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EFFECTS OF LANDSCAPE CONTEXT ON POPULATIONS OF BUMBLEBEES

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ANIMAL ECOLOGY DEPARTMENT OF BIOLOGY LUND UNIVERSITY 2011

Effects of Landscape Context on Populations of Bumblebees

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Doctoral Thesis
Effects of Landscape Context on Populations of Bumblebees

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The thesis is based on the following papers, referred to by their roman numerals:

I Persson, A. S., Olsson, O., Rundlöf, M. and Smith, H. G. (2010). **Land use intensity and landscape complexity - Analysis of landscape characteristics in an agricultural region in Southern Sweden.** Agriculture Ecosystems & Environment, 136, 169-176. 45

II Persson, A.S. and Smith, H.G. **Seasonal persistence of bumblebee populations is affected by landscape context.** Manuscript. 57

III Persson, A.S, Rundlöf, M. and Smith, H.G. **Bumblebees show trait-dependent tolerance to structural simplification of agricultural landscapes.** Manuscript. 77

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Effects of landscape context on populations of bumblebees

1. INTRODUCTION

Why is it interesting and important to study populations of wild bees? Why study them in regions dominated by agriculture rather than in more "natural" habitats? And what is the usefulness of applying a landscape ecological approach? I will try to answer these questions here, by drawing from the experience and the knowledge I have gained from my PhD studies and the chapters enclosed in this thesis.

1.1 Background

It is widely recognised that pollinating insects have declined since the early 20th century, especially in regions with intensive agriculture. Recent studies have highlighted dramatic declines of bumblebees from areas where natural and semi-natural habitats have been lost and fragmented as a consequence of agricultural practices. Since pollination is essential for plant reproduction and bumblebees are an important group of pollinators, this has gained attention both in scientific and popular media. However, results from studies of bumblebees in farmland regions differ and a few species are actually still common. To be able to suggest measures to reverse the negative trends of bumblebees, as well as other pollinators and plants, we therefore need to know more about how biodiversity respond to past and present changes in land-use and landscape structure. It is within this scenario that I have studied bumblebees, *Bombus spp.*, in a region in southernmost Sweden which is dominated by agriculture.

1.2 Agriculture and landscape transformations

In Scandinavia human populations began using agriculture to sustain themselves around 4000 BC. Skåne, or Scania, the focal region for this thesis, has thus been shaped by human activities connected to animal husbandry and crop production for a period of ca. 6000 years (Emanuelsson 1985). Up until the Middle Ages, farming in much remained of very low intensity, with low inputs of manure, low harvests and with large portions of broad-leaved forest in between small fields. From the Middle Ages much of the forest was however cleared and grazing, fodder production, grains and vegetables for human consumption dominated land-use in southern and western Skåne, where the soils are more fertile than further to the northeast. However, the landscape was small-grained, with large variations in land-use and land cover. Regarding landscape types and biodiversity, the agricultural landscapes of the 17th and 18th centuries are believed to have been the most diverse that have existed historically in this region (Berglund 1991, p 94).

From the mid 18th century however, farming was no longer only for self-sustenance, and large-scale improvements of the land began in order to increase productivity. This led to pronounced changes to the landscape. Fields were enlarged, new rotational schemes were introduced and the proportion of land under fallow decreased. A major transition occurred around 1850, when large-scale draining allowed for cultivation of land which was previously too wet or otherwise difficult to use (Emanuelsson 1985). At the same time, artificial fertilisers were introduced and relieved the dependence on manure, which allowed further expansion of crop fields on behalf of pastures and meadows (Emanuelsson 1985). New crops such as wheat, potatoes and sugar beet were introduced and legumes e.g. red clover (*Trifolium pratense*) became important both for fodder and for soil improving qualities via nitrogen fixation (Berglund 1991, p 98).

Modernisation and intensification of agriculture have accelerated further during the last 70 years. In post-war Europe and with the birth of the European Union (EU), agricultural policy became a common European concern. In the 1950's the focus of policies was to ensure food security for its citizens and profitability for farmers within the EU. Via subsidy systems based on production, intensification was encouraged (European Commision 2011). This resulted in that also small non-crop habitats were removed, larger amounts of nutrients and pesticides were used and farm specialisation on either a few crops or animal production increased. As a result, species rich farmland habitats (hay meadows and unimproved pastures) as well as non-crop refuges for wildlife was lost to a large degree (Ihse 1995;Stoate et al. 2001). Contemporary agricultural landscapes are thus void of most of their historical complexity regarding habitat types and management practices (Benton, Vickery & Wilson 2003;Tscharntke et al. 2005).

In the light of over-production of agricultural produce and abandonment of marginal areas during the 1980's, it was agreed that the Common Agricultural Policy (CAP) should shift focus away from promoting production only. Since the reform in 1999 the aim of the CAP is now, among other things, to encourage continued farming and make agriculture possible also in less favoured rural areas of the union, as well as to ensure "environmentally sound farming" (European Commision 2011). However, a landscape wide loss of biodiversity from farmlands has already been manifested over much of Europe, presumably resulting from landscape simplifications over several spatial scales (Benton, Vickery & Wilson 2003;Tscharntke et al. 2005;Wretenberg et al. 2007). Exceptions to this occur in so called marginal regions, where climate, topography and soil quality makes conventional farming unprofitable (Gabriel et al. 2009;Stoate et al. 2009).

1.3 Loss of biodiversity in agricultural landscapes

In a global perspective, roughly half of all land (not classified as desert, rock or permafrost) is used by humans for either crop production or as rangelands for cattle (Millennium Ecosystem Assessment 2005). Agricultural practices and management strategies thus directly influence a large part of the earth's surface. In addition, there are indirect influences since farming activities, fields and pastures are not isolated but indeed connected to other habitats (Swinton et al. 2007), e.g. via waterways and winds as well as through dispersal and *landscape complementation* of organisms (Dunning, Danielson & Pulliam 1992), (see section 1.5 below).


Bombus pascuorum
foto M. Rundlöf


Bombus hypnoruom


Bombus terrestris


Bombus pratorum


Bombus subterraneus


Bombus humilis


Bombus ruderarius
foto M. Rundlöf


B. terrestris nest


B. terretris pupae

From a biodiversity perspective, one consequence of agricultural intensification is loss, fragmentation and decreased quality of natural and semi-natural habitats situated within an agricultural matrix (Vandermeer & Perfecto 2007). Since World War II several groups of organisms inhabiting or connected to the agricultural landscape have indeed declined dramatically (reviewed by Krebs et al. 1999;Stoate et al. 2001). It has been suggested that both the loss of habitat and loss of spatial and temporal habitat heterogeneity is the general cause of this decline of biodiversity (Benton, Vickery & Wilson 2003;Shrubb 2003;Tscharntke et al. 2005). Also land-use intensity *per se* has been related to declining biodiversity (Kleijn et al. 2009), as the quality of fields for non-crop organisms decrease e.g. when the use of agro-chemicals increase.

1.4 Loss of ecosystem services in agricultural landscapes

Organisms interact with their surroundings and are part of processes that shape the environment in which they, and we, exist. In some cases these processes are clearly beneficial for human wellbeing and are then called *ecosystem services*, *ES* (Millennium Ecosystem Assessment 2005). Such processes can for example be water retention, nutrient uptake and CO_2-sequestration by plants as well as natural pest control and improvement of soil properties by soil organisms. Lately, widespread declines of pollinators in regions dominated by agriculture have received increased attention because of the risk posed to the ES of pollination (Kremen & Ricketts 2000;Kremen, Williams & Thorp 2002;Potts et al. 2010;Ricketts et al. 2008;Steffan-Dewenter & Westphal 2008). Around 35% of the world production of crops, fruits and vegetables are indeed dependent on animal pollinators for proper fruit and seed set (Klein et al. 2007). Furthermore, in fragmented landscapes a major threat to wild plant reproduction is in fact pollination failure. This can be caused either by lack of mates or of pollinators (Wilcock & Neiland 2002) and large-scale losses of pollinators have also been paralleled by losses of out-crossing plant species (Biesmeijer et al. 2006;Gabriel & Tscharntke 2007).

Although managed honey bees, *Apis mellifera*, carry out a substantial part of crop pollination (Klein et al. 2007), the service offered by a diverse assembly of wild pollinators have several advantages. Honey bees are domesticated and, although sometimes feral, they mostly occur where beekeepers chose to place them, i.e. their services do not necessarily cover all areas. It is also highly risky to depend on only one species for pollination, as was highlighted in the wake of the Colony Collapse Disorder which whipped out a large part of North American honey bee colonies (Stokstad 2007). It has also been shown that if many different pollinator species visit a flower, this can lead to higher seed and fruit-set (Greenleaf & Kremen 2006;Klein, Steffan-Dewenter & Tscharntke 2003). Furthermore, the pollinator community is highly variable between years, due to yearly differences in e.g. weather, land management, parasites and deceases. A diverse pollinator community buffers these variations and increases the chance of successful pollination even if some species are low in abundance during a particular year (Kremen, Williams & Thorp 2002).

In the light of this, it is interesting that responses of bumblebees to landscape changes imposed by agriculture differ between species. Many species have declined, but some remain common even in very simplified regions (Goulson, Lye & Darvill 2008;Williams 1982;Williams, Colla & Xie 2009). Also, groups differ in their response to farming of mass flowering crops (MFCs) (Diekötter et al. 2010;Goulson et al. 2010;Herrmann et al. 2007;Knight et al. 2009;Westphal, Steffan-Dewenter & Tscharntke 2009) and in the spatial scale at which populations and colonies respond to resource rich habitats (Goulson et al. 2010;Hines & Hendrix 2009;Westphal, Steffan-Dewenter & Tscharntke 2006). These differences may reflect both species-specific responses and specific qualities of the studied landscapes. Such variability of responses, together with the great importance of bumblebees as pollinators of crops and wild plants throughout much of the world (e.g. Cederberg, Pettersson & Nilsson 2006;Goulson 2003;Winfree et al. 2008), calls for continued research on the mechanisms underlying their responses to past and present landscape changes.

1.5 Useful theories and models

Bumblebees are social insects, constructing colonies of worker bees (in most cases all full sisters (Schmid-Hempel & Schmid-Hempel 2000) around one reproducing queen (Goulson 2003). The existence of a nest makes bumblebees *central place foragers*; their fitness being dependent on the distance between the nest and the flower resources necessary for survival and reproduction (Goulson 2003). During the life cycle of a bumblebee queen, she is also dependent on having within reach: a mate, a good hibernation site and, in spring, a good nest site close to plentiful nectar and pollen resources. This *habitat* or *landscape complementation* (Dunning, Danielson & Pulliam 1992) clearly restricts the areas where bumblebees can persist.

Natural and semi-natural habitats within landscapes converted for agriculture predominantly consist of a patchwork of habitat fragments within a matrix of production systems (Vandermeer & Perfecto 2007). A large part of biodiversity of these landscapes also resides in such fragments (Tscharntke et al. 2002). Populations inhabiting agricultural landscapes may therefore consist of sub-populations, connected via dispersal of individuals between fragments. This is called a *meta-population* (Hanski 1999). Both the number of fragments and sub-populations in the system and the degree of dispersal between them affects the likelihood of persistence of the greater population. A special case of meta-population is *source-sink population dynamics* (Dias 1996;Pulliam 1988). This occurs when one habitat fragment is qualitatively superior to another one. The sub-population in a high quality fragment produces a surplus of offspring, which disperse to habitat fragments with a reproductive deficiency and thus keep up population numbers there despite a poor environment.

The tolerance and adaptability of a species to changes in the surrounding habitat, depend on its *morphological*, *ecological* and *life history traits*. Traits connected to e.g. reproductive strategy, physiology, phenology, foraging preferences, climatic tolerance and resistance to deceases affect the ability to produce offspring. However, combinations of certain habitats and traits may be more or less successful and lead to either persistence or to decrease and extinction of populations, and eventually also of species (Bommarco et al. 2010;Öckinger et al. 2010;Williams et al. 2010).

The mechanisms behind sustenance of organisms in simplified landscapes presumably act via *habitat preferences* and *habitat selection*. Also the ability to reach and efficiently exploit preferred habitats is crucial. The combination of habitat selection and landscape effects on separate trait groups may therefore inform us about the mechanisms behind population decreases, as well as possible measures to mitigate these.

1.6 Conservation biology and conservation action

The goal of *conservation biology* is to provide a basis for management of disrupted ecosystems in the light of an exploding human population (Groom, Meffe & Carroll 2006, p 7). We therefore study rare and declining organisms and habitats, in order to gain knowledge of the reasons for and effects of their declines. It is however crucial to also turn this knowledge into conservation action and practise (Goulson et al. 2011;Sutherland 2002). Not the least to justify the money spent on research. The dependency of agricultural production on ecosystems services originating in non-crop habitats (Klein et al. 2007;Millennium Ecosystem Assessment 2005), as well as the large nutritional and economical value of this production (Klein et al. 2007;Swinton et al. 2007), further justifies large-scale conservation actions to retain these services within farmland landscapes (Sutherland 2002).

