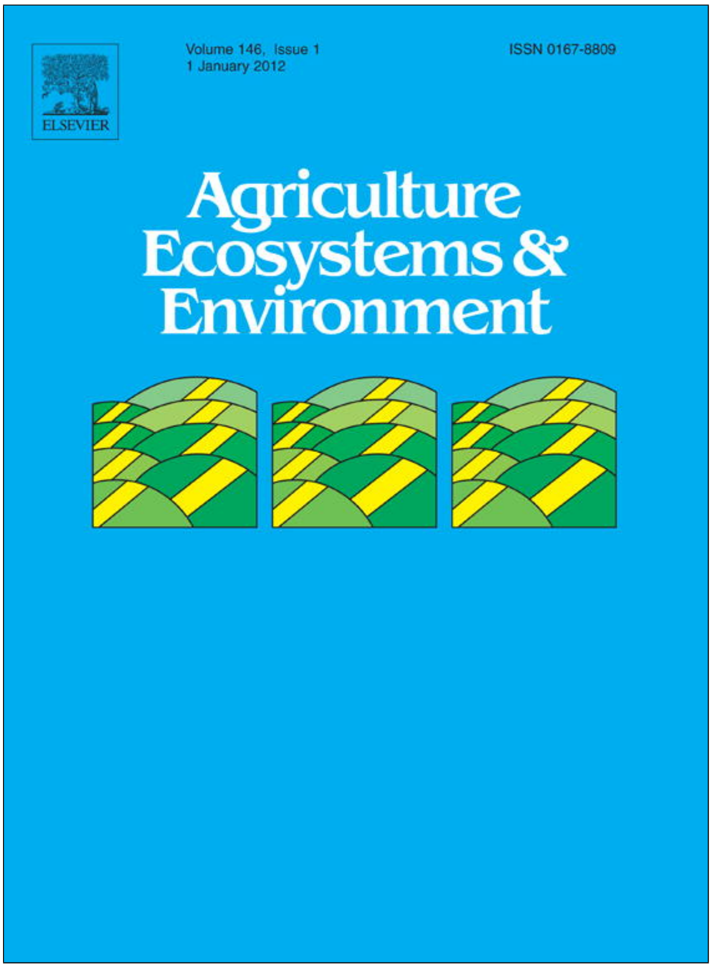

Volume 146, Issue 1
1 January 2012

ISSN 0167-8809

Agriculture
Ecosystems &
Environment

Agriculture, Ecosystems and Environment 165 (2013) 201–209

Contents lists available at SciVerse ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Seasonal persistence of bumblebee populations is affected by landscape context

Anna S. Persson[a,*], Henrik G. Smith[a,b]

[a] Department of Biology, Lund University, SE-223 62 Lund, Sweden
[b] Centre of Environmental and Climate Research, Lund University, SE-223 62 Lund, Sweden

ARTICLE INFO

Article history:
Received 3 January 2012
Received in revised form 7 December 2012
Accepted 8 December 2012

Keywords:
Bombus
Agriculture
Floral resources
Landscape structure
Mass flowering crop
Oilseed rape
Pollinator

ABSTRACT

Bumblebee communities and their foraging resources were surveyed in south Swedish agricultural landscapes of contrasting complexity, defined by the size of arable fields and the amount of permanent grazed pastures. After the flowering of oilseed rape (OSR), simplified landscapes contained substantially less herbaceous flower resources and a lower proportion of perennials, compared to complex ones. The seasonal pattern of bumblebee abundance differed between landscape types. Initial bumblebee abundances were equal in both landscape types. However, by late July there was a sharp decline of bumblebees in simple landscapes, while the abundance continued to increase in complex landscapes. This suggests that a larger proportion of bumblebee colonies may fail to reproduce in simple landscapes despite a beneficial early season. Overall, bumblebee abundance in late July was positively related to three inter-related variables: area of permanent pasture, area of ley fields and total amount of herbaceous flowers, while early abundances (June to early July) did not relate to these variables. We suggest that in simplified landscapes of this region, bumblebee abundance is limited by floral resources mainly from midsummer and onward. Spring and early summer resources may indeed be sufficient for colony establishment and initial growth even in simplified landscapes, possibly as a result of large scale farming of OSR. The initially equal abundances of workers in simple and complex landscapes, as well as the fact that also many of the regionally rare species seem to persist in simple landscapes, suggest that rare species can survive in pockets of beneficial habitat and/or there may be an inflow of queens from nearby complex landscapes. If the latter is true, further simplification or abandonment of complex landscapes may threaten bumblebee populations also in neighbouring simple landscapes.

1. Introduction

Pollinating insects have decreased dramatically in Western Europe, North America and Asia since the 1950s (e.g. Potts et al., 2010). This is also true for bumblebees (*Bombus* spp.), which are important pollinators of wild plants and crops (e.g. Winfree et al., 2008). The 20th century has seen a massive intensification of agricultural practices (Stoate et al., 2001), which has left much of Western Europe with only fragments of natural or semi-natural habitats and simplified agricultural-dominated landscapes (Benton et al., 2003; Tscharntke et al., 2005). In Europe, the combined decrease in bumblebee diversity and species distribution has been suggested to relate to such agricultural intensification and the concomitant loss of food plants (reviewed by Goulson et al., 2008; Potts et al., 2010; Williams and Osborne, 2009; Winfree, 2010). As a result of intensification both permanent, low-input grasslands and leguminous fodder crops have declined (Ihse, 1995; Stoate et al., 2001). This may have had particularly negative effects on bumblebees since these habitats provide both nesting habitat and foraging resources (e.g. Goulson et al., 2008). Remaining permanent grasslands may however still act as a source of bumblebees to the surrounding landscape (Öckinger and Smith, 2007) and the amount of semi-natural habitats in the surrounding positively affects species richness of both bumblebees and bees in general (Le Féon et al., 2010).

A large plant species pool may increase the probability that bumblebees find forage during their whole colony cycle. However, agricultural intensification has reduced plant diversity, both within crop fields and in field borders (Ma, 2008; Rundlöf et al., 2010). Perennials are preferred by bumblebees (Fussell and Corbet, 1992; Potts et al., 2009), but have declined more than annuals in simplified agricultural landscapes (Smart et al., 2006). Thus, forage quality has most likely declined. Bumblebee populations have been suggested to benefit from mass flowering crops (MFCs); in North Western Europe predominantly oilseed rape (OSR), *Brassica napus*. The overwhelming, but short flush of resources (approximately three to four weeks) offered by OSR occurs in May to early June in south Scandinavia, which is during an early stage of the bumblebees' colony cycle. It could therefore aid colonies during establishment and early

---

* Corresponding author. Tel.: +46 046 2223820; fax: +46 046 2224716.
E-mail addresses: anna.persson@biol.lu.se (A.S. Persson), henrik.smith@biol.lu.se (H.G. Smith).

