers.

The proportion of individuals with evidence of dry pollen distributed on their bodies differed between bee taxa ($F_{2,15}$=8.50, $p<0.01$; Fig. 1), with the likelihood of both honeybees and solitary bees having pollen on their bodies being higher than that for the bumblebees. Stigmal contact by foraging bees also differed between the three taxa ($F_{2,15}$=3.55, $p<0.05$; Fig. 1). Both bumblebees and solitary bees made contact with the stigma on a far greater proportion of visitations to oilseed rape flowers than was observed for the honeybees. The product of the probabilities of free pollen being present on bee bodies and stigmal contact were used to estimate the percentage likelihood that an individual bee visitation would result in pollen transfer. We found that for solitary bees, 71.3 % of visitations had the potential to result in pollen transfer to the stigma (based on a dry pollen probability = 0.82; stigmal contact probability = 0.87). This was higher than that of the 34.0 % chance of pollen transfer observed for honeybees (dry pollen = 0.81; stigmal contact = 0.42) or the 35.1 % chance of pollen transfer seen for the bumblebees (dry pollen = 0.39; stigmal contact = 0.90). Note that the probabilities of free pollen being present and stigmal contact were not correlated ($F_{1,14}$=2.61, $p>0.05$).

Observations of pollen collecting behaviour differed between the honeybees, bumblebees and solitary bees ($F_{2,15}$=9.41, $p<0.01$; Fig.1). Over half of the visitations by solitary bees involved pollen collecting, although this behaviour was rarely observed for either the honeybees or bumblebees. The only behaviour that was not seen to differ between the honeybees, bumblebees and solitary bees was the proportion of individuals actively collecting nectar ($F_{2,15}$=0.37, p>0.05). This was generally high at 0.92 (SE ±0.01).

3.2 Bee visitation rates

Overall a total of 866 bees (honeybees = 375; bumblebees = 275; Solitary bees = 216) were observed from the fixed quadrats in the 24 farms of the landscape study. At the smallest scale, the within field effect of sampling 'location' relative to the field boundary (either at 30 or 90 m from the field edge) had no effect on visitation rates of either honeybees, bumblebees or solitary bees (p>0.05). However, the location of oilseed rape fields relative to honeybee hives did influence the visitation rates of the honeybees ($F_{1,20}$=7.58, p=0.01: with hives: mean=6.78 m^2 $hour^{-1}$ SE±1.60; without hives mean=1.58 m^2 $hour^{-1}$ SE±0.38) and bumblebees ($F_{1,22}$=6.80, p=0.02: with hives: mean=3.77 m^2 $hour^{-1}$ SE±0.41; without hives mean=1.91 m^2 $hour^{-1}$ SE±0.32). In all cases, visitation rates were highest for both groups where honeybee colonies were in close proximity to the study fields, although this effect was most pronounced for the visitation rates of honeybees themselves. Visitation rates of solitary bees were not affects by proximity to a honeybee colony (p>0.05).

The explanatory variable of 'overall habitat quality' had a significant effect on honeybee visitation rates ($F_{2,20}$=6.11, p=0.01; Fig. 2), which were considerably higher where habitat quality was high. Honeybee visitation rates then declined in farms from medium to low habitat quality. No effect of overall habitat quality was found for visitation rates of bumblebees or solitary bees (p>0.05). No other significant effects or interaction terms were found to explain visitation rates of any of the three taxa.