1.7 The landscape perspective

Landscape ecology is “the study of how landscape structure affects the abundance and distribution of organisms” (Fahrig 2005). I have applied the theories and models presented above in spatially explicit systems, where landscapes were selected based on criteria of structure and management. By applying experimental landscape designs where we selected study sites based on *a priori* hypothesis about how landscapes affect foraging and reproduction of wild bees, we were able to combine population dynamic theory and models with a landscape ecological approach. We thus used the region of Skåne as a “lab”, letting landscape structure or management practice be the “treatments” under study. Traditionally, ecologists and conservationists have focused on the local habitat and its’ quality and on interactions between organisms within local populations or communities. However, as meta-population, source-sink and meta-community theory (e.g. Leibold et al. 2004) implies, processes at larger spatial scales also affect population and community dynamics. To my knowledge, there have been no previous studies exploring the spatial and temporal dynamics of both resources and bumblebee communities in regions composed of differently structured agricultural landscapes.

In 2000 the Council of Europe (COE) launched the European Landscape Convention. This convention urges member states to adopt a landscape perspective on planning, management and conservation of our natural and cultural heritage. The convention recognises that landscapes surrounding us are important for several aspect of our wellbeing and encourages authorities to develop policies to maintain and improve landscape quality (Jones-Walters 2008). In the light of this it becomes important to understand what landscape quality is and how to maintain and improve it.

2. AIMS OF THE STUDIES

If we are to turn the negative trends of pollinators in agricultural regions, the study and understanding of how wild bees are affected by present day landscape changes are perhaps crucial. In order to suggest ways to mitigate pollinator losses there is a need to know not only how, but also why, groups of pollinators respond differently to landscape changes. In short, to ordinate a cure one needs to know both the illness and the peculiarities of one's patient. The overall aim of this project was to reveal mechanisms behind recent losses of wild bees in regions highly modified by agriculture, via a landscape perspective on habitat selection and population dynamics of bumblebees. The aims of the individual chapters were:

Chapter I To investigate if it is possible to distinguish measures of agricultural intensity from measures of landscape complexity and if so, which proxies might be used to represent them. Furthermore, to investigate if the interrelationship between measures of complexity and intensity are dependent on the spatial scale at which the analysis is performed.

Chapter II To study seasonal effects of landscape context on populations of bumblebees and their resource flowers. To this end we performed surveys in two landscape types: Complex, with mixed farming and high proportion permanent grasslands and simple, with mainly crop production and practically lacking permanent grasslands. Also, oilseed rape (*Brassica napus*) was grown in different proportions within the studied landscapes.

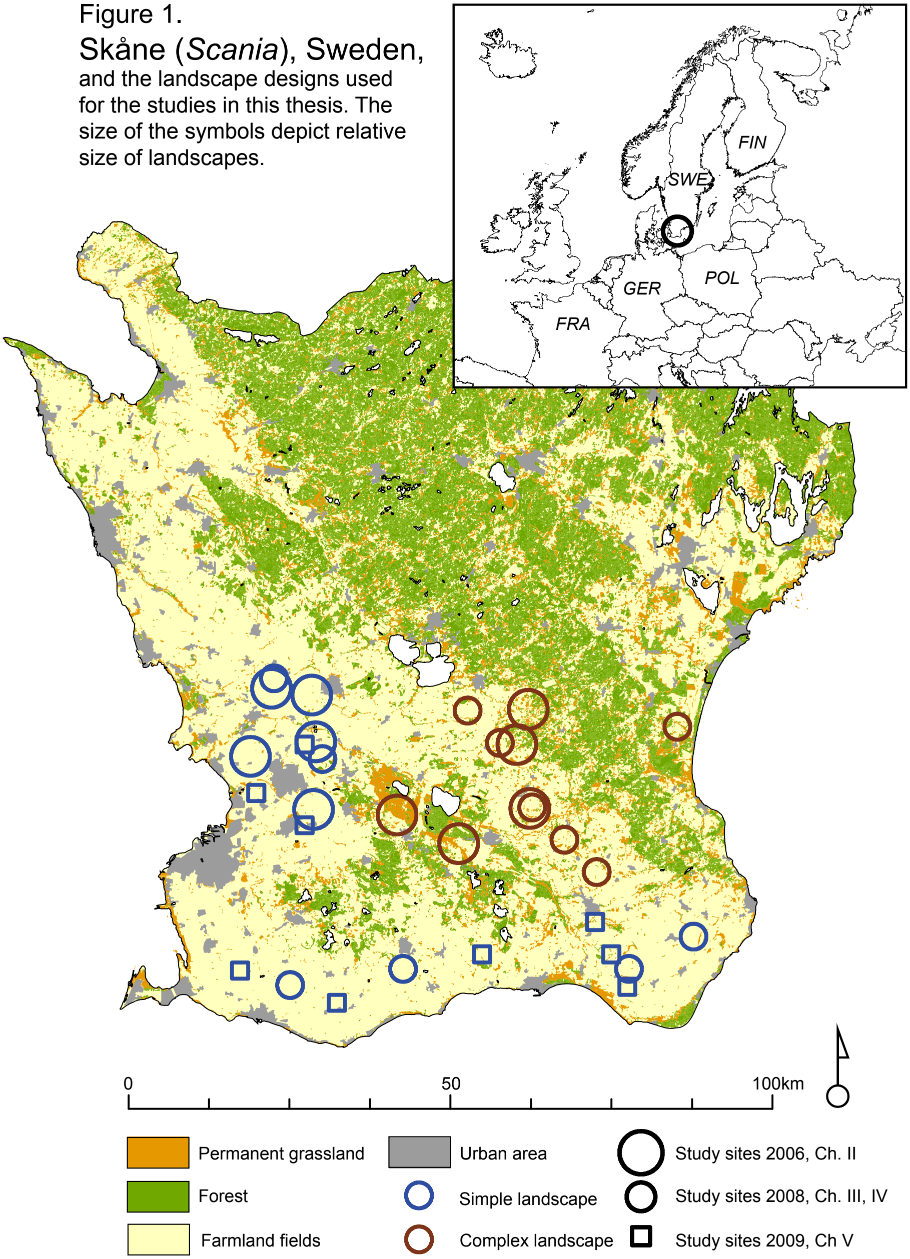
Chapter III To study if ecological, morphological and life-history traits affect bumblebees' tolerance to loss of landscape complexity and their choice of foraging habitat. We analysed effects of thorax width, proboscis length, colony size, nesting habitat, queen emergence date and length of the colony reproductive cycle in simple and complex landscapes.

Chapter IV To investigate if the amount and distribution of non-crop habitats (i.e. a component of landscape complexity) affect the mean size of bumblebee workers. We performed our study in simple and complex landscapes that differed in the mean size of agricultural fields as well as in correlated land-use variables.

Chapter V To investigate if domestic gardens can act as sources of pollinators, and

Figure 1.

Skåne (*Scania*), Sweden, and the landscape designs used for the studies in this thesis. The size of the symbols depict relative size of landscapes.



subsequently benefit pollination and seed set of wild out-crossing plants, in landscapes highly dominated by agriculture.

3. METHODS

3.1 Study region

All studies were carried out in Sweden's southernmost province Skåne (figure 1). This province boasts some of Europe's most fertile soils in particular to the southwest (Emanuelsson 1985), and this region is consequently highly dominated by agriculture, mainly crop production on large fields. In the central, eastern and north eastern parts we find a more mixed farmland landscape with smaller crops fields interspersed with leys and pastures for horses, milk and beef production. In the northern and eastern parts we also increasingly find small forests and woodlots.

3.2 Study organisms

Bumblebees are wasps of the genus Apoidea, family *Bombus*. 29 species of social bumblebees are native to Sweden (see photos, p 9). To date two of those are considered regionally extinct, two are severely threatened and two nearly so (ArtdataBanken 2010). Just as their close relative the honeybee (*Apis mellifera*) they are social insects, constructing colonies around one reproducing queen. However, bumblebee colonies are annual. The following description of the bumblebee and its life cycle is based on Goulson (2003) and Benton (2006).

The colony cycle starts in spring (March-May) when queens wake from hibernation, search for a nest site, start to forage and hopefully lay eggs. The queen provisions and cares for the first generation of ca. 10 to 20 worker bees herself, and proximity to abundant pollen (protein) and nectar (carbohydrates) is essential for a successful nest establishment. When the first workers emerge and start to forage, the queen remains in the nest, continues to lay eggs and governs worker behaviour. Some time in early to late summer the food influx to the colony is high enough to enable production of new sexual offspring; males and daughter queens. The number of sexuals produced varies a lot, both between species, habitats and climatic regions. Social wasps have haplo-diploid sex determination. Males develop from unfertilized eggs and are thus haploid, while females derive from fertilized eggs and are diploid. The queen is larger than workers, and is the only bee in the colony that has mated. Worker bees can thus potentially lay unfertilised, haploid (male) eggs. Studies indicate that queens of most bumblebee species mate only once (Schmid-Hempel & Schmid-Hempel 2000), so in most cases all daughters (i.e. workers and new queens) are full sisters with a mean relatedness of 75%. Furthermore, the colony is the reproductive unit, which drastically reduces the effective population size in comparison to census counts of worker bees. After queen production has taken place the colony degenerates and dies. Because of phenological differences between species there are still active colonies in the beginning of September. Before autumn the new queens and males mate. Males die as autumn progresses, while queens forage to build up an energy reserve, search for a hibernation site and over-winter there. Hopefully the site was of good quality and her energy reserves enough to enable her to wake up and start a new colony the following spring.

Bees feed exclusively on flower resources; i.e. mainly pollen and nectar but the degree of specialisation towards forage plants varies. Bumblebees are (with some exceptions) oligo- or polylectic.

3.3 Experimental design and landscape selection

In all studies I have used information from the Integrated Administration and Control System (IACS, Swedish Board of Agriculture) to select individual landscapes and sites for surveys and experiments. IACS is 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.). In IACS, fields are reported in units of "blocks", which typically consist of one or several adjacent fields surrounded by a border that can be identified on an aerial photograph. The area covered by individual crops within each block is also known. We have defined farmland as all blocks of fields in the database with annual crops, leys, pastures or fallow. In some studies, block data was also used to estimate the amount of non-crop field borders via block shape.

For the study of landscape complexity and land-use intensity (Ch. I) I extracted IACS data for 156 plots using GIS (ArcMap 9.1, ESRI). I also used other sources of information regarding land cover and habitat types. Detailed habitat data (including information on small parcels of non-crop habitats e.g. stonewalls and ditches) was collected during field surveys 1995 to 2002 (Svensson 2001). By studying aerial photographs (black and white ortho-photos from the Swedish Land Survey, Lantmäteriet) of each inventory plot, semi-natural habitats such as stone walls, ditches, small wood lots and single trees, field islands, permanent pastures and grasslands could be identified or verified and digitised. From the satellite data of the EU programme CORINE (Coordination of Information on the Environment, 25 × 25m resolution), data on forests, wetlands, water bodies and built up areas for the concerned areas was extracted and used to complement information from the above mentioned sources. We also used data from Statistics Sweden (SCB) on normalised harvest of spring-sown barley in 2006. For each plot, data was compiled for two spatial scales: 1 × 1km and 5 × 5km.

In Chapter II we selected landscapes (radius 3km) of two classes, simple with large fields and without permanent pasture, versus complex with smaller fields and a large proportion of pasture (n=5+5), figure 1, photos p 17. We surveyed bumblebees and flowers in randomly selected transects of three common farmland habitats and their non-crop borders. In Chapters III and IV, landscape classes were composed of landscapes (radius 2km) of either large or small fields, but all with low proportions of pasture (n=6+6), figure 1. However, in connection to small fields the amount of ley was higher and there was also slightly more pasture and forest. We aimed at collecting a large data set of as many bumblebee species as possible and therefore surveyed only flower-rich non-crop

simple and intensively farmed landscape

cut road verge

complex landscape with permanent pastures

flower-rich field border

flowering oilseed rape *Brassica napus*

Trifolium pratense in ley border

habitats and domestic gardens. In Chapter V, we only used simple landscapes (2.5 × 2.5km, n=8) dominated by annual crops, with large fields and practically lacking permanent pasture. Within an individual landscape two isolated domestic gardens were identified and inspected to ensure reasonable similarity with respect to features beneficial to pollinators (Osborne et al. 2008;Smith et al. 2006). One of the gardens in each pair was used for pollinator surveys and the other for assessing seed set of potted plants.

3.4 Wild bee surveys

In 2006, (Ch. II), bumblebees (*Bombus spp.*) were recorded during transect walks adopted from the standard line transects method developed for butterfly surveys (Pollard 1977;Rundlöf, Nilsson & Smith 2008). We counted bumblebees (workers, males and queens) seen within a 1m by 200m zone on each side of transects, i.e. one zone lying within the crops/leys/pastures and the other side being the non-crop border habitat. We surveyed bumblebees on days with predominantly clear skies, temperatures above 15°C and no strong winds. 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 & Corbet (1987) and Holmström (2002). In case of uncertainty, the bumblebee was noted as the most common species. The species of the visited flower was also noted. Because of the difficulty of separating *B. lucorum* and *B. terrestris* in the field (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. Transects were sampled three times from 9 June to 27 July.