0167-8809/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.agee.2012.12.008

growth (Knight et al., 2009; Westphal et al., 2006b). However, it has been questioned if it also boosts reproduction (Herrmann et al., 2007; Westphal et al., 2009). To date only a few studies have related bumblebee abundance or colony growth to actual flower resources to provide a mechanistic link between observed losses of wild bees and landscape changes (Goulson et al., 2010; Knight et al., 2009; Williams et al., 2012).

Bumblebees are social species and census counts of workers may therefore be poor estimates of effective population size, i.e. the number of reproducing queens (Winfree, 2010). However, temporal dynamics of worker numbers could indirectly inform about colony growth, and thereby the potential for reproduction (Ings et al., 2006; Schmid-Hempel and Schmid-Hempel, 1998). To our knowledge, there are few previous studies exploring both the spatial and temporal dynamics of total bumblebee communities in differently simplified agricultural landscape and relating this to total availability of flower resources (Williams et al., 2012). On the other hand several studies have focused on surveys of bumblebee density in one or a few particular habitats, such as semi-natural or flower enriched habitats (e.g. Herrmann et al., 2007; Kells et al., 2001; Pywell et al., 2006, 2011). However, if landscape comparisons are made from such surveys they may underestimate the difference in abundance between landscapes since bumblebee workers can be expected to aggregate into such habitats. Furthermore, the degree of aggregation depends on the availability of alternative resources, and therefore on the agricultural intensity, in the surrounding landscape (Heard et al., 2007). The occurrence of large but ephemeral resources such as MFCs could therefore increase the apparent abundance of bees in an area as they seek forage in other habitats after the MFC bloom. Consequently, it is important to evaluate the total abundance of pollinators, in this case bumblebees, within a landscape.

To study potential effects of differences in landscape structure and amount of permanent grasslands on both bumblebees and their resource flowers, surveys were performed in two landscape types: Complex, with small agricultural fields, mixed farming and a high proportion permanent grasslands (mainly pasture) and Simple, with large fields, mainly crop production and practically lacking permanent grasslands. During June and July 2006, bumblebees and their flower resources were surveyed in some common farmland habitats; edges and border zones of crop fields, leys and permanent pastures. To be able to follow changes in abundance over the season, three temporally separate survey rounds were performed. We expected to find higher abundance and species richness of floral resources and bumblebees in complex landscapes compared to simple ones, and that this difference should be more accentuated when comparing total density as compared to habitat specific densities.

2. Methods

2.1. Landscape selection and description

The study was carried out in the province of Skåne in southernmost Sweden (approx. 56°N, 13°30′E), a region dominated by agriculture but with a large variation in land use intensity and landscape complexity (Persson et al., 2010). Study landscapes were selected using data from the Integrated Administration and Control System (IACS), a yearly updated database on all registered farmland fields in Sweden, including spatially explicit data on crops and other land use on farmland (pasture, fallow, tree plantations, etc.). Based on the amount of permanent, grazed pastures and the mean size of farmland fields, 10 circular landscapes with a radius of 3 km were selected. This radius was chosen so as to cover the flight range of bumblebees (Knight et al., 2009; Westphal et al., 2006a), thereby ensuring that the majority of resources were actually drawn from the surrounding study landscape. Five landscapes were characterised as simple with large fields and without permanent pasture (<1% pasture) and five as complex and with small fields and with permanent pasture (>9% pasture). Data was processed in ArcGis 9.2 (ERSI, Redlands, CA). In this study complex landscapes also had a lower proportion of annual crops, more leys and less oilseed rape (*B. napus*) than simple ones (Table 1). According to the classification used here pastures are practically permanent, non-fertilised, semi-natural grasslands used exclusively for grazing. In contrast, leys are rotational crops where grass or grass mixed with clover (*Trifolium repens* or *Trifolium pratense*) is cultivated for grazing, hay or silage production. Typically, a field is used as ley for 2–5 years in sequence. There were no significant differences between landscape classes of three other potential bumblebee foraging habitats: fallow fields, *Salix* grown on farmland, and the number of houses, used here as an indicator of the amount of garden habitat per landscape (Table 1).

2.2. Inventory methods

From each 3 km radius landscape, six 500 m × 500 m evenly spaced square cells were selected along the north–south axis. In each such cell two 100 m × 2 m transects of each of the following habitats were identified during field visits: (1) non-flowering crop field, (2) ley field and (3) pasture. Following the methodology of Rundlöf et al. (2008), transects were positioned in the field/ley/pasture margin such that 1 m covered the field/ley/pasture, and 1 m covered its non-crop border zone. In simple landscapes, with a low proportion of pastures, it was naturally not possible to sample pastures in all cells.

Bumblebees (*Bombus* spp.) were recorded using transect walks adopted from the standard line transects method developed for butterfly surveys (Pollard, 1977; Rundlöf et al., 2008). It was noted if a bumblebee was seen within the crops/leys/pastures or in the corresponding border zone habitat. Transects were walked at a slow pace and bumblebees seen foraging were determined to species by eye or if necessary caught with a hand-net and identified using Prŷs-Jones and Corbet (1987) and Holmström (2002). In case of uncertainty, the bumblebee was noted as the more common species. Workers, queens or males were not discriminated. Because of the difficulty of separating *Bombus lucorum* and *Bombus terrestris* (Svensson, 2002) they were pooled and noted as *B. lucorum*-group. In order to prevent more than one record of the same individual, each bumblebee was monitored until it either left the transect or was lost from sight. Bumblebees flying over the inventory area without stopping to forage were not determined to species, but noted as a “flying” individual and only included in data on abundance. The survey was repeated three times during the summer of 2006; (1) 9–27 June, (2) 27 June–5 July, and (3) 17–25 July. There were on average 15.7 days (min. 8 and max. 20 days) between the 1st and 2nd survey in a particular landscape and on average 18.6 days (min. 17 and max. 21) between the 2nd and 3rd survey.

To assess the total amount of potential flower resources in each landscape flowering plants were surveyed at the start of the study in mid-June. Surveys were carried out in 12 500 m × 500 m cells per circular landscape, six along the north–south axis and six along east–west axis. This setup was used to detect and include potential spatial variations in resources within landscapes. Flowers were surveyed in five potential foraging habitats: pasture, ley, crop field, road verge and non-crop field border. In each of the 12 500 m × 500 m cells two squares of 0.25 m^2 were randomly positioned within in each of these five habitat types, i.e. in total 30 m^2 was surveyed in each circular landscape. Plant taxonomy followed Mossberg et al. (1992). Flower resources were assessed in different

Table 1
Land-cover in simple and complex landscapes within a 3 km radius. Differences analysed with *t*-tests. Dfs deviate from 1,8 when heterogeneous variances were allowed for because that decreased the AIC. Significant differences in bold.