3.3. Landscape scale impacts on bee species richness

The yellow water traps used to sample bee species richness collected a total of 578 individuals over the 48 hour sampling period, representing 42 species from seven bee genera. The most frequently collected species was *Andrena cineraria*, with a further 25 species comprising 95 % of the overall abundance of all individuals. Solitary bee species richness was not affected by the presence of 'honeybee' colonies ($p>0.05$). However, solitary bee species richness was affected by the categorical descriptor of overall habitat quality. Farms with high habitat quality supported more species than those of either moderate or low quality ($F_{2,21}=9.12$, $p<0.001$; AICc=106.4; Fig. 2). There was no significant interaction between overall habitat quality and presence of hives ($p>0.5$). The second model, considering only correlative landscape variables (cover of grassland, arable agriculture and nesting habitat) found a positive correlation with the proportion of species-rich grassland within a 2 km radii for the solitary bees ($F_{1,22}=18.96$, $p<0.001$, AICc=104.1; Fig. 3). Solitary bee species richness was not correlated with either the proportion of arable agriculture or the proportion of nesting habitat ($p>0.05$). This first correlative model was a poorer descriptor of variation in solitary bee species richness than the categorical model including only 'species-rich grassland'.

Bumblebee species richness showed no significant response to 'overall habitat quality', nor did it respond to the treatment of either presence of 'hives' or the interaction of that with overall habitat quality ($p>0.05$). The second model considering correlative relationships with landscape structure likewise failed to find a significant relationship with either the proportional coverage of species-rich grassland, arable agriculture or nesting habitat ($p>0.5$).

4. Discussion

4.1. Implications of behavioural differences between bees.

Differences in behavioural interactions with oilseed rape flowers are likely to mean that bee species differ in their effectiveness at achieving pollination per unit visit. While such differences between individual species are to be expected, our findings suggest that there are more general differences between different groups of bees. Considered in terms of a per unit visitation, a honeybee and solitary bee will not share the same probability of transferring pollen from their bodies to the flower stigmas. Two of the key behavioural differences that are expected to modulate pollination success are the probabilities of stigmal contact and the presence of free pollen on bee bodies (Bosch and Blas, 1994; Wallace *et al.*, 2002). We found that solitary bees show the greatest probability of achieving stigmal contact with their bodies. For solitary bees the greater likelihood of stigmal contact was probably influenced by a combination of the greater average time spent on individual flowers, as well at their tendency to collect pollen as opposed to just nectar. Interestingly, honeybees have a high probability of having pollen on their bodies even though they have a low probability of showing pollen collecting behaviour. This juxtaposition may be due to species specific characteristics relating to the frequency of body cleaning behaviour or individual characteristics of hair structure and location on their bodies. When the interaction between the probability of stigmal contact and the presence of body pollen was used as a correction factor for interpreting visitation rates, we found that on average across all sites only 1.42 of the 4.18 (m^{-2} $hour^{-1}$) honeybee visits observed would be expected to result in pollen transfer. While visitation rates for wild pollinators were lower than that seen for honeybees (bumblebees: 2.84 m^{-2} $hour^{-1}$; solitary bees: 2.54 m^{-2} $hour^{-}$), a comparable number of these visitations have the potential to result in pollen transfer (solitary bees: 1.71 m^{-2} $hour^{-1}$;

bumblebees: 0.99 m^{-2} $hour^{-1}$). Clearly this is a simplification and represents an upper limit to the probability of a bee visitation resulting in pollen transfer, but these behavioural differences have implications for the relative worth of different bee taxa. Importantly, visitation rates are not everything, and less abundant groups of bee may still make a disproportionate contribution to pollination services for this crop. Conversely where honeybee hives are in close proximity to oilseed rape fields their greater frequency of visitations would easily compensates for their lower efficiency in transferring pollen. When considered across the wider landscape, where hives are likely to be patchily distributed, such differences in efficiency may have far greater implications in achieving seed set for oilseed rape. In the current study, we do not directly measure seed set resulting from individual taxa. As a result we can only infer the impact of differences in behaviour between honeybees, bumblebees and solitary bees on seed set. However, experimental evidence does exist linking increased pollinator density to increased seed set and seed weight (Bommarco *et al.*, 2012; Jauker *et al.*, 2012).