In 2008 (Ch. III, IV), all bumblebees found during a 10min survey of each of sixteen100m^2 flower-rich sites (including domestic gardens) per landscape, were collected by hand netting and preserved in 70% ethanol, (photo p 19). Sites were sampled 3 times over a period from 25 June to 31 August 2008, on days with predominantly clear skies, temperatures above 15°C and no strong winds. We also placed four sets of three pan-traps in each landscape sector. Pan-traps were 6 cm deep, Ø15 cm plastic cups, sprayed with yellow, blue and white fluorescent colours and containing 50% propylene glycol (photo p 19). Pan-traps were emptied in connection to each survey, i.e. three times per landscape. We avoided collecting queens in order not minimize effects on population numbers. Bumblebees were determined to species and caste in the lab following Löken (1973), Prŷs-Jones & Corbet (1987) and Holmström (2007) and we also separated between *B. lucorum* and *B. terrestris*. The thorax width of each individual was measured using digital callipers.

In 2009 we used only pan-traps to collect insects. The traps consisted of a set of three plastic cups as described above. They were placed on the ground in road verges at two different distances from domestic gardens, either within 15 meters from the edge of a garden or approximately 140m away. Insects caught in traps were collected and stored in 70% ethanol and all bees were later determined to species in the lab.

3.5 Flower and habitat surveys

In 2006 (Ch. II) we specifically wanted to quantify both bumblebees and flower resources from non-crop border habitats, and we therefore carried out a separate survey of non-crop landscape elements and flowering plants during the bumblebee survey. We noted length and width of all border habitats in twelve 500×500m squares per individual landscape. In the same squares, an inventory of flowering plant species was carried out at the start of the study. Two 0.25m^2-plots of each of five habitat-types (pasture, leys, crop field, road verge, crop border zone) were randomly selected from maps of the squares. Together, this data was used to estimate total numbers of bumblebees and flowers. To make flower resources more comparable between plant species and also easier to count, they were noted in units based number of flower heads or equivalents. For *Asteraceae* and *Dipsaceae* the number of flower heads was counted, for *Fabaceae* the numbers of racemes, and for *Campanulaceae*, *Lamiaceae* and *Scrophulariaceae* flower stalks.

In 2008 (Ch. III, IV) all plants flowering in transects were noted and the number of flower units estimated in conjunction with the bumblebee survey.

3.6 Seed set of bellflower

In order to evaluate potential positive effects of gardens on pollination in simple landscapes, we assessed seed set of peach-leaved bellflower, *Campanula persicifolia*, (see photo this page). This species is a wild and self-incompatible flower native to Sweden (Nyman 1992). Plants


hand-netting in field border
Photo M. Lind


pan-traps in ruderal patch
Photo A. Jönsson


seed set experiment with *C. persicifolia*, photo U.Samnegård

were purchased from a local garden centre at the beginning of May 2009 and replanted in 7.5l pots. We placed two sets of two plants each, along road verges reaching out from the gardens; one set within 15 m from the garden and the other set ca. 140 m away. We did not use the same garden for both plants and traps because of the risk of pollinator depletion due to the traps. Plants and traps were kept in the field during three weeks, from end of June until mid July, and were visited and watered twice a week. To be able to determine date of flowering, we marked all flowers that had started to bloom since the last visit with coloured thread and used one colour for each visit.

All capsules (n=233) from *C. persicifolia* marked in the field, except those marked at the last visit, were harvested between 30 July and 20 August when ripe. Seeds were weighed and we used the weight as a proxy for seed set. In two landscapes plants had all flowers and capsules eaten by slugs, resulting in six complete pairs of plants and one with only distant plants.

3.7 Statistical methods

For the landscape study (Ch. I), the variation of the selected variables was analysed using Factor Analysis in R 2.8.1 (R Development Core Team, 2008) with the procedures factanal and cor in package stats, and gls in package nlme. Factor analysis has the advantage of letting us combine variables into a set of factors, which are more or less independent depending on the rotation method used. Factors are interpreted through the loadings (correlations) they have of the

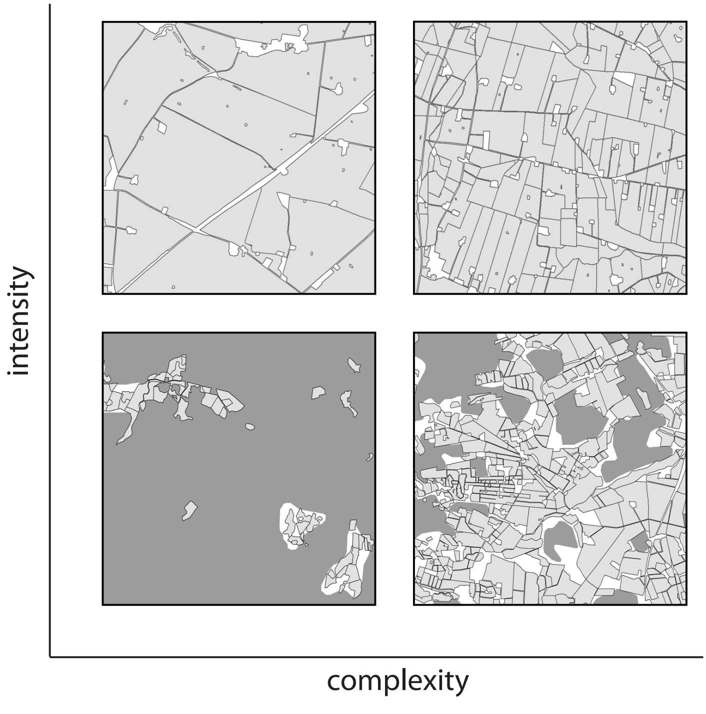


Figure 2: A conceptual graph of how two of the factors from the analysis, representing intensity and complexity, can be visualised. As an example, four landscapes from the study area are placed in the graph to depict the landscape types indicated at the four positions respectively. Medium grey represents farmland and dark grey represents forest.

original variables (Quinn & Keough 2002). We ran two separate factor analyses, one on each spatial scale of measurement (1km and 5km), which included 11 and 8 variables respectively.

The bee studies (Ch. II-IV) and seed set (Ch. V) were analysed in SAS 9.2 for Windows (SAS Institute Inc., Cary, NC), using General Linear models (SAS Proc GLM), Linear Mixed model (SAS Proc Mixed), Generalized Mixed models (SAS Proc Glimmix) and Linear Correlations (SAS Proc Corr). Non-parametric goodness-of-fit tests (SAS Proc Freq, options Fisher, Trend and JT) were used to assess correlations of bumblebee traits. By using Mixed models we accounted for dependencies of bumblebee and flower counts in, e.g. habitats within a survey round and within a landscape. By using a Generalized Mixed model we also allowed for non-normal distribution, which is often the case in data sets containing zeros, for example bumblebee or flower counts from one 100m^2 transect in simple landscapes.

4. RESULTS AND DISCUSSION

4.1 Landscape complexity and land-use intensity: same same, but different

The goal of agricultural intensification is to increase the yield per unit area, and intensification can thus be estimated from crop harvest data (Donald, Green & Heath 2001;Vepsäläinen 2007). The degree of landscape heterogeneity (complexity) is a result of the mix of habitat types within an area, i.e. the number of land-use classes and the distribution and configuration of these (Turner, Gardner & O'Neill 2001;Vepsäläinen 2007). In Ch. I we used Factor Analysis to extract factors to describe landscape structure and agricultural intensity. We performed the same type of analysis at two spatial scales, at 1 x 1km and at 5 x 5km. At both spatial scales, the first factor was dominated by proportion farmland, the proportion of annual crops and field size. In addition it was highly correlated with harvest data. We therefore interpret this factor as reflecting *agricultural intensity*. At the smaller scale the second factor was dominated by land-use diversity and contagion, a measure of how interspersed land-use classes are. We consequently interpret this factor as reflecting *landscape configuration* or degree of *complexity*. Factor three contained field size and area of field borders, trees and bushes, thus reflecting another component of complexity which is connected to the abundance of small non-crop habitats. Proportion leys and pastures dominated factors four and five, respectively. These land-uses are connected to dairy and cattle production, i.e. the direction of farming in a focal landscape. When we looked at the same data at the larger 5 × 5km scale, we retained three factors. These factors were not as clearly differentiated as at the smaller scale; factors two and three were mixtures of complexity and farming direction. Pastures, leys and land-use diversity indicate a mixed farming with crops, dairy and beef production while leys and much border zones indicate milk production with fodder production for dairy cattle.

We have shown that in real agricultural landscapes, complexity and intensity are indeed separable from each other. In other words, a landscape of intense farming is not necessarily also a simple one, but can consist of many small fields with borders of herbaceous vegetation, trees and hedgerows in between (figure 2). As a consequence it should be possible to maintain a certain degree of landscape complexity despite intensive farming and high yields. We could also see that the amount of leys and pastures were somewhat separate from the complexity and intensity factors. We interpret these variables as indicators of farming directions, namely toward dairy and meat production. This separation was, however, clearer at the 1 × 1km scale compared to the 5 × 5km scale. This means that care must be taken about at which scale landscape data is to be used in combination with biodiversity data, i.e. the scale at which the organisms integrate resources in their surroundings. Our results also highlight the need to distinguish between intensity and complexity in studies of biodiversity in relation to landscape factors as well as in development of management policies.

4.2 The availability of flower resources in agricultural landscapes

Where do bumblebees find flowering plants in contemporary agricultural landscapes? Except when crops are flowering (e.g. oilseed rape and clover fields), conventionally managed crop fields offer very little for a foraging bee (Ch. II). However, fields within complex landscapes (Gabriel, Thies & Tscharntke 2005) and organically managed fields and field borders may contain higher abundances of nectar and pollen plants (weeds) (Gabriel & Tscharntke 2007;Rundlöf, Edlund & Smith 2010). Flower-rich grasslands, e.g. hay meadows of older times, have been almost completely lost from north western Europe (Emanuelsson 1985;Stoate et al. 2001), as has large scale farming of late flowering leguminous fodder crops as they are often harvested before flowering (Carvell et al. 2006;Fitzpatrick et al. 2007;Goulson, Lye & Darvill 2008). Permanent pastures compose a low intensity habitat, and if not fertilized, may act as refuges for plants demanding habitats of lower nutrient levels (Bignal & McCracken 1996;Ihse 1995). However, many pastures support high numbers of livestock and are intensively grazed, leaving little of flowering plants for pollinating insects (Sjödin 2007). So, in rural areas foraging bees are in much left with a few mass flowering crops, linear non-crop border habitats and some domestic gardens.

The amount of borders (Ch. I) and the amount and composition of flowering plants in those borders differed between landscape types (Ch. II, III), as did the amount of trees and bushes growing in field borders and road verges (Ch. I). This was because of a higher abundance of flowering plants (Ch. II) as well as higher species richness (figure 2 in Ch. III) and proportion of perennials (Ch. II) in borders of complex and low intensity landscapes, compared to simple, high intensity landscapes. Bumblebees are known to prefer perennials (Fussell & 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, Mänd & Williams 2002). Borders of complex landscapes thus contained both more and higher quality forage for bumblebees and a more diverse array of flowers was indeed visited in complex compared to simple landscapes (Ch. I). Low pollen and protein diversity in forage has been shown to negatively affect the colony immune response for honeybees (Alaux et al. 2010). Both low flower abundance and diversity may thus contribute to the decrease in worker numbers detected in simple landscapes during the course of summer (Ch. II, below).

By multiplying flower density of borders and pastures with the area of these habitats we estimated that complex and pasture-rich landscapes had approximately 30 times more herbaceous forage plants for bumblebees than did simple ones in June (Ch. II). There was however more of another potentially important resource, oilseed rape (*B. napus*), in simple landscapes (Ch. II). Oilseed rape has previously been shown to increase colony sizes of *B. terrestris* (Westphal, Steffan-Dewenter & Tscharntke 2009) and to boost worker numbers of other species too (Herrmann et al. 2007;Knight et al. 2009, but see Goulson et al. 2010). On the other hand it has been argued that production of offspring is not positively affected, since neither the daughter queen production (Westphal, Steffan-Dewenter & Tscharntke 2009) nor the number of colonies found were significantly related to the area of oilseed rape within landscapes (Herrmann et al. 2007).

An additional resource, often over-looked, is domestic gardens situated in agricultural landscapes and surrounded by crop fields. Previous studies of pollinators in gardens have mainly focused on urban or suburban regions (e.g. Goddard, Dougill & Benton 2010;Goulson et al. 2002a;Smith et al. 2006). Lately, gardens also in rural areas have received attention as they have been found to contain higher numbers of bumblebee nests than the surrounding farmland (Osborne et al. 2008) and have positive effects on both the number of bumblebee nests in the surrounding (Goulson et al. 2010) and on pollination of wild plants (Cussans et al. 2010; Ch. V).

In Ch. III we selected and surveyed flower-rich habitats composed of borders of leys, pastures, crops fields, fallows and domestic gardens. We found both more resource flowers and a higher species richness of flowering plants in domestic gardens compared to the other habitats surveyed (figure 2 in Ch. III). In the studied region, leys are mainly composed of grasses and either white or red clover (*Trifolium repens* and *T. pratense*). Ley borders were relatively species poor, probably because clover dominated, but contained more flower units than did borders of crops and pastures and fallows (figure 2 in Ch. III).

4.3 Habitat preferences of foraging bumblebees

When comparing bumblebee density in three common farmland habitats and their non-crop borders, we found that border habitats had higher densities of bumblebees (Ch. II). When specifically surveying flower-rich habitats (field borders, fallows and gardens) we found that gardens and borders of leys were generally preferred over the other habitats, but also that preference changed over time (Ch. III, figure 2c in Ch. II).