Landscape type (number of sites)	Complex (5)		Simple (5)		Test of difference between groups	
Landscape variables	Mean	std	Mean	std	F_{df}	P
Fieldsize (ha)	6.08	4.37	21.52	7.32	$\mathbf{16.39}_{1,8}$	**0.0037**
Pasture (ha)	487.43	178.29	17.61	10.38	$\mathbf{34.60}_{1,4.0}$	**0.0041**
Oilseed rape fields (ha)	48.16	62.80	208.58	42.29	$\mathbf{22.44}_{1,8}$	**0.0015**
Leys (ha)	797.86	158.85	72.27	33.03	$\mathbf{100.00}_{1,4.4}$	**0.004**
Annual crops (ha)	605.55	370.71	2325.76	60.45	$\mathbf{104.87}_{1,4.2}$	**0.004**
Fallow (ha)	79.42	17.74	93.11	21.70	$1.19_{1,8}$	0.31
Salix fields (ha)	0.78	1.75	5.28	7.93	$1.53_{1,4.4}$	0.28
Forest (ha)	505.90	282.35	7.01	13.82	$\mathbf{15.52}_{1,4.0}$	**0.017**
Field borders (ha)	25.87	11.03	5.68	6.32	$\mathbf{12.61}_{1,8}$	**0.0075**
Road verges (ha)	14.71	5.52	20.52	12.14	$0.95_{1,8}$	0.36
Border zones to ditches (ha)	8.75	5.11	18.38	15.23	$1.80_{1,4.9}$	0.24
Number of houses	163.4	42.5	148.8	37.4	$0.33_{1,8}$	0.58

units depending on the flower-type (sensu Williams and Kremen, 2007). The following was noted: for Convolvulaceae, Papaveraceae and Rosaceae (except Filipendula) individual flowers, for Brassicaceae and *Filipendula* number of "umbels", for Asteraceae, Dipsaceae and Plumbaginaceae the number of flower heads, for Fabaceae and Boraginaceae the numbers of racemes and for Campanulaceae, Caryophyllaceae, Clusiaceae, Lamiaceae, Onagraceae and Scrophulariaceae number of flower stalks.

We gathered data on land-cover to describe landscapes, to use as a basis to calculate total numbers of bumblebees and resource flowers and to estimate the amount of potential resource rich habitats (see Section 2.1, Table 2). Information of farmland fields was taken from IACS. To estimate the amount of linear non-crop habitats we noted the quantity (length and width) of all border habitats during field surveys to 12 500 m × 500 m cells per circular landscape (same cells as the flower survey). Land-cover data was processed in ArcGis 9.2.

2.3. Calculations and statistical methods

All statistical analyses were done in SAS 9.2 for Windows (SAS Institute Inc., Cary, NC). In one case a General Linear Model (SAS Proc GLM) was used, whereas otherwise Linear Mixed Models with Normal (SAS Proc Mixed, Normal distribution) or Poisson error (SAS Proc Glimmix) were used to account for non-independence of data. To account for the dependence of observations in habitats within survey rounds, and within a landscape, random factors nested at several levels were used (details are given conjunction to each test below). Fixed effects were tested using *F*-tests with the degrees of freedom estimated with the Kenward–Roger method. When covariance estimations of random factors were occasionally non-significantly negative the Nobound option was used, since the Kenward–Roger method otherwise gives inflated denominator degrees of freedom. Significant interactions were interpreted with simple main effects (SAS option slice). The least square means estimates (lsm est) predicted from the models are presented and were used for further calculations. When log(density) was used as response variable, the smallest non-zero value was added to all values to avoid zeros.

If the only bumblebees noted were "flying" ones, i.e. individuals not determined to species, the number of species in that habitat was set to 1. Species richness was analysed using a Generalised Linear Mixed Model (SAS Proc Glimmix) and used Tukey's post hoc test to evaluate differences between habitat type least square means. The fixed part of the model was: N species = landscape class, survey round, habitat type, surveyed area and landscape type × survey round, with random factor landscape id. The model was checked for over-dispersion, but this was not the case.

For habitat specific density, log bumblebee density per habitat type within a landscape was used as response variable. The three survey rounds were kept separate to be able to compare seasonal patterns between the two landscape types. A Linear Mixed Model was used with the fixed factors: landscape type, habitat type, survey round, survey round × landscape type, survey round × habitat type. The random structure was landscape id, habitat type × landscape id and survey round × landscape id.

To estimate total abundances of bumblebees per landscape, data on habitat and landscape specific densities of bumblebees from model predictions were multiplied with the area of each habitat type per circular landscape. To estimate bumblebee abundance in different border habitats the mean density from the surveys of borders of pasture, leys and annual crops fields were used. This mean density was also used to estimate bumblebee abundance in linear non-crop elements where bumblebees were not surveyed (mainly road verges and borders of open ditches). During field visits it was noted that borders of open ditches differed in structure and flora between landscape types such that these habitats in complex landscapes resembled other non-crop borders, while in simple landscapes they were often several meters wide, grassy protective zones of small water courses. Because of this they constituted a large part of all non-crop habitats in simple landscapes but contributed few flower resources. Ditch borders in simple landscapes had on average only 16% of the flower density found in other border habitats, while those in complex landscapes had 78%. The number of bumblebees found in a habitat was assumed to be positively related to the amount of flower resources (e.g. Bäckman and Tiainen, 2002). It was therefore possible to crudely correct for the lower resource value of ditch borders by multiplying ditch area with 0.78 and 0.16 for complex and simple landscapes, respectively.

Total bumblebee abundance (Linear Mixed Model) was analysed using the following model: log n.o. bumblebees per landscape = survey round, landscape type, survey round × landscape type, with random factor landscape id.

From the flower survey, the density per habitat type and landscape of all species considered potential nectar and/or pollen resources for bumblebees was calculated (Fussell and Corbet, 1992; Rundlöf et al., 2008; Appendix, Table A2). As for total bumblebee numbers, density was then multiplied with the total area of each habitat per circular landscape, resulting in an estimation of total amount of flower resources present. Flower abundance per landscape was analysed using a Linear Mixed Model with response variable log (flower units + 1), fixed factors landscape type, habitat type, landscape type × habitat type, and with random factors landscape id and habitat type × landscape id.

Perennial flowers are preferred by bumblebees (Fussell and Corbet, 1992), so to test for qualitative differences in the flora

Table 2
Results of the statistical analyses. Statistically significant results in bold. Non-significant interaction terms were removed and models re-run to obtain the final models. See Section 2.3 for details.