4.2 Within-field and landscape scale spatial effects.

Contrary to our prediction no evidence was found for visitation rates differing in response to the distance from the field edge for honeybees, bumblebees or solitary bees. If there were diminishing energetic returns for pollinators foraging further into oilseed rape crops past viable flowers at field edges, this finding is certainly counter to what may be expected (Fahrig, 2003; Chacoff and Aizen, 2006). However, this assumes that peak nectar availability occurs in a homogenous fashion across oilseed rape fields. If spatial variation in nectar availability is independent of the distance from the field edge (i.e. due to response to soil moisture and nutrient availability), then pollinator abundance may track this resource resulting in an absence of an edge effect (Cartar, 2004). Certainly there is evidence that visitation rates by bumblebees on oilseed rape are influenced by differences in nectar availability between individual plants (Cresswell, 1999). However, without direct evidence of spatial variation in the quality of individual plants across oilseed rape fields this explanation is supposition only.

While no evidence of a field edge effect were found, honeybee visitation rates were strongly affected by their proximity to hives, with four times as many individuals per unit area found foraging around such locations. In addition, bumblebee visitation rates were also higher in the proximity of honeybee hives. While it is no surprise that honeybee visitation rates would be greater around their colonies, why this would have a positive effect on the bumblebees is not clear. Certainly negative competitive interactions are known to occur between honeybees and bumblebees, resulting in reduced bumblebee body size (Goulson and Sparrow, 2009). In addition, we can find no evidence of facilitation between these two taxa that may explain such a positive effect of hives on bumblebee abundance. It is possible that there may have been some initial bias in the choice of honeybee hive location by apiarists towards areas with relatively good foraging resources. If this was the case such areas may also have attracted larger numbers of bumblebees. Independent of this, there was no evidence that the presence of honeybee hives reduced visitation rates of solitary bees. The absence of direct negative competitive effects of honeybees on wild pollinators suggests that they can act in complementary fashion to promote crop pollination for oilseed rape. This absence of a negative effect of honeybees on wild pollinators has been reported elsewhere. For example, Steffan-Dewenter and Tscharntke (2000) found that the abundance of wild European bees was not negatively correlated with honeybee colony density.

The categorical descriptor of overall habitat quality affected the visitation rates of honeybees, although not that of either bumblebees or solitary bees. To define low, moderate and high quality habitats, this categorical descriptor incorporated information on the availability of non-crop foraging habitat, nesting habitat and the intensity of agricultural land use. In the case of the honeybees, high quality habitats could have provided a greater availability of foraging resources in periods preceding peak oilseed rape flowering, which may have led to increased colony provisioning and so colony growth (Avni *et al.*, 2009). Greater numbers of workers per colony would have had a knock on impact on visitation rates. While visitation rates of solitary bees did not respond to overall habitat quality, the species richness of this group was greatest both in farms that represented high quality habitats. Solitary bee species richness was also positively correlated with the availability of species rich grassland; a key foraging and nesting habitat important for this group (e.g. Steffan-Dewenter *et al.*, 2002). Bee species richness has been shown to be linked with increased seed set of some crops, although the diversity of pollinator functional groups may be as important in determining seed set (Hoehn *et al.*, 2008). As solitary bees are characterised by high variation in traits linked with body size, diet breath, foraging range and nesting preferences (Banaszak-Cibicka and Zmihorski, 2012) the observed increases in species richness could be likely to increased functional group diversity. The failure of bumblebee species richness to respond to either overall habitat quality or landscape structure may reflect the limited species pool found in the current study. Certainly the majority of species were habitat generalists capable of persisting in event the most intensively managed landscapes, making overall responses in species richness unlikely (Edwards and Jenner, 2005).