Furthermore, morphological, ecological and life-history traits modify habitat preferences of bumblebees since all traits except queen emergence significantly interacted with foraging habitat type to explain bumblebee abundances (Ch. III). Most likely this occurs via the composition of pollen and nectar-producing plants characteristic of the different habitats since bumblebees are known to prefer to forage on flowers that fit their morphology (Peat, Tucker & Goulson 2005). In the case of individual based traits (thorax width, tongue length) this is quite intuitive. A bumblebee worker would prefer the habitat where it can contribute the highest rate of resource influx to the colony. Subsequently we found most workers of small species with short tongues and low or medium intra-specific variation, foraging in borders of leys and fields, fallows and ruderal patches, where we expect a high proportion of white clover, annual and biennial plants which are readily visited by small and short tongued bumblebees (Fussell & Corbet 1992). Large species with long tongues and a large variation on the other hand, were mostly found in gardens, where human preferences result in a large variety of ornamental plants, often with more complex flower morphology and a deeper corolla. Regarding males, they generally preferred to forage in gardens. This makes sense as they mainly search for nectar-rich flowers, are slightly larger (Persson,A.S. & Rundlöf,M., unpubl) and therefore also have somewhat longer tongues than workers (Inoue & Yokoyama 2006), as these variables are positively (non-linearly) related within a species (Goulson et al. 2002b).

Regarding colony-based traits and habitat preferences, queen emergence did not show any significant interaction with habitat at all. The groups with medium and large colonies were more abundant in gardens and ley borders than in fallows and border of crops and pastures. This indicates a higher ability for large colonies to detect and utilize resource hot-spots, e.g. gardens or flowering clover ley borders. This is possible if a larger colony indeed searches and forages over a larger area than a small colony. In contrast, small colony workers were equally common in all habitats, possibly because fewer workers decrease the chances of detecting hot-spots. Below-ground species were also more commonly found in gardens and ley borders. This could however be caused by the inter-relation between colony size and nesting habitat. The group with a long reproductive cycle was equally common in all habitats, possibly because of a need to utilize a broader variety of resources and habitats over their extended cycle, compared to shorter cycled species.

4.4 Bumblebee response to agricultural intensification and complexity

In Ch. II we show that, despite the substantially lower availability of wild flowers in simple landscapes, the abundance of bumblebees in June and early July was actually similar in complex and simple landscapes (figure 3). However, simple landscapes contained more oilseed rape. It is likely that oilseed rape has subsidies a high initial growth rate in those landscapes such that those landscapes may host fewer but larger colonies at that time period. There is an east-west gradient which coincides with the landscape classification such that the simple sites have a more westerly position than the complex ones (figure 1). Since spring and summer temperatures are somewhat higher in western compared to inland landscapes (SMHI 2010), this could results in that bumblebee activity in simple landscapes started some days earlier. The high early abundance of bumblebees there may thus in part be caused by earlier emergence of queens and establishment of colonies. In combination with the more abundant MFC resources, colonies in simple landscapes may therefore have reached a stage of more rapid growth by the first survey in mid June, compared to complex landscapes.

However, this high abundance of bumblebees came to an abrubt end already by mid to late July (figure 3). At the same time the increase instead continued in complex landscapes. In late July, the peak bumblebee season in this region, complex landscapes contained around 30 times more bumblebees than did simple ones (Ch. II). The change is dramatic, and may be explained by a sharp decline in available flower resources when oilseed rape stopped flowering. The decline in numbers is so dramatic that there is even a risk that a large proportion of colonies may not manage reproduction before the crash. Furthermore, since we did not discriminate between workers, males and queens, a part of the large difference in total abundance may indeed be attributed to a higher production of sexual offspring in complex landscapes. In that case subsistence of bumblebee populations in simplified landscapes is clearly at risk.

By classifying bumblebee species according to morphological, ecological and life-history traits,

ceral field border

garden in farmland landscape
Photo A. Jönsson

white clover strip
Photo A. Jönsson

we show that the abundance of bumblebees in complex and simple landscapes was related to these traits. For example, in spite of the general difference in abundance between landscape types, species with certain colony-based traits were actually equally common in simple and complex landscapes (Ch. III). Species that start activity early, form large colonies and have short reproductive cycles seemed to manage to reproduce even in simplified landscapes (figure 4). We propose that their traits make them better fit to find and attain resources that are highly scattered or appear in clumps (such as MFCs), and also to efficiently turn these resources into offspring. Therefore populations of these species can persist even in simplified landscapes. In addition, nesting under-ground is most likely a better choice in simple landscapes, as suitable aboveground nest sites in tall and withered grass are most likely more difficult to find in these landscapes. The successful combination of traits is in sharp contrast to the less successful ones and late emerging, small colony, long cycled and aboveground nesters are subsequently more common in complex than in simple landscapes.

The reasons for the trait dependent landscape effects on bumblebee abundance, is most likely that landscape changes especially during the last 70 years, have influenced the relative competitiveness of bumblebees with these combinations of traits. Contemporary agricultural landscapes favour the "large, early and below ground" colony strategy, especially in combination with a short colony cycle. A large part of early flower resources are composed of trees and bushes and large stands of a few common "nitrophilic" or ruderal plants such as white dead nettle, *Lamium album* (Goodwin 1995;Lye et al. 2009; paper II). Agricultural intensification may have had a more negative effect on the abundance of high and late summer flora compared to early flowering plants. Late flowering habitats e.g. hay meadows, legume-based fodder crops and un-cropped habitats, which composed quite a large part of historical farmland landscapes, have to date largely been lost (Fitzpatrick et al. 2007;Goulson, Lye & Darvill 2008;Stoate et al. 2001). Trees and bushes have most certainly also declined but the few remaining may still provide the resources necessary for the critical phases of colony growth. Furthermore, the increased farming of winter-sown oil seed rape may aid early, large and short cycled colonies, since it would take a large work force already by mid May to efficiently localise and exploit this abundant but ephemeral resource (Westphal, Steffan-Dewenter & Tscharntke 2006). It may thus not only be the decrease of forage per se but the spatial and temporal match (or mis-match) between colony cycle, foraging ranges and resources, which result in today's patterns of bumblebee abundance; a few relatively successful species, but many more facing a downward spiral. If the match is good it enables population sustenance (and perhaps also growth) even in simplified landscapes. Early species also have the advantage of already having a relatively large colony as the later species emerge. This gives them a competitive advantage, especially when resources are scarce and scattered, which is indeed the case in simple landscapes after the flowering of trees, shrubs and oilseed rape (Ch. II).

However, even the more successful species may face problems in simplified landscapes. In Ch. IV we show that independent of species, workers from simple landscapes were smaller than those caught in complex ones (figure 2 in Ch. IV). The size of adult worker bees is determined by the amount of food they are fed as larvae (Goulson 2003;Schmid-Hempel & Schmid-Hempel 1998). Smaller and fewer workers as well as fewer males in response to food shortage has been demonstrated in a lab environment (Schmid-Hempel & Schmid-Hempel 1998). In a field study, competition from managed honeybees resulted in decreased mean body size of co-occurring bumblebees (Goulson & Sparrow 2009). It has been suggested that production of smaller workers is an adaptive response to starvation, since smaller bumblebees survive longer during low colony nectar intake rates (Couvillon & Dornhaus 2010). This could mean that colonies in simple landscapes adjust to food scarcity by producing more, smaller and hardier workers rather than fewer, larger and more energy demanding ones. However, this still implies that the colonies sampled in simple landscapes experience a shortage of resources. Another way to view these results is that smaller workers may fit the flora of simplified landscape better, i.e. annuals with disc shaped corollas and small flower heads (Goulson et al. 2002b;Peat, Tucker & Goulson 2005), why a colony of many equally small workers may indeed be competitive under these circumstances. To complicate things further, small bumblebees are actually also able to enter and extract nectar from deep flowers, and may therefore in fact functionally act as a large and long tongued bee (Williams N.M., pers. comm.).

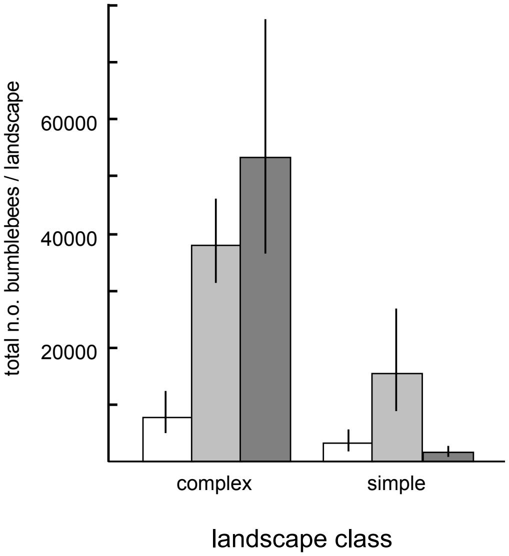


Figure 3: Bumblebee abundance over time. Open bars: 9-27 June, light grey: 27 June-5 July, dark grey: 16-25 July. Total numbers (mean±sem) of bumblebees per landscape class, estimated from habitat specific densities and total area of each habitat per landscape. The difference between landscape classes in the last survey-round is statistically significant.

4.5 Pollination in simplified landscapes; positive effects of domestic gardens

We found that both seed set of peach-leaved bellflower, *Campanula persicifolia* and the abundance and species diversity of bees were higher close to domestic gardens than just 140m further away (Ch. V). From this we draw two main conclusions: First, domestic gardens can serve as refuges for wild bees in simplified landscapes and second, there seems to be a lack of full pollination of at least the here studied plant species. The fact that a lower seed set coincided with lower bee abundance and that we used two plant individuals at each site to allow cross-fertilisation, suggest that lower seed set is indeed caused by too few visits by insect pollinators rather than by a lack of mates. Also, the distance from a non-crop habitat, at which pollination is enhanced, is indeed quite short. Thus, we have presented evidence that the ecosystem service of pollination is already at risk in simplified landscapes with intensive agriculture in southernmost Sweden. Our results are further corroborated by those of Cussans et al. (2010), who found higher seed set of *Lotus corniculatus* and *Glechoma hederacea* when grown in gardens compared to next to crop fields. Gardens should thus not be overlooked when discussing population dynamics and ecosystem processes, whether in an urban (Goddard, Dougill & Benton 2010) or rural setting.

Interestingly, large scale parallel declines of pollinators and out-crossing plants have been documented in Great Britain, and The Netherlands (Biesmeijer et al. 2006), but it is not yet clear if they are decreasing from external factors such as agro-chemicals (Rundlöf, Edlund & Smith 2010) and field border management or from lack of food/lack of pollination respectively (Gabriel & Tscharntke 2007). The most probable cause would of course be that several factors are working in synergy. The fact that a higher abundance and diversity of plants were found in field borders and road-verges of more complex landscapes, both in our (Ch. II, III) and other studies (e.g. Smart et al. 2006), demonstrate that an increased amount of linear non-crop habitats can have a positive effect on the plant community also in regions otherwise dominated by agriculture. This positive effect is presumably caused both by providing more suitable habitats for plants and a richer pollinator community.

4.6 Mechanism behind detected patterns

The crucial question for persistence of bumblebee populations in agricultural landscapes is if colonies have enough resources to complete reproduction. In 2006 we detected a crash in total numbers of bumblebees in simple landscapes by late July (Ch. II, figure 3), suggesting an over-all lower reproduction of colonies in these areas. Analyses of separate trait groups (Ch. III) indicated that some combinations of traits increase the chances of successful reproduction (of males) in simple landscapes, while others do not. Successful traits seem to be early queen emergence, large colony, below ground nests and a short colony cycle. These traits, especially in combination, allowed for equal production of males in both complex and simple landscapes , (figure 4). The opposite: late queen, small colonies, surface nesting and with a long cycle, resulted in lower production of both workers and males in simple landscapes (Ch. III). Although we do not have any data on production of daughter queens, production of males may give us an indication. Despite these findings, the number of detected species was actually relatively high also in simple landscapes during all three years of surveying (table 1), and during surveys of similar landscapes in 2003 and 2004 (Rundlöf, Nilsson & Smith 2008). How can this be? How do vulnerable species persist (although at very low abundances) in simplified landscapes? We suggest two mechanisms. Firstly, survival and a low rate of reproduction may be possible even for vulnerable species in pockets of beneficial habitats, e.g. domestic gardens (Ch. V), certain non-crop border zones, ruderal patches and brown-fields. Secondly, there may be an annual dispersal of queens into simple landscapes from nearby complex regions. The latter case would imply source-sink population dynamics (Dias 1996;Pulliam 1988) where simple landscapes act as sinks, at least for a subset of the species. Quite possibly a combination of these scenarios could be the case, and the dominating mechanism would depend on species specific traits such as foraging range, colony size, habitat preferences and proneness and ability of queens to disperse.