Response variable	Basic model	F_{df}	P	Interactions	F_{df}	P
Number of species per habitat and landscape	Landscape type Survey round Habitat type Log (area)	$0.41_{1.11.3}$ $9.49_{2,25.8}$ $6.98_{5,30.8}$ $16.4_{1,78.5}$	0.54 0.0008 **0.0002** **0.0001**	Landscape type × survey round	$7.00_{2,25.7}$	**0.0038**
Bumblebee habitat specific density per landscape	Landscape type Survey round Habitat type	$1.16_{1,7.4}$ $18.21_{2,17.4}$	0.31 <0.0001	Landscape type × survey round Habitat type × survey round Landscape type × habitat type Landscape × survey round × habitat	$7.46_{2,16}$ $2.93_{10,78.6}$ $0.69_{5,39.0}$ $1.17_{9,68.9}$	**0.0051** **0.0036** 0.63 0.33
Total number of bumblebees per landscape	Landscape type Survey round	$23.85_{1,8}$ $6.59_{2,16}$	0.0012 0.0082	Landscape type × survey round	$5.84_{2,16}$	**0.013**
Total amount of flowers per habitat	Landscape type Habitat type	$11.03_{1,8.3}$ $0.24_{3,27}$	**0.010** 0.87	Landscape type × habitat type	$1.87_{3,24}$	0.17
Flower density per habitat and plant type	Landscape type Habitat type Plant type	$0.54_{1,8.2}$ $8.77_{1,36.2}$ $2.16_{1,43.0}$	0.065 <0.0001 0.15	Landscape type × plant type Habitat type × plant type	$0.51_{1,42.0}$ $6.31_{5,43.0}$	0.48 **0.0002**

between landscape classes and habitat types, plants were divided into perennials vs. annuals and biennials. A Mixed Model was used with log (flower density + 0.167) as dependent variable and the fixed factors: landscape type, habitat type, plant type, landscape type × plant type and habitat type × plant type. The random structure included landscape id and habitat type × landscape id.

3. Results

Out of a total of 1560 bumblebee individuals, 1130 were found in complex and 430 in simple landscapes. 1007 bumblebees were determined to species while 553 were noted as individuals flying past. Eleven different species were observed (12 if *B. lucorum* and *B. terrestris* are treated separately), the most common being *B. lucorum/terrestris*-group (212), *Bombus lapidarius* (206), *Bombus ruderarius* (184) and *Bombus hortorum* (159) (Appendix, Table A1).

3.1. Bumblebee species richness

We found in total 11 species in complex and 9 species in simple landscapes (*B. terrestris* and *Bombus lucorum* pooled, Appendix, Table A1). There was a significant interaction between survey round and landscape type (Table 2). The interaction was caused by a significantly higher species richness in complex landscapes during the 3rd survey (simple main effect: $F_{1,20.6} = 8.56$, $P = 0.0082$), while there was a non-significant tendency for the opposite during the 1st survey ($F_{1,45.0} = 3.34$, $P = 0.074$) and no difference during the 2nd survey ($F_{1,16.4} = 0.57$, $P = 0.46$) (Fig. 1(a)). There was also a significant difference in species richness between habitats (Table 2). Tukey's post hoc test showed that this was because border zone habitats (of crop fields, leys and pastures) were richer than crop fields and leys (data not shown).

3.2. Bumblebee habitat specific density

We detected seasonally dependent effects of both landscape context and habitat type on the density of bumblebees in the surveyed habitats (Table 2 and Fig. 1(c) and (d)). There was no difference in density between landscape types during the 1st and 2nd survey rounds (simple main effects: $F_{1,19.8} = 1.96$, $P = 0.18$; $F_{1,15.9} = 1.47$, $P = 0.24$), but during the 3rd survey round there was approximately a threefold higher density in complex landscapes ($F_{1,15.5} = 8.11$, $P = 0.012$; Fig. 1(c)).

There was furthermore seasonal variation in abundance in some but not all habitat types, as verified by the significant interaction of survey round × habitat type (Table 2). Significant simple main effects revealed that seasonal effects occurred in all border habitats (crop border $F_{2,88.7} = 6.48$, $P = 0.0024$; ley border $F_{2,88.7} = 4.87$, $P = 0.0098$; pasture border $F_{2,102} = 9.59$, $P = 0.0002$), and to some degree crop fields ($F_{2,88.7} = 6.85$, $P = 0.0017$), although at much lower density than in border habitats (Fig. 1(d)). In contrast, there was no difference in bumblebee density over time in leys or pastures ($F_{2,89.2} = 2.53$, $P = 0.085$; $F_{2,88.2} = 0.90$, $P = 0.41$, respectively). The pattern was the same in both landscape types (non-significant interactions habitat type × survey-round × landscape type, Table 2). During the first round no bumblebees were found in borders of pastures or crop fields.

3.3. Total number of bumblebees

The total number of bumblebees within a landscape depended on both survey round and landscape type (significant interaction survey round × landscape type, Table 2, Fig. 1(b)). This was because significantly more bumblebees were estimated in complex landscapes during the 3rd survey round (simple main effect $F_{1,24} = 31.60$, $P < 0.0001$), while significant difference between landscape types were found during the 1st and 2nd surveys ($F_{1,24} = 2.05$, $P = 0.16$; $F_{1,24} = 2.17$, $P = 0.15$, respectively). Complex landscapes had ca. 30 times more bumblebees than simple ones at the 3rd survey in late July (Fig. 1(b)).

3.4. Flower resources

Complex landscapes held more floral resources in pastures, leys, road verges and field borders than did simple landscapes. There were on average (mean ± std at total of) 17.9 ± 16.9 flower units (log-scale) in complex landscapes and 14.4 ± 13.2 in simple ones; i.e. approximately 30 times more floral resources in complex landscapes. Non-flowering crop fields were surveyed but contributed no resource flowers at any site. Habitats not included in the estimation were flowering crops (other than clover leys), fallows, flowering