4.3. Conclusion

Managed honeybee hives represent a pro-active measure to support pollination services within oilseed rape crops, their relative mobility allowing them to track crop rotation patterns across farming systems. However, the impact of such hives is localised, and so their role in promoting oilseed rape pollination must be considered in context with the real world availability of honeybee hives. This is particularly so given our results that highlight the possible reduced efficiency in achieving pollen transfer per unit visit relative to solitary bees. Resent predictions suggest that in the UK there currently exist sufficient numbers of hives to support 34 % of required crop pollination services (Breeze *et al.*, 2011). In addition, hives are typically clumped together for reasons linked with ease of access by apiarists. For this reason honeybee visitation rates may be unduly aggregated relative to the actual number of hives in a landscape. While it is certainly possible to disperse hives and so increase the landscape scale spread of visitation rates, this is likely to be an advantage to farmers rather than those managing the hives, and so may necessitate financial compensation. Without considerable increases in the availability of hives, wild pollinators will be fundamental to the maintenance and improvement of crop pollination services for oilseed rape (Potts *et al.*, 2010; Breeze *et al.*, 2011; Ollerton *et al.*, 2012). Indeed outside of the immediate vicinity of managed hives they are likely to be both numerically dominant, and show behavioural adaptations that increase the likelihood of pollination relative to honeybees . An increased emphasis on wild pollinators, at least as a complementary resource to honeybees, will require habitat modification at landscape scales to create new foraging and nesting resources. Mass flowering crops, such as oilseed rape, are likely to represent a bonanza of food resources, although only over a few months (Westphal *et al.*, 2003). Continuity of foraging resources outside of mass flowering periods is likely to represent an important bottleneck that must be overcome to increase population viability of some wild pollinators. A possible solution to this is the development of new flower rich field margins that target species less for their ease of establishment and cost, and more for their peak periods of flowering.

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References

Aebi, A., Vaissière, B.E., Vanengelsdorp, D., Delaplane, K.S., Roubik, D.W., Neumann, P., 2012. Back to the future: Apis versus non-Apis pollination-a response to Ollerton et al. TREE 27, 142-143.

Avni, D., Dag, A., Shafir, S., 2009. Pollen sources for honeybees in Israel: Source, periods of shortage, and influence on population growth. Isr. J. Plant Sci. 57, 263-275.

Banaszak-Cibicka, W., Zmihorski, M., 2012. Wild bees along an urban gradient: winners and losers. J. Insect Conserv. 16, 331-343.

Bommarco, R., Marini, L., Vaissiére, B.E., 2012. Insect pollination enhances seed yield, quality, and market value in oilseed rape. Oecologia 169, 1025-1032.

Bosch, J., Blas, M., 1994. Foraging behaviour and pollinating efficiency of *Osmia cornuta* and *Apis mellifera* on almond (Hymenoptera, Megachilidae and Apidae). Appl. Entomol. Zoolog. 29, 1-9.

Breeze, T.D., Bailey, A.P., Balcombe, K.G., Potts, S.G., 2011. Pollination services in the UK: How important are honeybees? Agric.Ecosyst.Environ. 142, 137-143.

Cartar, R.V., 2004. Resource tracking by bumble bees: Responses to plant-level differences in quality. Ecology 85, 2764-2771.

Chacoff, N.P., Aizen, M.A., 2006. Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. J. Appl. Ecol. 43, 18-27.

Chifflet, R., Klein, E.K., Lavigne, C., Le Feon, V., Ricroch, A.E., Lecomte, J., Vaissiere, B.E., 2011. Spatial scale of insect-mediated pollen dispersal in oilseed rape in an open agricultural landscape. J.Appl.Ecol. 48, 689-696.

Cresswell, J.E., 1999. The influence of nectar and pollen availability on pollen transfer by individual flowers of oil-seed rape (Brassica napus) when pollinated by bumblebees (Bombus lapidarius). J.Ecol. 87, 670-677.

Defra, 2012. Crop areas, yields and production, livestock populations and the size of agricultural workforce: 2011. UK - Final results. Defra, Petersborough, UK.

Edwards, M., Jenner, M., 2005. Field Guide to the Bumblebees of great Britain & Ireland. Ocelli Ltd, Eastbourne, UK.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Ecol.Ecol.System. 34, 487-515.

Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhoffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H., Szentgyorgyi, H., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecol. Lett. 14, 1062-1072.

Goulson, D., Sparrow, K., 2009. Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. J.Insect Conserv. 13, 177-181.

Hayter, K.E., Cresswell, J.E., 2006. The influence of pollinator abundance on the dynamics and efficiency of pollination in agricultural Brassica napus: implications for landscape-scale gene dispersal. J.Appl.Ecol. 43, 1196-1202.

Heard, M.S., Carvell, C., Carreck, N.L., Rothery, P., Osborne, J.L., Bourke, A.F.G., 2007. Landscape context not patch size determines bumble-bee density on flower mixtures sown for agri-environment schemes. Biol. Lett. 3, 638–641.

Hoehn, P., Tscharntke, T., Tylianakis, J.M., Steffan-Dewenter, I., 2008. Functional group diversity of bee pollinators increases crop yield. Proc.Roy.Soc.B-Biol.Sci. 275, 2283-2291.

Jauker, F., Bondarenko, B., Becker, H.C., Steffan-Dewenter, I., 2012. Pollination efficiency of wild bees and hoverflies provided to oilseed rape. Agric.For.Entomol. 14, 81-87.

Jauker, F., Diekotter, T., Schwarzbach, F., Wolters, V., 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landsc. Ecol. 24, 547-555.

Morandin, L.A., Winston, M.L., Abbott, V.A., Franklin, M.T., 2007. Can pastureland increase wild bee abundance in agriculturally intense areas? Basic Appl.Ecol. 8, 117-124.

Morton, D., Rowland, C., Wood, C., Meek, L., Marston, C., Smith, G., Wadsworth, R., Simpson, I.C., 2011. Final Report for LCM2007 - the new UK Land Cover Map. Centre for Ecology & Hydrology, Lancaster.

Öckinger, E., Smith, H.G., 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes J. Appl. Ecol. 44, 50-59.

Ollerton, J., Price, V., Armbruster, W.S., Memmott, J., Watts, S., N.M., W., Totland, O., Goulson, D., Alarcón, R., Stout, J.C., Tarrant, S., 2012. Overplaying the role of honey bees as pollinators: a comment on Aebi and Neumann (2011). TREE 27, 141-142.

Pollard, E., Yates, T.J., 1993. Monitoring Butterflies for Ecology and Conservation. Chapman and Hall, London.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. TREE 25, 345-353.

Potts, S.G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'Eman, G., Willmer, P., 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecol.Entomol. 30, 78-85.

Pywell, R.F., Warman, E.A., Carvell, C., Sparks, T.H., Dicks, L.V., Bennett, D., Wright, A., Critchley, C.N.R., Sherwood, A., 2005. Providing foraging resources for bumblebees in intensively farmed landscapes. Biol. Conserv. 121, 479–494.

Richards, S.A., Williams, N.M., Harder, L.D., 2009. Variation in Pollination: Causes and Consequences for Plant Reproduction. Am.Nat. 174, 382-398.

Rodwell, J.S., 1992. British Plant Communities. Volume 3. Grassland and Montane Communities. Cambridge University Press, Cambridge.

Steffan-Dewenter, I., 2003. Seed set of male-sterile and male-fertile oilseed rape (Brassica napus) in relation to pollinator density. Apidologie 34, 227-235.

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., Tscharntke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83, 1421-1432.

Steffan-Dewenter, I., Tscharntke, T., 2000. Resource overlap and possible competition between honey bees and wild bees in central Europe. Oecologia 122, 288-296.

Vazquez, D.P., Morris, W.F., Jordano, P., 2005. Interaction frequency as a surrogate for the total effect of animal mutualists on plants. Ecol. Lett. 8, 1088-1094.