A recent study shows that queens can indeed disperse several kilometres (Lepais et al. 2010). If dispersal mainly takes place in spring, the availability of fields of flowering oilseed rape and possibly also flowering trees and bushes,

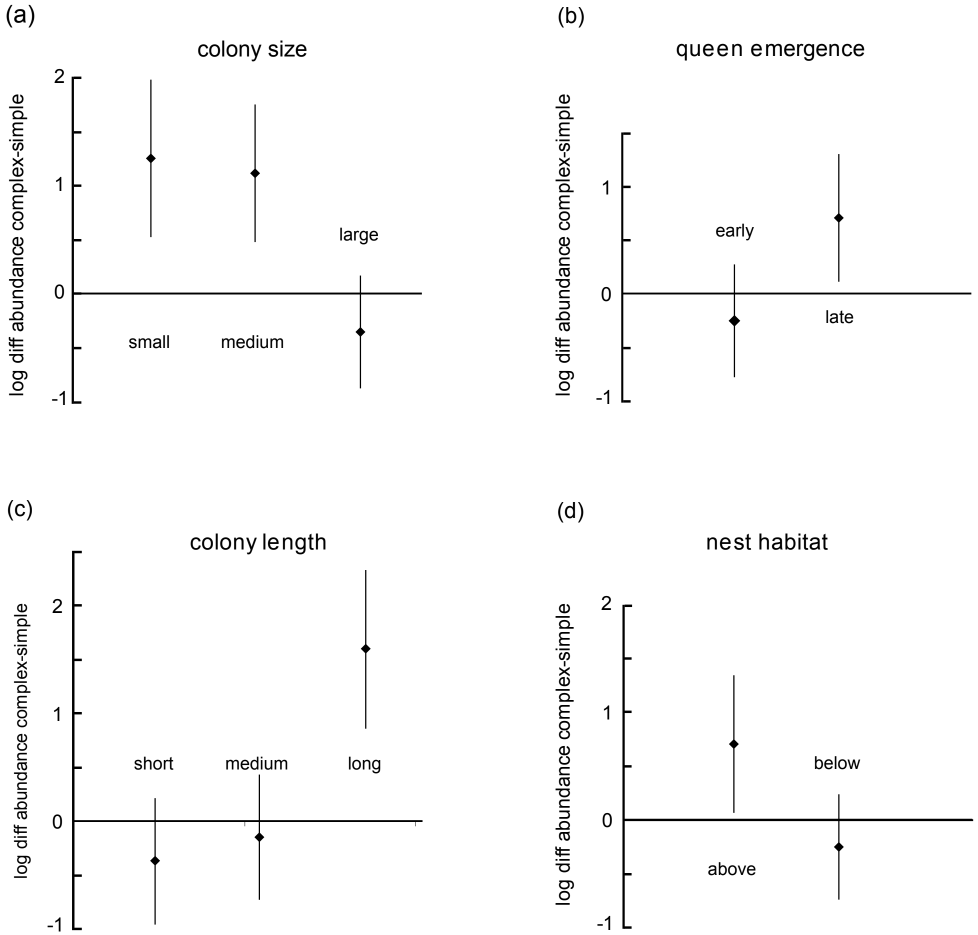


Figure 4: Landscape effects of colony colony-based traits on male abundances. Graphs show difference in mean abundance between complex and simple landscapes for (a) effect of colony size, (b) effect of queen emergence time, (c) effect of colony cycle length, (d) effect of nesting habitat. Error bars show 95% CI. Landscape effects were detected where the difference was statistical significantly separated from zero.

may lead queens to settle in landscapes where resources will later practically disappear. This would make possible a source-sink system to be at work, where south western Skåne receives input of queens from central and north eastern parts of the province. It would be interesting to investigate if the genetic structure of bumblebee populations in this region shows signs of source-sink dynamics. Another interesting topic is to study potential differences in nest establishment vs. successful reproduction of daughter queens between differently structured landscapes (Goulson et al. 2010). Also to follow variation in bumblebee numbers more closely over the whole season, and relate this to the spatial separation of potential foraging resources and nest habitat could reveal more on the mechanisms behind persistence vs. decline of bumblebee species.

In contrast to the large landscape differences found in 2006 (Ch. II), we found neither landscape differences in bumblebee density nor seasonal differences between landscapes in 2008 (Ch. III). We did however sample only flower-rich habitats, and although survey sites in simple landscapes contained a lower abundance and richness of flowers (figure 3 in Ch. III), they were still highly rewarding for bumblebees compared to the surrounding habitats. If total numbers of bumblebees in simple landscapes are indeed as low as suggested by our estimation from the 2006 survey, then the lack of a landscape difference in 2008 suggests a relatively higher attraction of bees in simple landscapes into the few existing flower-rich habitats (Heard et al. 2007). This is expected if bees utilise the foraging landscape according to an *ideal free*

Table 1: Sample sizes of bumblebees during three years of surveys, divided between simple and complex landscapes. In 2006 we did not discriminate between workers (w), males (m) and queens (q). In 2008 workers, males and males of *Psityris spp.* were separated and queens were not collected. In 2009 only workers were considered. There was no difference in species richness between landscape classes in 2006 (based on n.o. species per landscape), see text for details.

	2006 (workers+males)		**2008 (workers)**		**2008 (males)**		**2009 (workers)**
Bombus sp.	Simple	Complex	Simple	Complex	Simple	Complex	Simple
B. hortorum	29	130	80	76	69	62	22
B. hypnorum	0	32	20	27	7	15	8
B. jonellus	0	0	1	0	0	0	0
B. lapidarius	80	126	479	275	176	146	32
B. lucorum	39	173	8	13	9	15	4
B. muscuorum	1	19	1	1	1	0	2
B. pascuorum	9	77	40	111	1	37	2
B. pratorum	1	18	5	11	4	10	3
B. ruderarius	58	126	8	14	3	5	1
B. soroëensis	0	1	6	22	3	2	2
B. subterraneus	6	22	24	18	8	1	14
B. sylvarum	24	36	109	130	11	67	13
B. terrestris	comb. w. *B. lucorum*		325	238	382	402	45
B. bohemicus					3	2	
B. campestris					0	1	
B. rupestris					91	20	
B. sylvestris					1	4	
B. vestalis					49	6	

distribution (Goulson 2003;Roulston & Goodell 2010). This highlights one of the problems of surveying pollinating insects: how to evaluate landscape scale abundances of pollinators when we naturally only find them where their preferred forage flowers are. One way to go about this is a stratified sampling of farmland habitats in combination with information on the amount of each habitat available to bees within an area (Ch. II). Hence, evaluations of conservation actions to increase forage of bumblebees, e.g. creation of flower-rich field margins (e.g. Pywell et al. 2005) could benefit from using this method, if the aim is to evaluate the effect on bumblebee populations rather than the attraction of a specific habitat on worker bees. Such information is of course still useful as it indicates the value of a specific habitat for foraging bees. But to increase the pollination service to both wild plants and crops, we need to find ways to boost population numbers so that more individuals also spill over into other habitats to forage.

5. CONCLUSIONS & FINAL REMARKS

Conservation of wild bees and pollination

In accordance with several other studies from around the world, my results suggest that the amounts and quality of non-crop semi-natural habitats and flower resource in landscapes highly dominated by agriculture are not enough to sustain population of bumblebees. Since bumblebees are important pollinators of both crops and wild plants, together with solitary bees (Winfree et al. 2008), it is urgent to design and implement large scale conservation actions to reverse the negative trends of these groups of pollinators in contemporary agricultural landscapes.

Both social and solitary bees need sufficient amount of pollen and nectar from flowers to survive and reproduce. Bumblebees prefer to forage from perennials, and because of morphological and seasonal variation of both plants and bumblebee activity, higher plant diversity will potentially benefit the diversity also of bumblebees (and solitary bees). We have shown that landscapes containing >9% permanent pastures and sufficient amounts of non-crop linear elements between fields can indeed harbour substantially higher numbers of bumblebees, also of species that are considered more vulnerable to habitat loss and fragmentation (Ch. II, III). Other studies have confirmed the value of permanent grasslands as sources of pollinators (e.g. Morandin et al. 2007;Öckinger & Smith 2007;Steffan-Dewenter & Tscharntke 1999). This type of landscape could thus be considered as of good quality to wild bees. We have also seen that even an isolated garden in a sea of crop fields can harbour bees and enhance pollination, but that the pollination service provided decreased already by 140m from the source (Ch. V).The rate of decay of flower visitation by pollinators has further been shown to decease more sharply with distance than species richness of pollinators does (Ricketts et al. 2008). To simply restore and properly manage the available non-crop habitats of simplified landscapes would most probably not suffice to reverse the decline of bees and insect pollinated plants.

Actions to conserve wild bees and pollination services must therefore include both *restoring* and *recreating* flower-rich non-crop habitats. For example, the stocking rate on pastures can be adjusted to allow more flowering plants, management of linear elements like field borders can allow for both more flowering trees, shrubs and forbs and cutting of road verges can be timed to allow plants to flower. Importantly, a diversity of flower-rich habitats must become available, both in sufficient amounts and close enough to benefit species which utilise different flower resources and forage at different spatial scales. My results suggest that there may be an inflow of queens into simple landscapes from nearby complex landscapes. If so, further simplification or abandonment of complex landscapes could threaten bumblebee populations also in simple landscapes were they still persist. To create viable wild bee populations, conservation action and management clearly needs to be implemented at the landscape scale, rather than in isolated habitats. In agricultural regions the farmer is the main landscape manager. By taking a small percentage of land out of production and create habitats benefiting biodiversity, farmers can increase their benefits from the ecosystem services that biodiversity provides; hence we have a win-win situation (Swinton et al. 2007). For example recreated species-rich grasslands may provide both increased hay yields (Bullock, Pywell & Walker 2007) and habitat for beneficial insects (Potts et al. 2009). As we have shown, increasing landscape complexity does not necessarily mean that intensity (as measured from harvest data) will decrease accordingly (Ch. I). Indeed, if ES are promoted by an increased landscape and habitat complexity it may actually benefit production.

This information need to be conveyed to both farmer and authorities. If not we may be facing a “tragedy of the commons” regarding farmland landscapes and their associated ES, where everyone would benefit from ES but no-one wants to set aside land to secure biodiversity and these benefits. Perhaps regulations and Agri-Environment Schemes are therefore vital for sustainable landscapes to have a chance to develop. Correct information on landscape and management effects on biodiversity constitutes the basis for sound conservation action. To turn science into practice and promote biodiversity and ES in agricultural landscapes of Europe, we therefore need to transfer scientific knowledge both to the farmer and to EU authorities (Scherr & McNeely 2008;Sutherland 2002). The results presented in this thesis can be useful when considering farmland management regulations and regional landscape planning. However, any potential regulations should be adjusted to the ecological conditions and cultural history of regional landscapes. Together with other recent studies (e.g. Ahrne, Bengtsson & Elmqvist 2009;Goddard, Dougill & Benton 2010;Osborne et al. 2008), my results also acknowledge that the interested general public can contribute to maintain biodiversity and ES by “gardening for diversity” and that urban and garden wildlife is a part of nature, as are (agri) cultural landscapes.

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7. REFERENCES

Ahrne,K., Bengtsson, J. & Elmqvist, T. (2009) Bumble Bees (Bombus spp) along a Gradient of Increasing Urbanization. PLoS ONE 4.

Alaux,C., Ducloz, F., Crauser, D. & Le Conte, Y. (2010) Diet effects on honeybee immunocompetence. Biology Letters.

ArtdataBanken. (2010) Rödlistan -Sök arter. http://snotra.artdata.slu.se/artfakta/GetSpecies.aspx?SearchType=Advanced. Accessed 2010-12-01

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

Benton,T.G., Vickery, J. A. & Wilson, J. D. (2003) Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology & Evolution 18, 182-188.

Berglund,B.ed. (1991) The cultural landscape during 6000 years in southern Sweden - the Ystad project Copenhagen.

Biesmeijer,J.C., Roberts, S. P. M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J. & Kunin, W. E. (2006) Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. Science 313, 351-354.

Bignal,E.M. & McCracken, D. I. (1996) Low-Intensity Farming Systems in the Conservation of the Countryside. Journal of Applied Ecology 33, 413-424.

Bommarco,R., Biesmeijer, J. C., Meyer, B., Potts, S. G., Poyry, J., Roberts, S. P., Steffan-Dewenter, I. & Ockinger, E. (2010) Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. Proceedings of the Royal Society Biological Sciences Series B 277, 2075-2082.

Bullock,J.M., Pywell, R. F. & Walker, K. J. (2007) Long-term enhancement of agricultural production by restoration of biodiversity. Journal of Applied Ecology 44, 6-12.

Carvell,C., Roy, D. B., Smart, S. M., Pywell, R. F., Preston, C. D. & Goulson, D. (2006) Declines in forage availability for bumblebees at a national scale. Biological Conservation 132, 481-489.

Cederberg,B., Pettersson, M. W. & Nilsson, L. A. (2006) ArtDatabanken, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Couvillon,M. & Dornhaus, A. (2010) Small worker bumble bees (Bombus impatiens) are hardier against starvation than their larger sisters. Insectes Sociaux 57, 193-197.

Cussans,J., Goulson, D., Sanderson, R., Goffe, L., Darvill, B. & OSBORNE, J. L. (2010) Two Bee-Pollinated Plant Species Show Higher Seed Production when Grown in Gardens Compared to Arable Farmland. PLoS ONE 5, e11753.

Dias,P.C. (1996) Sources and sinks in population biology. Trends in Ecology & Evolution 11, 326-330.

Diekötter,T., Kadoya, T., Peter, F., Wolters, V. & Jauker, F. (2010) Oilseed rape crops distort plant-pollinator interactions. Journal of Applied Ecology 47, 209-214.

Donald,P., Green, R. & Heath, M. (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. Proceedings of the Royal Society Biological Sciences Series B 268, 25-29.