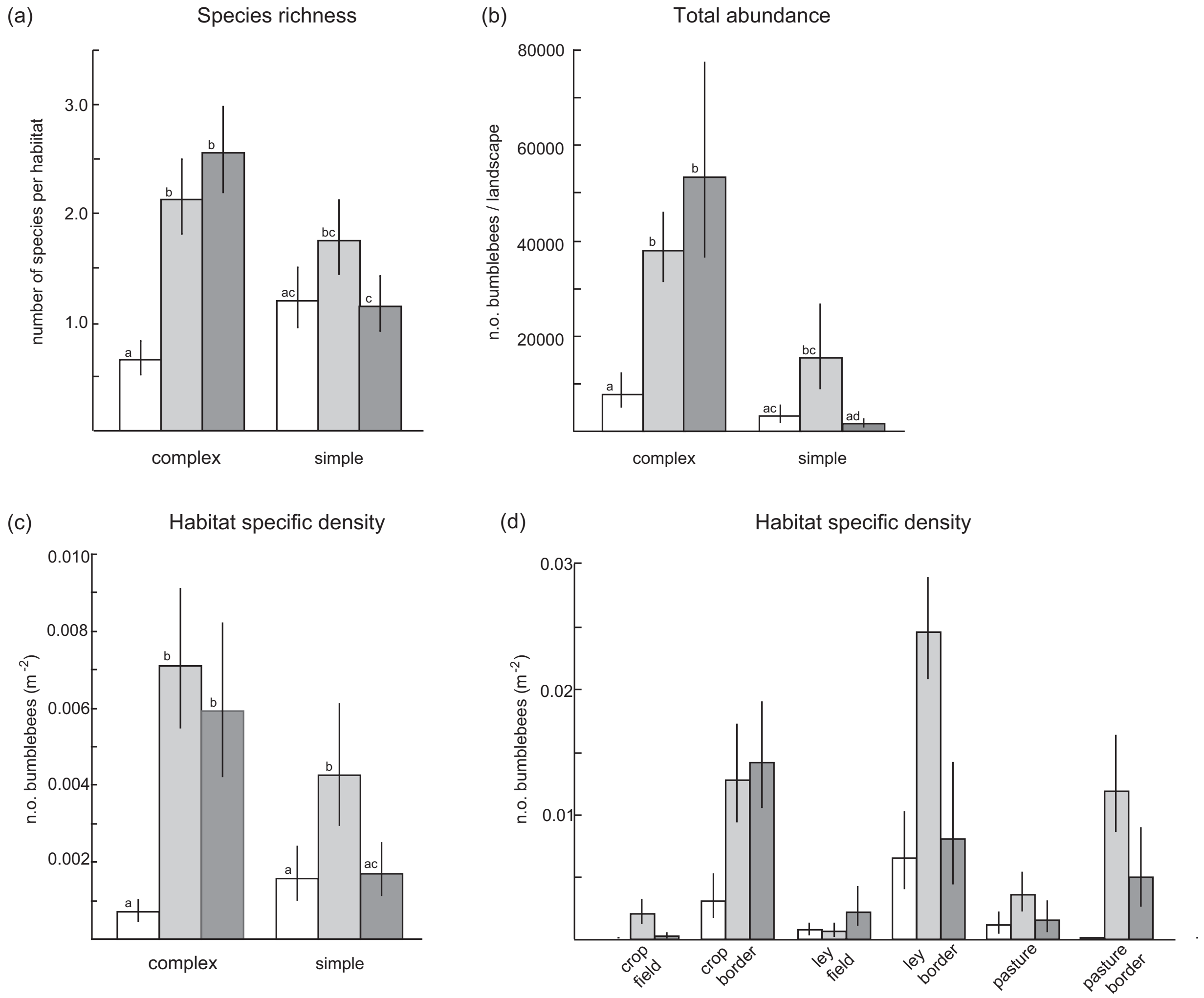

Fig. 1. Bumblebee species richness and abundance over time in simple and complex landscapes. Open bars: 1st survey, light grey: 2nd survey, dark grey: 3rd survey. Results shown are back-transformed model derived least square means, with standard errors (sem) calculated from data aggregated at the level they were tested at, using SAS Proc Means, if nothing else is stated. Significant differences are noted with letters in (a)–(c). (a) Species richness of bumblebees (mean ± sem), both mean and sem from model derived data. (b) Total numbers of bumblebees (mean ± sem) per landscape type and survey. (c) Habitat specific density of bumblebees (mean ± sem) per landscape type and survey. (d) Density of bumblebees (mean ± sem) in the six habitats surveyed over time.

trees and shrubs and domestic gardens. However, except for OSR (which had almost ceased to flower at the time of this survey), the amount of these were either similar between landscape types (Table 1) or higher in complex sites, since complex landscapes in this region contain more non-crop margins with trees and bushes (Persson et al., 2010).

There was a non-signficant tendency for habitats in complex landscapes to hold more perennials, compared to habitats in simple landscapes (Table 2). The density of perennials compared to that of annuals/biennials was also habitat dependent; as shown by the significant interaction between habitat type and plant type (Table 2). There were more perennials than annuals/biennials in pastures, leys, road verges and field borders (simple main effects of habitat, pasture: $F_{1,43} = 25.10$, $P < 0.0001$; ley: $F_{1,43} = 13.58$, $P = 0.0006$; road verge: $F_{1,43} = 13.58$, $P = 0.0006$; field border: $F_{1,43} = 6.78$, $P = 0.013$), while fallows instead had more annuals/biennials than perennials ($F_{1,43} = 8.72$, $P = 0.0051$). There was no significant difference between the relative density of the two plant types in crop fields ($F_{1,43} = 0.10$, $P = 0.75$), but densities of flowers were very low altogether in this habitat.

The total number of bumblebees during the 3rd survey round was positively correlated to the area of pasture ($r_{10} = 0.87$, $P = 0.0008$), ley ($r_{10} = 0.91$, $P = 0.0002$) and total flower resources ($r_{10} = 0.71$, $P = 0.019$) and negatively so to the area of oilseed rape in the landscape ($r_{10} = -0.74$, $P = 0.015$). However, the 1st and 2nd survey rounds did not show any such relation (all correlations $P > 0.19$). The area of pasture, ley and total amount of flowers were also positively correlated to each other and negatively correlated to area of OSR (data not shown, but see Table 1 for land-cover data).

4. Discussion

This study shows that the relationship between bumblebee abundance and surrounding landscape complexity incorporates a seasonal component. Patterns of bumblebee abundance in a region dominated by agriculture interacted with both time and landscape context, such that numbers gradually increased over the whole survey period in complex landscapes, whereas numbers in simplified landscapes initially increased but then declined sharply by mid/late July. Bumblebee abundance in late season (but not early season) was furthermore positively related to three potential nesting habitats and foraging resources in the surrounding landscape: leys, pastures and total amount of herbaceous flowers. Despite a substantially lower availability of wild herbaceous flowers and leys in simple landscapes the early season bumblebee abundances and species richness were similar in both landscape types. This suggests that nest establishment and early season growth was subsidised by other resources in simple landscapes, possibly flowering trees and shrubs and/or OSR, which was grown on a larger area in those landscapes. However, colony growth and species richness was sustained until the end of July only in complex landscapes with a higher availability of flower resources throughout the season.

4.1. *Effects of seasonal variation in flower resources*

Westphal et al. (2009) showed that bumblebees produced larger colonies, but not more sexual offspring per colony, in response to high abundance of early season flowering OSR and Williams et al. (2012) suggested that sufficient resources during both early and late season is crucial to positively affect production of daughter queens. The results presented here suggest negative mid/late-season effects of a simplified surrounding landscape dominated by relatively intensive agriculture and including OSR-fields. In comparison a complex surrounding landscape, with plenty of non-crop, semi-natural habitats such as grassy field borders and permanent unfertilised pastures, exhibited a continuous increase in bumblebee numbers throughout the study period. If a negative effect of intensive agriculture mainly works through affecting early or late season resources depends on the farming systems of a particular region and the type, amount and phenology of flowering crops grown in relation to phenology of the bumblebee community. Williams et al. (2012) found that landscapes in northern California dominated by agriculture provided plenty of flowering crops late in the season, while early season growth of experimental colonies in such landscapes seemed to be resource limited. Contrary to this, the results presented here indicate a lack of late season resources in simplified agriculture dominated landscapes. However it is possible that the lack of a difference in early bumblebee abundance between landscape types was actually caused by the larger area of OSR grown in simple landscapes, if OSR subsidised colony establishment and growth there. Complex landscapes instead offered substantially more of wild herbaceous flower resources (ca. 30-fold more) and a tendency for a larger proportion of perennials. At the end of July, some six weeks after the end of OSR flowering, 1:30 was actually the approximate relation in bumblebee numbers between the two landscape types (Fig. 1(b)). It is therefore likely that a lack of resources during the mid and late season limited continued growth of colonies in simple landscapes, while early growth was well catered for. The area of semi-natural habitats in the surrounding has been shown to positively affect abundance of bumblebees (Morandin et al., 2007) and species richness of bumblebees and bees in general (Le Féon et al., 2010). It is likely that bumblebees in agricultural landscapes with "adequate" amounts of wild flowers from semi-natural habitats will be buffered through periods without MFCs. Colonies are then able to make the most of the superabundant MFCs once they appear (Williams et al., 2012). This study therefore adds strength to the link between landscape complexity/quality via flower resources to bumblebee abundance and colony growth also documented by others (Goulson et al., 2010; Knight et al., 2009; Williams et al., 2012).