Wallace, H.M., Maynard, G.V., Trueman, S.J., 2002. Insect flower visitors, foraging behaviour and their effectiveness as pollinators of Persoonia virgata R. Br. (Proteaceae). Aust. J. Entomol. 41, 55-59.

Westphal, C., Bommarco, R., Carre, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S.G., Roberts, S.P.M., Szentgyorgyi, H., Tscheulin, T., Vaissiere, B.E., Woyciechowski, M., Biesmeijer, J.C., Kunin, W.E., Settele, J., Steffan-Dewenter, I., 2008. Measuring bee diversity in different European habitats and biogeographical regions. Ecol. Monogr. 78, 653-671.

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2003. Mass flowering crops enhance pollinator densities at a landscape scale. Ecol. Lett. 6, 961-965.

Wittkop, B., Snowdon, R.J., Friedt, W., 2009. Status and perspectives of breeding for enhanced yield and quality of oilseed crops for Europe. Euphytica 170, 131-140.

Figure captions

Fig. 1. Behavioural differences between honeybees (HB), bumblebees (BB) and solitary bees (SB) in the average time spent on oilseed rape flowers and the probability of dry pollen being present on their bodies, stigmal contact and pollen collecting behaviour.

Fig. 2. Effect of overall habitat quality on: a) honeybee visitation rates in oilseed rape; b) solitary bee species richness. Overall habitat quality is a categorical descriptor that considers agricultural management intensity and availability of foraging and nesting habitats.

Fig. 3. Response of solitary bee species richness to the proportion of semi-natural grassland within a 2 km radii surrounding oilseed rape fields.

Appendix A: Map showing the location of the 24 farms used to assess honeybee, bumblebee and solitary bee visitation rates and species richness responses to landscape structure. Semi natural Grassland cover data from LCM2007 © NERC (CEH) 2011. All rights reserved. © Crown copyright 2007. Licence number 100017572 © third party licensors.