Dunning,J.B., Danielson, B. J. & Pulliam, H. R. (1992) Ecological Processes That Affect Populations in Complex Landscapes. Oikos 65, 169-175.

Emanuelsson,U. (1985) Det Skånska kulturlandskapet. Signum, Lund, Sweden.

European Commision. (2011) The CAP explained. http://ec.europa.eu/agriculture/publi/capexplained/cap_en.pdf. Accessed 2011-03-28.

Fahrig,L. (2005) When is landscape perspective important? Issues and perspectives in landscape ecology. pp. 3-10. (eds Wiens,J. & Moss,M.), Cambridge University Press, Cambridge, UK.

Fitzpatrick,U., Murray, T. E., Paxton, R. J., Breen, J., Cotton, D., Santorum, V. & Brown, M. J. F. (2007) Rarity and decline in bumblebees - A test of causes and correlates in the Irish fauna. Biological Conservation 136, 185-194.

Fussell,M. & Corbet, S. A. (1992) Flower Usage by Bumble-Bees: A Basis for Forage Plant Management. The Journal of Applied Ecology 29, 451-465.

Gabriel,D., Carver, S. J., Durham, H., Kunin, W. E., Palmer, R. C., Sait, S. M., Stagl, S. & Benton, T. G. (2009) The spatial aggregation of organic farming in England and its underlying environmental correlates. Journal of Applied Ecology 46, 323-333.

Gabriel,D., Thies, C. & Tscharntke, T. (2005) Local diversity of arable weeds increases with landscape complexity. Perspectives in Plant Ecology, Evolution and Systematics 7, 85-93.

Gabriel,D. & Tscharntke, T. (2007) Insect pollinated plants benefit from organic farming. Agriculture, Ecosystems & Environment 118, 43-48.

Goddard,M.A., Dougill, A. J. & Benton, T. G. (2010) Scaling up from gardens: biodiversity conservation in urban environments. Trends in Ecology & Evolution 25, 90-98.

Goodwin,S. (1995) Seasonal phenology and abundance of early-, mid- and long-season bumble bees in southern England, 1985-1989. Journal of Apicultural Research 34, 79-87.

Goulson,D., Lye, G. C. & Darvill, B. (2008) Decline and Conservation of Bumble Bees. Annual Review of Entomology 53, 191-208.

Goulson,D. (2003) Bumblebees: Their behaviour and ecology. Oxford University Press, Oxford, UK.

Goulson,D., Hughes, W., Derwent, L. & Stout, J. (2002a) Colony growth of the bumblebee, Bombus terrestris, in improved and conventional agricultural and suburban habitats. Oecologia (Berlin) 130, 267-273.

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. Journal of Applied Ecology 47, 1207-1215.

Goulson,D., Peat, J., Stout, J. C., Tucker, J., Darvill, B., Derwent, L. C. & Hughes, W. O. (2002b) Can alloethism in workers of the bumblebee, Bombus terrestris, be explained in terms of foraging efficiency? Animal Behaviour 64, 123-130.

Goulson,D., Rayner, P., Dawson, B. & Darvill, B. (2011) Translating research into action; bumblebee conservation as a case study. Journal of Applied Ecology 48, 3-8.

Goulson,D. & Sparrow, K. (2009) Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. Journal of Insect Conservation 13, 177-181.

Greenleaf,S.S. & Kremen, C. (2006) Wild bees enhance honey bees' pollination of hybrid sunflower. Proceedings of the National Academy of Sciences 103, 13890-13895.

Groom,M.J., Meffe, G. K. & Carroll, C. R. (2006) Principles of conservation biology, 3rd edn. Sinauer Press, Inc., Sunderland, MA, USA.

Hanski,I. (1999) Metapopulation ecology. Oxford University Press, Oxford, UK.

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. Biology Letters 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. Molecular Ecology 16, 1167-1178.

Hines,H.M. & Hendrix, S. D. (2009) Bumble Bee (Hymenoptera: Apidae) Diversity and Abundance in Tallgrass Prairie Patches: Effects of Local and Landscape Floral Resources. Environmental Entomology 34, 1477-1484.

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. Landscape and Urban Planning 31, 21-37.

Inoue,M.N. & Yokoyama, J. (2006) Morphological variation in relation to flower use in bumblebees. Entomological Science 9, 147-159.

Jones-Walters,L. (2008) Biodiversity in multifunctional landscapes. Journal for Nature Conservation 16, 117-119.

Kleijn,D., Kohler, F., Baldi, A., Batary, P., Concepcion, E., Clough, Y., Diaz, M., Gabriel, D., Holzschuh, A., Knop, E., Kovacs, A., Marshall, E., Tscharntke, T. & Verhulst, J. (2009) On the relationship between farmland biodiversity and land-use intensity in Europe. Proceedings of the Royal Society Biological Sciences Series B 276, 903-909.

Klein,A., Steffan-Dewenter, I. & Tscharntke, T. (2003) Pollination of Coffea canephora in relation to local and regional agroforestry management. Journal of Applied Ecology 40, 837-845.

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. Proceedings of the Royal Society B: Biological Sciences 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 Conservation and Diversity 2, 116-124.

Krebs,J.R., Wilson, J. D., Bradbury, R. B. & Siriwardena, G. M. (1999) The second Silent Spring? Nature 400, 611-612.

Kremen,C. & Ricketts, T. (2000) Global perspectives on pollination disruptions. Conservation Biology 14, 1226-1228.

Kremen,C., Williams, N. M. & Thorp, R. W. (2002) Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences of the United States of America 99, 16812-16816.

Leibold,M., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J., Hoopes, M., Holt, R., Shurin, J., Law, R., Tilman, D., Loreau, M. & Gonzalez, A. (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7, 601-613.

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. Molecular Ecology 19, 819-831.

Löken, A. (1973) Studies on Scandinavian Bumble Bees (Hymenoptera, Apidae). Norwegian Journal of Entomology 20, 1-218.

Lye,G., Park, K., Osborne, J., Holland, J. & Goulson, D. (2009) Assessing the value of Rural Stewardship schemes for providing foraging resources and nesting habitat for bumblebee queens (Hymenoptera: Apidae). Biological Conservation 142, 2023-2032.

Mänd,M., Mänd, R. & Williams, I. H. (2002) Bumblebees in the agricultural landscape of Estonia. Agriculture, Ecosystems & Environment 89, 69-76.

Millennium Ecosystem Assessment (2005) World Resource Institute, Washington, DC.

Morandin,L.A., Winston, M. L., Abbott, V. A. & Franklin, M. T. (2007) Can pastureland increase wild bee abundance in agriculturally intense areas? Basic and Applied Ecology 8, 117-124.

Nyman,Y. (1992) Pollination Mechanisms in Six Campanula Species Campanulaceae. Plant Systematics and Evolution 181, 97-108.

Öckinger,E. & Smith, H. G. (2007) Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. Journal of Applied Ecology 44, 50-59.

Öckinger,E., Schweiger, O., Crist, T. O., Debinski, D. M., Krauss, J., Kuussaari, M., Petersen, J. D., Poyry, J., Settele, J., Summerville, K. S. & Bommarco, R. (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecology Letters 13, 969-979.

Osborne,J.L., Martin, A. P., Shortall, C. R., Tod, A. D., Goulson, D., Knight, M., Hale, R. J. & Sanderson, R. A. (2008) Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. Journal of Applied Ecology 45, 784-792.

Peat,J., Tucker, J. & Goulson, D. (2005) Does intraspecific size variation in bumblebees allow colonies to efficiently exploit different flowers? Ecological Entomology 30, 176-181.

Pollard,E. (1977) A method for assessing changes in butterfly abundance. Biological Conservation 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. Journal of Applied Ecology 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. Trends in Ecology & Evolution 25, 345-353.

Prys-Jones,O.E. & Corbet, S. A. (1987) Naturalist's Handbooks 6. Bumblebees. Cambridge University Press.

Pulliam,H.R. (1988) Sources Sinks and Population Regulation. American Naturalist 132, 652-661.

Pywell,R., Warman, E., Carvell, C., Sparks, T., Dicks, L., V, Bennett, D., Wright, A., Critchley, C. & Sherwood, A. (2005) Providing foraging resources for bumblebees in intensively farmed landscapes. Biological Conservation 121, 479-494.

Quinn,G.P. & Keough, M. J. (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK.

Ricketts,T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S. S., Klein, A. M., Mayfield, M. M., Morandin, L. A., Ochieng, A. & Viana, B. F. (2008) Landscape effects on crop pollination services: are there general patterns? Ecology Letters 11, 499-515.

Roulston,T.H. & Goodell, K. (2010) The Role of Resources and Risks in Regulating Wild Bee Populations. Annual Review of Entomology 56, 293-312.

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. Biological Conservation 141, 417-426.

Scherr,S.J. & McNeely, J. A. (2008) Biodiversity conservation and agricultural sustainability: towards a new paradigm of Çÿecoagriculture ÇÖ landscapes. Philosophical Transactions of the Royal Society B: Biological Sciences 363, 477-494.

Schmid-Hempel,R. & Schmid-Hempel, P. (1998) Colony performance and immunocompetence of a social insect, Bombus terrestris, in poor and variable environments. Functional Ecology 12, 22-30.

Schmid-Hempel,R. & Schmid-Hempel, P. (2000) Female mating frequencies in Bombus spp. from Central Europe. Insectes Sociaux 47, 36-41.

Shrubb,M. (2003) Birds, Scythes and Combines: A History of Birds and Agricultural Change. Cambridge

University Press, New York, NY, USA.

Sjödin,N. (2007) Pollinator behavioural responses to grazing intensity. Biodiversity and Conservation 16, 2103-2121.

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. Journal of Applied Ecology 43, 1128-1137.

SMHI (2010) Swedish Meteorological and Hydrological Institute, Norrköping, Sweden.

Smith,R., Warren, P., Thompson, K. & Gaston, K. (2006) Urban domestic gardens (VI): environmental correlates of invertebrate species richness. Biodiversity and Conservation 15, 2415-2438.

Steffan-Dewenter,I. & Tscharntke, T. (1999) Effects of habitat isolation on pollinator communities and seed set. Oecologia (Berlin) 121, 432-440.

Steffan-Dewenter,I. & Westphal, C. (2008) The interplay of pollinator diversity, pollination services and landscape change. Journal of Applied Ecology 45, 737-741.

Stoate,C., Baldi, A., Beja, P., Boatman, N., Herzon, I., van Doorn, A., de Snoo, G., Rakosy, L. & Ramwell, C. (2009) Ecological impacts of early 21st century agricultural change in Europe - A review. Journal of Environmental Management 91, 22-46.

Stoate,C., Boatman, N. D., Borralho, R. J., Carvalho, C. R., Snoo, G. R. & Eden, P. (2001) Ecological impacts of arable intensification in Europe. Journal of Environmental Management 63, 337-365.

Stokstad,E. (2007) The Case of the Empty Hives. Science 316, 970-972.

Sutherland,W.J. (2002) Restoring a sustainable countryside. Trends in Ecology & Evolution 17, 148-150.

Svensson,B. (2002) Foraging and Nesting ecology of bumblebees (Bombus spp.) in agricultural landscapes in Sweden. Department of Ecology and Crop Production Science, Swedish University of Agricultural Scienses, Uppsala, Sweden

Svensson,S. (2001) Övervakning av jordbrukslandskapets fåglar i Skåne, manual för fältarbetet. Ekologiska institutionen, Lunds Universitet, Lund.

Swinton,S.M., Lupi, F., Robertson, G. P. & Hamilton, S. K. (2007) Ecosystem services and agriculture: Cultivating agricultural ecosystems for diverse benefits. Ecological Economics 64, 245-252.

Tscharntke,T., Klein, A. M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. Ecology Letters 8, 857-874.

Tscharntke,T., Steffan-Dewenter, I., Kruess, A. & Thies, C. (2002) Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. Ecological Applications 12, 354-363.

Turner,M.G., Gardner, R. H. & O'Neill, R. V. (2001) Landscape Ecology in theory and practice. Springer Science+Business Media, LLC, New York, NY.

Vandermeer,J. & Perfecto, I. (2007) The Agricultural Matrix and a Future Paradigm for Conservation. Conservation Biology 21, 274-277.

Vepsäläinen,V. (2007) Farmland birds and habitat heterogeneity in an intensively cultivated boreal agricultural landscape. PhD Faculty of Biosciences, University of Helsinki, Finland.

Westphal,C., Steffan-Dewenter, I. & Tscharntke, T. (2009) Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. Journal of Applied Ecology 46, 187-193.

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

Wilcock,C. & Neiland, R. (2002) Pollination failure in plants: Why it happens and when it matters. Trends in Plant Science 7, 270-277.

Williams,N.M., Crone, E. E., Roulston, T. H., Minckley, R. L., Packer, L. & Potts, S. G. (2010) Ecological and life-history traits predict bee species responses to environmental disturbances. Biological Conservation 143, 2280-2291.

Williams,P.H. (1982) The Distribution and Decline of British Bumble Bees Bombus. Journal of Apicultural Research 21, 236-245.

Williams,P., Colla, S. & Xie, Z. (2009) Bumblebee Vulnerability: Common Correlates of Winners and Losers across Three Continents. Conservation Biology 23, 931-940.

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. Journal of Applied Ecology 45, 793-802.