It is known that bumblebees prefer to forage on perennials (e.g. Fussell and Corbet, 1992) and a lower proportion of perennials among food plants have been suggested as a reason behind declines in species richness of bumblebees on Estonian farmland (Mänd et al., 2002). In addition to a higher abundance of flowers, complex landscapes contained a higher proportion of perennials, i.e. both more and higher quality forage for bumblebees. Low pollen and protein diversity in forage have been shown to negatively affect the immune response at the colony level for the honeybee, *Apis mellifera* (Alaux et al., 2010). This may also have contributed to the decline in bumblebee abundance in simple landscapes.

4.2. *Implications for bumblebee reproduction*

Bumblebee queens establish colonies in early spring and the ability to reproduce at the end of the colony cycle depends on the build-up of a force of workers to provision the brood (e.g. Benton, 2006; Schmid-Hempel and Schmid-Hempel, 1998). Thus, reproductive success is expected to depend on the resource availability throughout the season, as well as the spatial distribution of those resources in relation to the foraging range of a particular colony. As a consequence, production of young queens and males is positively related to colony size (Ings et al., 2006; Williams et al., 2012) and the number of workers and males produced is positively related to the total amount of resources in the surrounding foraging landscape (Williams et al., 2012). There was a sharp decline in the number of bumblebees in simple landscapes by mid/late July, a decline which may have occurred before new queens and males were produced, at least for species with a long colony cycle and/or late phenology (Benton, 2006). Furthermore, because foragers, males and queens were not discriminated, a part of the large difference in total abundance in late-season might actually be attributed to a higher production of sexual offspring in complex landscapes. The results presented here therefore suggest a lower reproduction of colonies within simplified agricultural landscapes in this region. Larger numbers of males in complex compared to simple landscapes were indeed found in a later study in the same region (Persson, 2011). The long-term persistence of bumblebee populations in simplified agricultural landscapes of this region may therefore be at risk. This poses a serious threat to adequate pollination because bumblebees are major pollinators of both wild plants and crops in this and other regions of the northern hemisphere (e.g. Cederberg et al., 2006; Winfree et al., 2008). In fact, a pollination deficit has been indicated in a study in simplified landscapes within this same region in Scania (Samnegård et al., 2011).

The present study is based on one season only, but demonstrates a (mid/late season) lack of flowers in simple landscapes that most likely occurs every year, and which may result in a concomitant decline in bumblebees. Despite this, simple landscapes hosted an early abundance and species richness equal to complex ones. Out of the 17 social bumblebee species present in the province of Scania (of which four are considered very rare and one regionally extinct (Holmström, 2007)), nine species were encountered in the five simple and eleven in the five complex landscapes. Other studies in the same region with similar landscape classifications have also detected relatively rare species in simplified landscapes, albeit in small numbers (Persson, 2011; Rundlöf et al., 2008; Samnegård et al., 2011). There are at least three potential explanations to this fact. Colonies in simple landscapes may reproduce earlier, i.e. have an earlier phenology with a higher initial growth rate (subsidised by flowering trees and OSR), making possible reproduction already during May and June. This could be the case for species with an early nest establishment and short reproductive cycle (Benton, 2006). In contrast several rare and declining species have a later peak season and a longer reproductive cycle (Benton, 2006; Persson, 2011). Some of these species (e.g. *Bombus muscorum*, *Bombus sylvarum*, *Bombus ruderarius* and *Bombus subterraneus*) were more numerous in complex landscapes, so the increase in both abundance and species richness in those landscapes during mid/late season could be caused by workers of more rare species appearing.

Another explanation to the relatively high abundance and diversity of bumblebees in simple landscapes in early season could be an annual inflow of queens to those landscapes from neighbouring complex areas, thus compensating a lower reproduction (i.e. source-sink population dynamics sensu Pulliam, 1988). Furthermore it is possible that some rare species persist in pockets of beneficial habitat within otherwise impoverished landscapes. Possibly a combination of the scenarios presented above is the case, where some early species (e.g. *Bombus terrestris*) are indeed able to efficiently utilise abundant early mass flowering resources (Westphal et al., 2006a) and grow large populations also in simple landscapes. Other species can most likely not adapt to the temporal and spatial distribution of resources and are either able to survive within small areas such as semi-natural grasslands or domestic gardens (Samnegård et al., 2011), or must rely on queen dispersal from more resource-rich areas back into simple landscapes. Queens are considered to have far better dispersal abilities than foragers and may travel several kilometres after hibernation before they have initiated a nest (Lepais et al., 2010). The distance between simple study landscape and the nearest region of complex landscapes is 10–20 km. If dispersal mainly takes place in spring the availability of spring flowering trees and shrubs and flowering OSR may lead queens to settle in landscapes where resources will later practically disappear. Alternative but less likely explanations to the patterns seen could be that fewer colonies manage reproduction but instead produce more queens per colony in simple compared to complex landscapes, or that winter survival and colony establishment is higher in simple landscapes.

4.3. Effects of bumblebee aggregation

The difference between landscape types during the last survey in mid/late July was much more pronounced when total numbers per landscape, instead of habitat specific densities, were considered. For example, habitat specific densities in the 3rd survey round were only a little more than 3-fold higher in complex compared to simple landscapes while the estimated total abundance was 30-fold higher. Thus, a comparison of habitat specific densities may drastically underestimate landscape differences, especially when measured in flower-rich habitats situated in otherwise impoverished landscapes (Heard et al., 2007). It may therefore be important to estimate total numbers, e.g. when evaluating effects of agri-environment schemes such as sown flower strips (Pywell et al., 2006, 2011) and when translating abundances of mobile pollinators such as bumblebees into pollination services, where the total number is likely to be more important than densities within particular habitats (Klein et al., 2007; Rader et al., 2009).