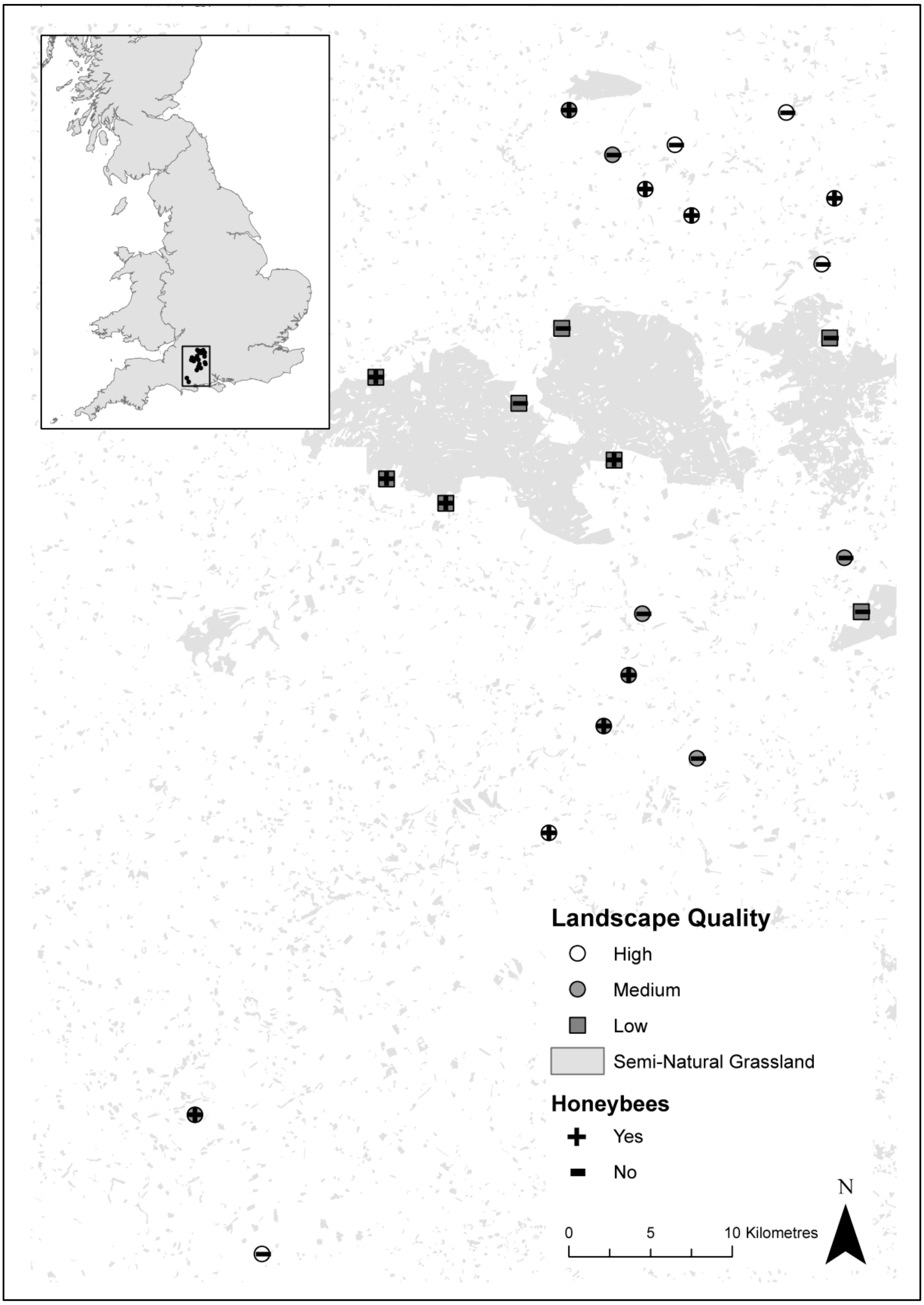
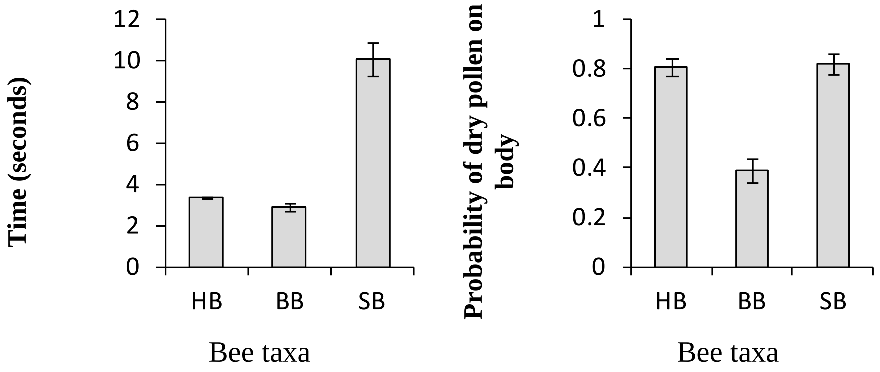
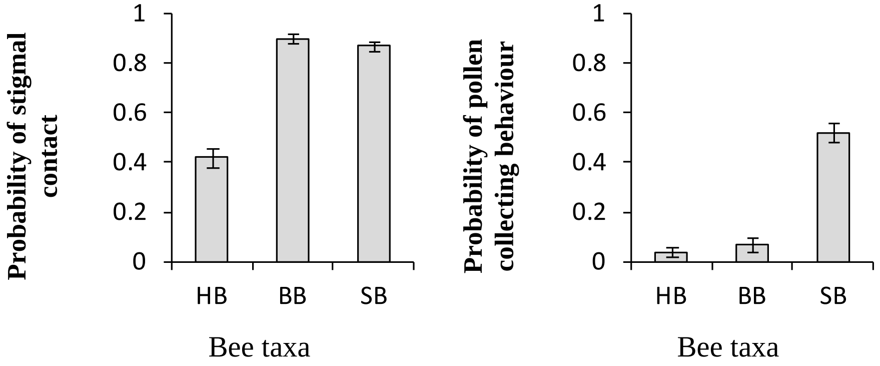