Wretenberg,J., Lindström, Å., Svensson, S. & Pärt, T. (2007) Linking agricultural policies to population trends of Swedish farmland birds in different agricultural regions. Journal of Applied Ecology 44, 933-941

Varför minskar humlorna?

Effekter av det omgivande landskapet på humlors fortlevnad

Under 1900-talet har man noterat att många grupper av organismer knutna till jordbrukslandskapet har minskat i utbredning och antal. Detta gäller t.ex. fåglar, kärlväxter och insekter. Bland insekter är minskningen av vilda bin särskilt oroande eftersom bin är viktiga pollinatörerna av både grödor och vilda växter i de flesta av världens ekosystem. Honungsbin kan användas för att pollinera många grödor, men det har visats att vilda bin, dvs. humlor och solitära bin, i flera fall är effektivare. Det finns fler fördelar med en mångfald av pollinatörer. Graden av pollinering, och därmed frösättningen, kan öka om en blomma besöks av flera olika arter av insekter. Dessutom varierar antalet pollinatörer av olika arter ofta mycket mellan åren, men om det finns många arter i ett område så kan en god pollinering ändå upprätthållas. Man kan säga att man sprider riskerna genom att investera in en mångfald av arter.

Det anses allmänt att det är den långtgående intensifieringen och strukturrationaliseringen av jordbruket som ligger bakom minskningen av biologisk mångfald i Europas jordbrukslandskap. I Sverige och EU regleras jordbruket bl.a. via CAP (Common Agricultural Policy) och för att åstadkomma ett hållbart jordbrukslandskap bör därför utformningen av CAP bygga på kunskap om hur landskapets struktur och skötsel påverkar ekosystemens funktioner och ekosystemtjänster.

För att förstå på vilket sätt viktiga pollinerande insekter påverkas av det omgivande landskapets struktur och innehåll, har jag studerat populationer av humlor (fam. *Bombus*). Jag har också gjort en analys av sambandet mellan jordbruksintensitet of landskapets komplexitet. Mina studier har utförts i Skåne och jag har valt studieområden bl.a. baserat på hur stora åkrar och hur mycket naturbetesmark de innehåller. Områden med små åkrar, omväxlande landskap och mycket betesmark kallar jag *komplexa* och motsatsen, med stora åkrar och nästan enbart växtodling, kallar jag *enkla* landskap. I dessa områden har jag inventerat humlor och blommande växter i kantzoner till åkrar, vallar, betesmarker och trädgårdar under juni till augusti. Humlor är sociala insekter som bildar ett-åriga kolonier av arbetare kring en drottning. Det är bara drottningen som är befruktad och kan lägga ägg som utvecklas till en ny drottning. När man räknar antalet humlor ute i naturen måste man därför betänka att antalet reproducerande individer, det man kallar effektiv populationsstorlek, är antalet drottningar eller antalet aktiva kolonier, och alltså inte antalet arbetare. Jag har dessutom gjort ett försök med en växt som är beroende av insekts pollinering, stor blåklocka (*Campanula persicifolia*), för att undersöka om privata trädgårdar i jordbrukslandskapet kan bidra till ökad pollinering genom att erbjuda vilda bin en gynnsam miljö.

Analysen av jordbruksintensitet och landskapets komplexitet visar att det inte nödvändigtvis är så att ett intensivt brukat landskap också är kraftigt förenklat. Vi identifierade delvis separata faktorer, uppbyggda av flera landskapsvariabler, som beskriver intensitet, komplexitet, mängd små-biotoper och jordbrukets inriktning (växtodling eller blandjordbruk). Detta bör betyda att en ökad grad av komplexitet inte nödvändigtvis måste innebära minskad avkastning från jordbruket. Jag visade också att sambandet mellan olika variabler som beskrev landskapet berodde på vilken skala man betraktade landskapet.

Mina resultat från 2006 visar att det från mitten av juli fanns ca 30 gånger färre humlor i enkla jämfört med komplexa landskap. Däremot var det ingen skillnad mellan mängden humlor i komplexa och enkla landskap i början av studien under juni månad. Eftersom mängden blommande, örtartade växter också skilde med en faktor 30 mellan landskapstyperna, tyder detta på att humlorna i de enkla landskapen utnyttjar andra resurser i början av säsongen (maj-juni). I andra studier har man visat att humlekolonier kan utnyttja blommande raps och att detta leder till en snabb tillväxt tidigt på säsongen. Så kan det vara också i skånska landskap fram till mitten av juni. När rapsen slutar blomma finns dock inte mycket alternativa resurser och humlepopulationerna minskar kraftigt. Vi ser en stor risk att denna minskning sker innan kolonier av alla arter hinner reproducera sig och att återväxten av humlor i enkla landskap därför är starkt hotad.

Trots de långtgående minskningarna av humlor och vilda bin från jordbruksområden så är en handfull arter alltjämt relativt vanliga. Orsakerna till detta är inte helt kända, men det har föreslagits att artspecifika egenskaper gällande födoval gör att några arter är bättre lämpade för att effektivt utnyttja de resurser som trots allt finns också i enkla landskap. För att undersöka detta delade jag upp arterna i grupper utefter deras egenskaper rörande kolonistorlek (antal arbetare per koloni), boplatsmiljö, kolonins livslängd och aktivitetsperiod och arbetarnas morfologi. Jag fann att de arter som är aktiva tidigt på säsongen, bildar stora kolonier, bygger sina bon under mark eller som är aktiva under en kort period, kan reproducera sig lika väl i enkla som i komplexa landskap. Motsatsen, dvs. arter som blir aktiva först på försommaren, bildar små kolonier, bygger bon ovan mark eller har en lång aktivitetsperiod, klarade sig betydligt sämre i enkla jämfört med komplexa landskap. Arbetarnas morfologi (medelstorlek och tunglängd) förklarade vilka miljöer de besöker när de samlar nektar och pollen, eftersom morfologin påverkar hur effektiv en arbetare är på att hantera en viss blomma. Jag tolkar dessa resultat som att egenskaper knutna till hur en koloni utnyttjar födo-resurser i tid och rum påverkar möjligheten att utnyttja resurser i olika typer av landskap, där tillgången på resurser varierar på olika skalor i både tid och rum. Humlor med egenskaper som gör att de kan utnyttja tidiga resurser över stora rumsliga skalor och som inte är beroende av boplatser ovan jord kan ha god reproduktionsframgång även i de enkla landskapen. Egenskaper på individnivå har istället en indirekt effekt på fortlevnaden i olika landskap. Detta då arbetarnas morfologi påverkar deras val av blommor, samtidigt som det finns skillnader mellan landskapen i både mängd och artsammansättning av blommande växter.

När jag jämförde arbetarnas medelstorlek i de båda landskapstyperna, fann jag att de i genomsnitt var 2% mindre i enkla jämfört med komplexa landskap. Detta resultat var generellt över arter, dvs. även de arter som fortfarande är vanliga var mindre till storleken i enkla landskap. Jag föreslår två möjliga orsaker till detta. Antingen att arbetarna lider brist på föda under larvstadiet, vilket resulterar i mindre kroppsstorlek som fullbildade humlor. Alternativ kan det vara ett sätt för kolonin att anpassa sig till resurstillgången; att tillverka fler men mindre arbetare. En mindre arbetare kan klara sig längre utan föda och att ha en större koloni innebär en fördel i enkla landskap. I båda fallen antyder resultatet att humlorna lider brist på födo-resurser i förenklade landskap.

Försöket med pollinering av stor blåklocka skedde enbart i enkla landskap. Resultaten visade att de plantor som placerats nära en trädgård (på ca. 15m avstånd) satte mer frö än de som stod på längre avstånd (ca. 140m). Dessutom fann vi fler arter och individer av vilda bin nära en trädgård än längre ifrån. Av dessa resultat drar jag slutsatsen att pollinering, åtminstone av den växtart vi studerat, redan är negativt påverkad i enkla landskap. Resultat som styrker detta har också presenterats från andra delar av Europa och världen. Det positiva är dock att också trädgårdar kan gynna biologisk mångfald och därför kan fungera som källor för ekosystemtjänster, åtminstone till den närmsta omgivningen.

Utifrån dessa resultat drar jag slutsatsen att för att gynna mångfalden av humlor och andra vilda bin är det brådskande att ta fram och tillämpa åtgärder för att öka tillgången av blommande växter i landskapet, särskilt i slättbygder med dess förenklade landskap. Dessutom måste blommor finnas tillgängliga under hela sommarhalvåret och blomrika miljöer ligga tillräckligt tätt, så att också de arter som är aktiva sent på säsongen och rör sig över begränsade områden kan finna och utnyttja dem. Generellt sett vore ett mer komplext landskap önskvärt för att gynna biologisk mångfald och därigenom de ekosystemtjänster som vilda organismer erbjuder samhället. Detta skulle kunna öka den ekologiska hållbarheten inom jordbruket. Vi bör även uppmärksamma de positiva effekter som trädgårdar kan ha på biologisk mångfald, både i urbana miljöer och på landsbygden.

Tack Danke Thank You Obrigada Merci Gracias

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Land use intensity and landscape complexity—Analysis of landscape characteristics in an agricultural region in Southern Sweden

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ABSTRACT

It is generally recognised that agricultural intensification has lead to simplification of landscape structure, but it has not been clarified if this is a ubiquitous relationship. That is, it has been an open question whether agricultural intensity and landscape simplicity should be regarded as one single or as two separate dimensions. To evaluate this we analysed landscape data in 136 different 1 km × 1 km study sites and within a buffer zone of 2 km around each site (i.e. approximately 5 km × 5 km). The sites were distributed over a large part of the region of Scania, southernmost Sweden, an area dominated by agriculture but with large variation in both intensity and complexity. We used spatially explicit digital data on land use, digitised aerial photographs, field surveys of landscape elements and agricultural statistics. Two separate factor analyses, one for each scale of measurements (1 km and 5 km), suggest that there are five and three relevant factors for each scale respectively. At the 1 km scale, the first factor can be interpreted as describing the intensity of land use in the form of proportion arable land which is highly correlated to crop yield. The second and third factors are more connected to landscape structure and amount of small patches of semi-natural habitats. The fourth and fifth factors contain one major variable each: proportion pasture and leys respectively. The division of intensity and complexity related variables is less clear at a larger spatial scale. At the 5 km scale, factor 1 is defined almost identically as at the 1 km scale. However, factors 2 and 3 are interpreted as descriptors of dairy and livestock farming systems but also include structural variables. Our analyses suggest that land use intensity and structural complexity of landscapes are more or less separate landscape level factors, at least at smaller spatial scales. This is important to bear in mind, especially when trying to explain patterns of biodiversity change in agricultural landscapes.

1. Introduction

In Europe and elsewhere agricultural development – modernisation and intensification – has accelerated during the last 50 years. This has lead to a transformation of landscape structure, generally towards a simpler one, via changes in management and land use (Benton et al., 2003). These changes act over several spatial scales where local changes for example include larger fields and changes of management practises (e.g. increased use of agrochemicals, choice of crops and rotation schemes) (Benton et al., 2003; Tscharntke et al., 2005). At a much larger scale, acting over the whole EU, the common agricultural policy (CAP) among other things affects the choice of crops and the amount of fallow via subsidy systems (Donald et al., 2001; Wretenberg et al., 2007).

During the last half-century many groups of organisms connected to the agricultural landscape have declined dramatically (Benton et al., 2003; Tscharntke et al., 2005). A decline in numbers is, for example, evident for farmland birds (Shrubb, 2003; Lindström and Svensson, 2005) as well as for plants and insects (Baessler and Klotz, 2006; Biesmeijer et al., 2006; Fitzpatrick et al., 2007). From a biodiversity perspective, intensification results in loss and fragmentation, as well as decreased quality, of natural and semi-natural habitats. Several authors suggest that the loss of spatial and temporal heterogeneity, i.e. farmland becoming ever more simplified, is the general cause of the decline in biodiversity (Meek et al., 2002; Benton et al., 2003; Shrubb, 2003; Pywell et al., 2005; Tscharntke et al., 2005). Also land use intensity has been related with declining biodiversity (Kleijn et al., 2009). The goal of agricultural intensification is to increase the yield per unit area, and intensification can thus be estimated from crop yield data

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(Donald et al., 2001; Vepsäläinen, 2007). The degree of landscape heterogeneity (complexity) is a result of the mix of habitat types within an area, i.e. the number of land use classes and the distribution and configuration of these (Turner et al., 2001; Vepsäläinen, 2007).

Intensification and loss of heterogeneity are often considered two sides of the same coin. Several studies on the effect of agricultural activities on biodiversity in a landscape perspective have used different definitions of and proxies for land use intensity and landscape structure, e.g. the proportion of arable land (per landscape and per farm), the proportion of permanent pasture or semi-natural habitats, size of arable fields, input of inorganic fertilisers and pesticides, crop harvest data, number of land use classes within an area or diversity indexes of land use (Donald et al., 2001; Steffan-Dewenter, 2002; Jeanneret et al., 2003; Kerr and Cichlar, 2003; Roschewitz et al., 2005; Sandkvist et al., 2005; Schweiger et al., 2005; Baessler and Klotz, 2006; Rundlöf and Smith, 2006; Firbank et al., 2008). Yet other metrics used to represent structure are for example length of and structural indices on non-crop field boundaries and semi-natural habitats within a landscape (Schweiger et al., 2005; Concepción et al., 2007).