Landscape variables and farming practices (e.g. land use, crop species and degree of specialisation of each farm) differed between landscape types (Table 1). As a consequence also pesticide use differed between landscape types. Agricultural statistics shows that the percentage of farmland treated with insecticide in the complex region is about one third compared to that in the simple region (13% vs. 36% of land classified as farmland), while the dosage seems to be slightly higher in the complex region (0.08 vs. 0.05 kg/ha) (SCB, 2007). For herbicide use both the area treated and the dosage is higher in the simple region. It is, thus, not possible to rule out that spraying of flowering crops (predominantly ORS) and/or drift of insecticide into bumblebee non-crop foraging habitats can have contributed to the landscape differences detected here. Previous studies in this region have shown that positive effects of organic farming (where pesticide use is prohibited) on bumblebee abundance mainly occur on farms situated within simple landscapes (Rundlöf et al., 2008). These effects can both be directly caused by insecticide use and indirectly by loss of flowering plants due to herbicide use and drift (Rundlöf et al., 2010). In the light of some recent papers pointing to correlations between flower or foraging habitat availability and bumblebee colony survival, density and growth (Goulson et al., 2010; Knight et al., 2009; Williams et al., 2012) it is still highly likely that the difference in flower abundance between landscape types played a major role in shaping the temporal patterns of abundance also in the present study region.

4.4. Conclusions and implication for management

In conclusion, it is shown that contrary to expectations, both simplified and complex agricultural landscapes of southern Sweden initially hosted equally high abundances and species richness of bumblebees. However, a sharp decline of both abundance and richness occurred in peak season only in simple, intensively managed landscapes. This decline is mainly explained by a lack of wild flower resources in simple landscapes in mid/late season, caused by fewer and poorer flower-rich semi-natural habitats, such as non-crop field borders and permanent grasslands. A promising method to counteract the loss of pollinators from farmland would thus be to reverse simplification by introducing more complexity into agricultural dominated landscapes, e.g. by adding non-crop habitats and mid/late flowering crops or wildflowers. Furthermore, the relatively high total species richness and initially high abundance also in simple landscapes might indicate that rare species can survive in pockets of beneficial habitat and/or that there is an in-flow from source populations inhabiting neighbouring complex areas. Thus, actions to avoid further simplification or land abandonment in complex regions may also benefit bumblebee population

Table A.1
Number of bumblebees of different species observed per landscape type and the total area surveyed during the three survey rounds. All individuals not determined to species are here denoted *Bombus* spp.

Survey round	1		2		3		Total
Landscape type	Complex	Simple	Complex	Simple	Complex	Simple	
Bombus spp.	54	44	197	77	119	62	553
B. hortorum	2	2	47	25	81	2	159
B. hypnorum	2	0	7	0	23	0	32
B. lapidarius	3	3	42	37	81	40	206
B. lucorum/terrestris	19	23	77	11	77	5	212
B. muscorum	0	1	5	0	14	0	20
B. pascuorum	4	0	31	8	42	1	86
B. pratorum	0	0	2	1	16	0	19
B. ruderarius	3	5	69	41	54	12	184
B soroeensis	1	0	0	0	0	0	1
B. subterraneus	0	1	3	1	19	4	28
B. sylvarum	6	14	13	4	17	6	60
Total	94	93	493	205	543	132	1560
Number of species	8	7	10	8	10	7	11
Total area surveyed (m^2)	27,950	16,950	32,700	18,000	31,750	18,150	

in adjacent simplified landscapes. If proper conservation measures are taken to ensure adequate flower resources there is indeed a potential to reverse the trend of bumblebee losses on farmland, also in simplified landscapes. Our results further highlight the urgent need for recreation of flower rich-habitats in intensively farmed landscapes, particularly to ensure abundant mid and late summer flora of preferred food plants, e.g. perennials.

Acknowledgements

We are grateful for field assistance by H. Hansson, Y. Hanell, G. Andersson, C. Hillerdal, C. Rönnås and J. Jönsson. Two anonymous referees provided valuable comments on a previous version of this manuscript. The project was funded by a grant from Formas to H.G.S.

Appendix.

See Tables A.1 and A.2 .

Table A.2
List of surveyed plant species considered important pollen and/or nectar resources.

Asteraceae
Achillea ptarmica
Carduus spp.
Centarurea scabiosa
Centaurea cyanea
Centaurea jacea
Chamomilla spp.
Chicorium intybus
Cirsium spp.
Crepis spp.
Eupatorium cannabinum
Helichrysum arenarium
Leontodon autumnalis
Leucanthemum vulgare
Matricaria perforata
Senecio vulgaris
Sonchus spp.
Taraxacum spp.
Tragopogon pratensis
Balsaminaceae
Impatiens spp.
Boraginaceae
Anchusa arvensis
Anchusa officinalis
Echuim vulgare
Symphytum spp.
Brassicaceae
Barbarea vulgaris
Bunias orientalis
Cardamine pratensis
Sinapis spp
Campanulaceae
Campanula spp.
Jasione montana
Caryophyllaceae
Lychnis flos-cuculi
Silene latifolia
Silene vulgaris
Clusiaceae
Hypericum spp.
Convolvulaceae
Calystegia sepium
Convolvulus arvensis
Crassulaceae
Sedum spp.
Dipsaceaea
Knautia arvensis
Fabaceae
Anthyllis vulneraria
Lathyrus linifolius
Lathyrus pratensis
Lotus corniculatus
Medicago spp.
Melilotus spp.
Ononis campestris
Ononis repens
Trifolim hybridum
Trifolium pratense
Trifolium repens
Vicia cracca
Vicia hirsuta
Lamiaceae
Galeopsis spp.
Lamium spp.
Prunella vulgaris
Stachys spp.
Onagraceae
Epilobium spp.
Papaveraceae
Papaver spp.
Plumbaginaceae
Armeria maritima
Primulaceae
Lysimachia spp.
Ranunculaceae
Aquilegia vulgaris
Ranunculus spp.
Trollius europaeus
Rosaceae
Filipendula ulmaria
Fragaria spp.
Geum spp.
Potentilla spp.
Rosa spp.
Rubus spp.
Scrophulariaceae
Linaria vulgaris
Rhinanthus spp.
Violaceae
Viola arvensis

References

Alaux, C., Ducloz, F., Crauser, D., Le Conte, Y., 2010. Diet effects on honeybee immuno competence. Biol. Lett. 6, 562–565.

Bäckman, J.P., Tiainen, J., 2002. Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera: *Bombus* and *Psithyris*). Agric. Ecosyst. Environ. 89, 53–68.

Benton, T., 2006. Bumblebees. Harper Collins, London.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? TREE 18, 182–188.

Cederberg, B., Pettersson, M.W., Nilsson, L.A., 2006. Slutrapport Svenska Vildbiprojektet 2002–2005, Restaurering av en ekologisk nyckelresurs. ArtDatabanken. Swedish University of Agricultural Sciences, Uppsala, Sweden.

Fussell, M., Corbet, S.A., 1992. Flower usage by bumble-bees: a basis for forage plant management. J. Appl. Ecol. 29, 451–465.

Goulson, D., Lepais, O., O‘Connor, S., Osborne, J.L., Sanderson, A., Cussans, J., Goffe, L., Darvill, B., 2010. Effects of land use at a landscape scale on bumblebee nest density and survival. J. Appl. Ecol. 47, 1207–1215.