Fig. 1



a) Time spent on flower head

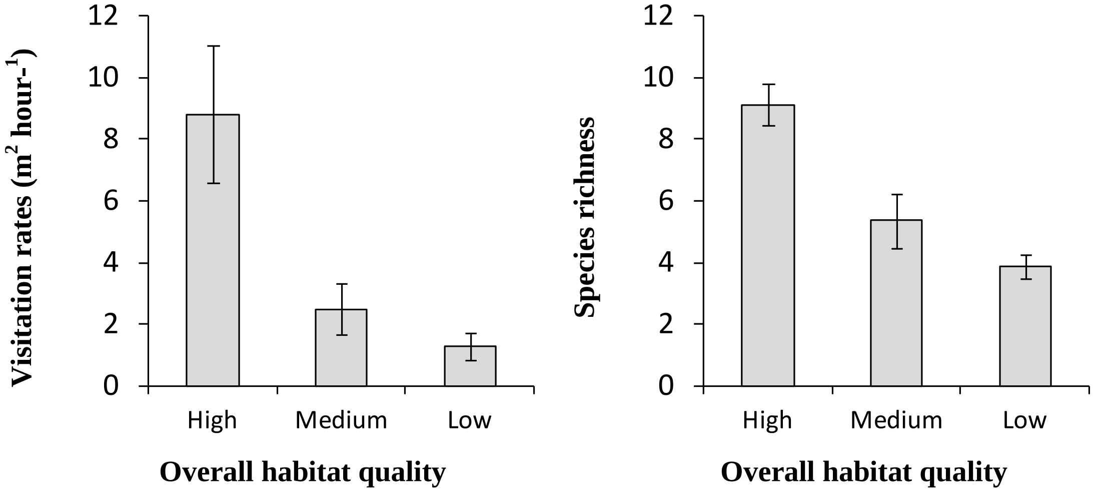
b) Dry pollen on body



c) Stigmal contact

d) Pollen collecting

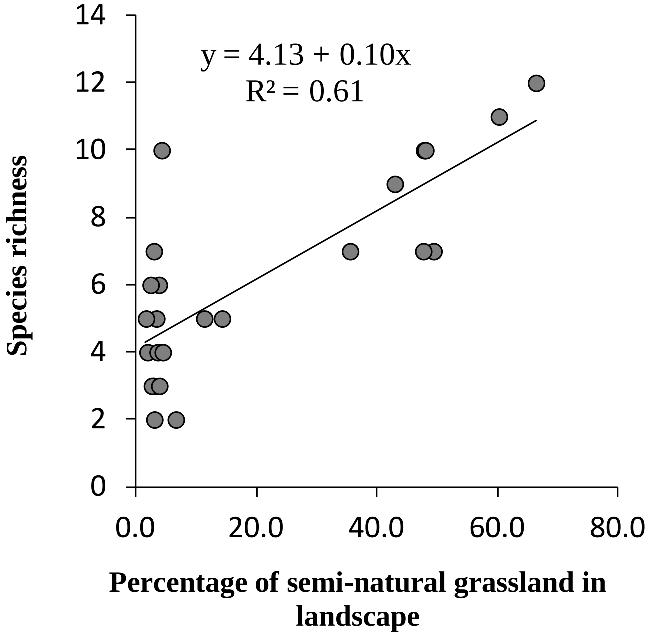
Fig. 2



a) Honeybee visitation rates

b) Solitary bee species richness

Fig. 3


y = 4.13 + 0.10x
R² = 0.61
Species richness
0
2
4
6
8
10
12
14
0.0
20.0
40.0
60.0
80.0
Percentage of semi-natural grassland in landscape