Goulson, D., Lye, G.C., Darvill, B., 2008. Decline and conservation of bumble bees. Annu. Rev. Entomol. 53, 191–208.

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.

Herrmann, F., Westphal, C., Moritz, R.F., Steffan-Dewenter, I., 2007. Genetic diversity and mass resources promote colony size and forager densities of a social bee (*Bombus pascuorum*) in agricultural landscapes. Mol. Ecol. 16, 1167–1178.

Holmström, G., 2002. Skånska humlor. Fazett 15, 25–33.

Holmström, G., 2007. Humlor – Alla Sveriges arter, så känner du igen dem i naturen och i trädgården. Symposion, Stockholm, Sweden.

Ihse, M., 1995. Swedish agricultural landscapes — patterns and changes during the last 50 years, studied by aerial photos. Landsc. Urban Plann. 31, 21–37.

Ings, T.C., Ward, N.L., Chittka, L., 2006. Can commercially imported bumble bees out-compete their native conspecifics? J. Appl. Ecol. 43, 940–948.

Kells, A.R., Holland, J.M., Goulson, D., 2001. The value of uncropped field margins for foraging bumblebees. J. Insect Conserv. 5, 283–291.

Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. Proc. Biol. Sci. 274, 303–313.

Knight, M., Osborne, J., Sanderson, R., Hale, R., Martin, A., Goulson, D., 2009. Bumblebee nest density and the scale of available forage in arable landscapes. Insect Conserv. Divers. 2, 116–124.

Le Féon, V., Schermann-Legionnet, A., Delettre, Y., Aviron, S., Billeter, R., Hendrickx, F., Burel, F., 2010. Intensification of agriculture, landscape composition and wild bee communities: a large scale study in four European countries. Agric. Ecosyst. Environ. 137, 143–150.

Lepais, O., Darvill, B., O'Connor, S., Osborne, J.L., Sanderson, R.A., Cussans, J., Goffe, L., Goulson, D., 2010. Estimation of bumblebee queen dispersal distances using sibship reconstruction method. Mol. Ecol. 19, 819–831.

Ma, M., 2008. Multi-scale responses of plant species diversity in semi-natural buffer strips to agricultural landscapes. Appl. Veg. Sci. 11, 269–278.

Mänd, M., Mänd, R., Williams, I.H., 2002. Bumblebees in the agricultural landscape of Estonia. Agric. Ecosys. Environ. 89, 69–76.

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.

Mossberg, B., Stenberg, L., Ericsson, S., 1992. Den Nordiska Floran. Wahlström & Widstrand, Stockholm, Sweden.

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

Persson, A., 2011. Effects of landscape context on populations of bumblebees. Ph.D. Thesis. Lund University, Sweden.

Persson, A.S., Olsson, O., Rundlöf, M., Smith, H.G., 2010. Land use intensity and landscape complexity-analysis of landscape characteristics in an agricultural region in Southern Sweden. Agric. Ecosyst. Environ. 136, 169–176.

Pollard, E., 1977. A method for assessing changes in butterfly abundance. Biol. Conserv. 12, 115–134.

Potts, S.G., Woodcock, B.A., Roberts, S.P.M., Tscheulin, T., Pilgrim, E.S., Brown, V.K., Tallowin, J.R., 2009. Enhancing pollinator biodiversity in intensive grasslands. J. Appl. Ecol. 46, 369–379.

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.

Prŷs-Jones, O.E., Corbet, S.A., 1987. Naturalist's Handbooks 6. Bumblebees. Cambridge University Press, Cambridge, UK.

Pywell, R., Warman, E., Hulmes, L., Hulmes, S., Nuttall, R., Sparks, T., Critchley, C., Sherwood, A., 2006. Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. Biol. Conserv. 129, 192–206.

Pywell, R., Meek, W.R., Hulmes, L., Hulmes, S., James, K.L., Nowakowski, M., Carvell, C., 2011. Management to enhance pollen and nectar resources for bumblebees and butterflies within intensively farmed landscapes. J. Insect Conserv. 15, 853–864.

Rader, R., Howlett, B.G., Cunningham, S.A., Westcott, D.A., Newstrom-Lloyd, L.E., Walker, M.K., Teulon, D.A., Edwards, W., 2009. Alternative pollinator taxa are equally efficient but not as effective as the honeybee in a mass flowering crop. J. Appl. Ecol. 46, 1080–1087.

Rundlöf, M., Edlund, M., Smith, H.G., 2010. Organic farming at local and landscape scales benefits plant diversity. Ecography 33, 514–522.

Rundlöf, M., Nilsson, H., Smith, H.G., 2008. Interacting effects of farming practice and landscape context on bumblebees. Biol. Conserv. 141, 417–426.

Samnegård, U., Pesson, A.S., Smith, H.G., 2011. Gardens benefit bees and enhance pollination in intensively managed farmland. Biol. Conserv. 11, 2602–2606.

SCB, 2007. Yearbook of Agricultural Statistics 2007 Including Food Statistics. Official statistics of Sweden, Statistics Sweden (SCB).

Schmid-Hempel, R., Schmid-Hempel, P., 1998. Colony performance and immunocompetence of a social insect, *Bombus terrestris*, in poor and variable environments. Funct. Ecol. 12, 22–30.

Smart, S.M., Marrs, R.H., Le Duc, M.G., Thompson, K., Bunce, R.G.H., Firbank, L.G., Rossall, M.J., 2006. Spatial relationships between intensive land cover and residual plant species diversity in temperate farmed landscapes. J. Appl. Ecol. 43, 1128–1137.

Stoate, C., Boatman, N.D., Borralho, R.J., Carvalho, C.R., Snoo, G.R., Eden, P., 2001. Ecological impacts of arable intensification in Europe. J. Environ. Manage. 63, 337–365.

Svensson, B., 2002. Foraging and nesting ecology of bumblebees (*Bombus* spp.) in agricultural landscapes in Sweden. Ph.D. Thesis. Swedish University of Agricultural Sciences, Uppsala, Sweden.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecol. Lett. 8, 857–874.

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2006a. Bumblebees experience landscapes at different spatial scales: possible implications for coexistence. Oecologia (Berlin) 149, 289–300.

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2006b. Foraging trip duration of bumblebees in relation to landscape-wide resource availability. Ecol. Entomol. 31, 389–394.

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2009. Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. J. Appl. Ecol. 46, 187–193.

Williams, N.M., Kremen, C., 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. Ecol. Appl. 17, 910–921.

Williams, P.H., Osborne, J., 2009. Bumblebee vulnerability and conservation worldwide. Apidologie 40, 367–387.

Williams, N.M., Regetz, J., Kremen, C., 2012. Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. Ecology 93, 1049–1058.

Winfree, R., 2010. The conservation and restoration of wild bees. Ann. N.Y. Acad. Sci. 1195, 169–197.

Winfree, R., Williams, N.M., Gaines, H., Ascher, J.S., Kremen, C., 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. J. Appl. Ecol. 45, 793–802.