To find one single proxy variable for both intensity and complexity at least two requirements must be fulfilled. First, this proxy needs to be related to intensity and complexity in a straightforward manner. Second, intensity and complexity need to be monotonically related to each other. Firbank et al. (2008) suggest that agricultural landscapes can be described along three axes: large scale land use, local field management and landscape structure. A study in northern Germany (Roschewitz et al., 2005) showed that proportion arable land per landscape was linearly related to land use diversity (referred to as complexity) but not correlated with the proportion arable land per farm (farm specialisation).

It might be possible to separate intensity related components (such as proportion arable land and harvest data) from structural ones (such as field size, amount of small semi-natural habitats and land use diversity). In an area where landscapes span a wide range of both intensity and complexity we may thus find structurally complex landscapes with intense farming. This allows detection of independent variation of at least these two landscape factors. Being able to separate these two dimensions of variation would allow us to design landscape scale study systems (Herzog, 2005; Rundlöf et al., 2008), to evaluate the effects of structural and complexity related components on biodiversity on a landscape scale, independently of field level intensity.

How important different variables are accounting for variation across landscapes may depend on the scale, i.e. size of the study sites analysed. Purtauf et al. (2005) showed that at small and medium scales (1 km × 1 km–3 km × 3 km), management variables and local site parameters (e.g. fertiliser application, pH-value) explained most of the variation between sites, while at a larger scale (4 km × 4 km) land use variables (% of land cover) explained more. The same authors also showed that the strength of correlations between variables increased with spatial scale. Furthermore, many organisms can be expected to react to or be affected by different mechanisms at different spatial scales. It would therefore be valuable to look at data on more than one spatial scale both when analysing landscape data only and when biodiversity data is added.

The purpose of this study was to investigate if it is possible to distinguish measures of agricultural intensity from measures of landscape complexity and if so, which proxies might be used to represent them. Furthermore, we investigate if the interrelationship between measures of complexity and intensity are dependent on the scale at which the analysis is performed. We perform these analyses for the agricultural landscapes of Scania (southernmost Sweden), because this region has an unusually large variation in agricultural landscapes over a small area (ca. 120 km × 120 km). These analyses constitute an important background to any further analysis in which spatial or temporal variation in biodiversity is to be explained by the ongoing intensification and simplification of agricultural landscapes (cf. Benton et al., 2003).

2. Methods

This study is based on land use data and agricultural statistics from several sources spanning over the period 1995–2002. The study system was originally designed to survey farmland birds (Svensson, 2001), but the bird data is not presented here. Two study sites of 1 km × 1 km each were selected from each 10 km × 10 km grid square of the Swedish National Grid System and were therefore systematically distributed over the region of Scania (approx. 56°N, 13°30′E), an area of approximately 120 km × 120 km (Fig. 1).

2.1. Habitat inventory

Detailed habitat data was collected during a survey 1995–2002. The inventory was conducted by volunteers and field assistants, who made an inventory of habitats and land use classes (Svensson, 2001). Larger continuous areas of forest were excluded from the survey. From this material we have collected information on the presence of small habitats with patches of semi-natural vegetation such as stonewalls and ditches.

2.2. Digital information from the Swedish Board of Agriculture

We have utilised information from the Integrated Administration and Control System (IACS, Blockdatabasen), a yearly updated database on all registered farmland fields in Sweden, including spatially explicit data on crops and other land uses on farmland (pasture, fallow, tree plantations, etc.). In IACS, fields are reported in units of "blocks", which typically consist of one or several adjacent fields surrounded by a border that can be identified on an aerial photograph. However, within the blocks the area covered by individual crops is known. To match the time of the habitat/bird inventory we used block data from 1999 and extracted information on crops as well as the size of blocks of fields and the proportion of arable land. We define farmland as all blocks in the database with either annual crops, leys, pastures or fallow. Block data was also used to calculate the amount of non-crop field borders. Since the delineation of fields provided by this digital dataset is based on border structures seen on aerial photographs, they are more in line with how fields are actually divided by non-crop border habitat, compared to the inventory maps created during bird/habitat surveys where all land parcels were drawn (Persson, pers. obs.). We used a template border width of 2.4 m to calculate border area, since this is the average width found by two independent habitat inventories in Scania (Persson and Rundlöf, unpublished data). Their analysis showed that the width of borders did not vary between different types of landscapes, defined as homogenous or heterogenous according to criteria similar to the ones used here (mixed model, difference between two landscape types when ca 900 borders were measured at 10 sites, $F_{1,8} = 0.56$, $P = 0.5$).

It should be noted that according to the classification we have used, pastures and leys are quite different. Pastures are practically permanent, semi-natural grasslands used exclusively for grazing. They may be fertilised but often they are not, or at least not much. In contrast, leys are rotational crops where grass, sometimes mixed with clover, is cultivated for grazing or hay or silage production.

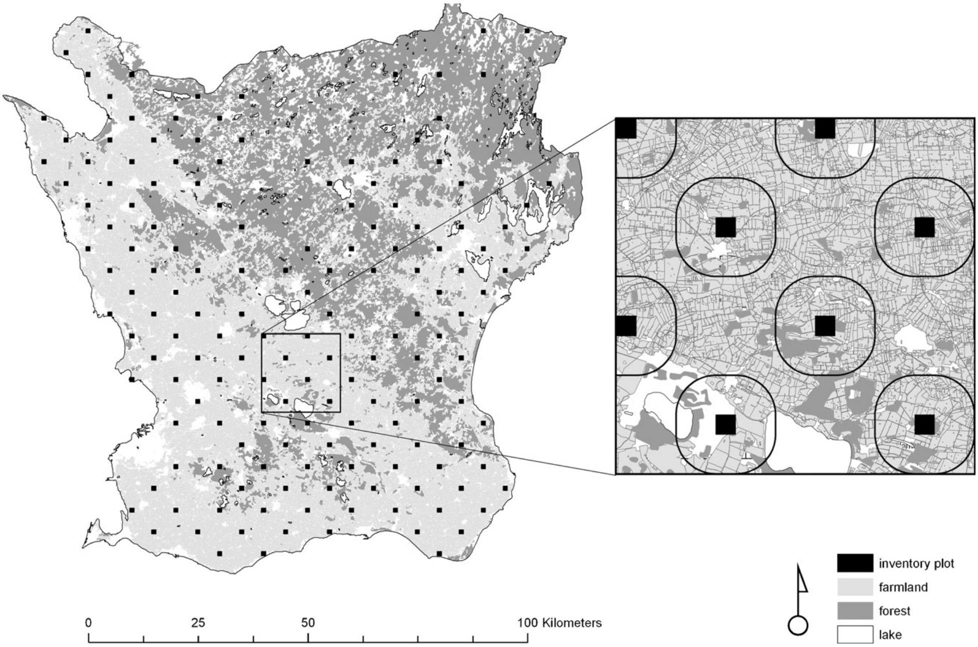

Fig. 1. Map of the study area; the region of Scania and the study sites used in the analyses. The inserted picture shows sites with 2 km buffer zones. Farmland fields, forest and lakes are drawn.

Typically, a field is used as ley for at least 2 and sometimes up to 5 years in sequence. After that it is used for other crops for some years.

2.3. Aerial photographs

By studying aerial photographs (black and white orthophotos from the Swedish Land Survey, Lantmäteriet) of each inventory plot, semi-natural habitats such as stone walls, ditches, small wood lots and single trees, field islands, permanent pastures and grasslands could be identified or verified and digitised. This gave us a detailed dataset of small, semi-natural habitats at the 1 km scale.

2.4. Corine land use data

From the satellite data of the EU programme CORINE (Coordination of Information on the Environment), data on forests, wetlands, water bodies and built-up areas for the concerned areas was extracted and used to complement information from the above mentioned sources. CORINE data is available at a 25 m × 25 m resolution.

2.5. Statistics on harvest

We used data from Statistics Sweden on normalised harvest of spring sown barley in 2006. The normalisation of harvest data results in a more robust estimate not affected by year to year variation. It describes the harvest expected in 2006 based on data for the past 15 years and so the in-data spans the whole period (1995–2002) of this study. The geographical basis for calculations of harvest is the 17 "harvest regions" of Scania; administrative regions originally based on collections of neighbouring parishes.

2.6. Data treatment

From the original 163 study sites we selected 136 sites, all containing more than 10% farmland and less than 50% of built-up areas or water bodies. All data was digitised and processed in ArcGis 9.1 (ESRI). The total area of different land use classes, field sizes and area of border habitats per landscape were calculated (Table 1). We also used a buffer zone of 2 km around each inventory plot (i.e. approximately 5 km × 5 km but with rounded corners, 2156 ha (Fig. 1)), and used block data and CORINE data to calculate average field size and area of major land use classes (Table 1). For calculation of average field size at the 1 km scale, fields were weighted by the proportion being contained within the landscape. In this way the influence of fields with only a small proportion actually within the landscape was lowered, while still being included in the calculation. All variables used in the analyses are briefly explained in Table 1.

Crop diversity was calculated for both spatial scales with the Simpson Diversity index calculated as $-\ln(D)$, where D is the sum of squared proportions of each crop type per study area (Magurran, 2004). Crops were classified as belonging to one of 11 classes of crops; spring sown cereals (mostly barley *Hordeum vulgare*, oat *Avena sativa*, but also some wheat *Triticum aestivum*), autumn sown cereals (mostly wheat and rye *Secale cereale*), sugar beet (*Beta vulgaris*), oilseeds (almost exclusively autumn sown oilseed rape *Brassica napus*), leys (cultivated grass and sometimes clover *Trifolium* sp.), potato (*Solanum tuberosum*), pea (*Pisum sativum*), fallow, pasture, other low crops (vegetables and berries), and other high crops (maize *Zea mayz*, fruit orchards and *Salix* sp.). We chose

Table 1
Definitions and characteristics of variables for the 136 sites analysed, at the two scales (1 km and 5 km) of analysis.

Variable	Explanation	1 km				5 km			
		Mean	sd	Min	Max	Mean	sd	Min	Max
Prop. farmland	Proportion crops, leys, pasture and fallow per landscape	0.717	0.254	0.122	0.987	0.675	0.264	0.063	0.976
Prop. crops	Proportion annually tilled land per landscape	0.458	0.320	0	0.953	0.456	0.284	0.002	0.938
Crop diversity	$-\ln(\text{Simpson}\,D)$ of crops divided into 11 categories	2.05	0.41	1.00	2.78	2.42	0.32	1.48	2.93
Field islands	Proportion of semi-natural habitat islands within farmland fields	0.003	0.006	0	0.040				
Contagion	Calculated in Fragstats on four land use classes: arable, semi-natural, water, forest	71.6	11.2	47.5	92.8				
Land use diversity	$-\ln(\text{Simpson}\,D)$ of arable, semi-natural, water, forest	0.538	0.331	0.042	1.182	0.774	0.372	0.109	1.857
Field size	Mean size of farm fields (ha)	12.0	16.5	0.9	108.9	9.6	6.6	1.2	29.3
Border area	Total area of field borders, stonewalls, ditches, road verges (ha)	0.030	0.011	0.009	0.068	0.028	0.009	0.005	0.051
Trees and hedges	Total area of tree- and hedgerows and solitary trees (ha)	0.037	0.029	0.002	0.227				
Prop. leys	Proportion of leys per landscape	0.116	0.140	0	0.771	0.093	0.072	0.006	0.327
Prop. pasture	Proportion permanent pasture per landscape	0.089	0.135	0	0.707	0.071	0.063	0	0.352
Spring barley	Normalised (15 year intervals) data on yield if spring sown barley (kg/ha)	5049	983	2591	6344	5049	983	2591	6344

to use only the Simpson index for diversity after we had made preliminary analyses showing that this index was very strongly correlated with the Shannon–Weaver index ($r = 0.98, p < 0.0005$ at both scales) and with total number of crops in a landscape (1 km: $r = 0.71$, $p < 0.0005$; 5 km: $r = 0.82$, $p < 0.0005$). The reason for choosing the Simpson index was that it had better statistical properties than the alternatives.

Land use diversity was calculated for both spatial scales with the Simpson Diversity index, as above, and land use was classified as belonging to one of four categories; arable land (annually tilled fields and leys), forest (larger areas of forest, production forest and small wood lots), wetland and water or semi-natural habitats (permanent pasture, non-crop border habitats, tree and hedge rows, solitary trees). Again, the Simpson index was chosen because it had better statistical properties than the Shannon–Weaver index, and they were nearly perfectly correlated (1 km: $r = 0.99$, $p < 0.0001$; 5 km: $r = 0.88$, $p < 0.0001$).

Fragstats 3.3 (McGarigal et al., 2002) was used for the calculation of another landscape index, Contagion, on raster data (vector to raster conversion in ArcGis, grid cell size 1 m), using the same four land use categories as mentioned above. This index was calculated only at the 1 km scale. The Contagion index is based on the probability of adjacent pixels belonging to the same category as the focal one and thus expresses to what degree the land use categories are inter-dispersed (McGarigal et al., 2002). We used a resolution of 1 m for the Fragstats calculations. The data extracted and used in the analyses is presented in Table 1. Where proportions of land uses were used they were arcsine-square-root transformed to normalise data and to avoid variance to be associated with the mean. Contagion is one of many landscape indices that can be calculated. We chose to use this, over the alternatives, because it has often been used in other studies, and because it is intuitively quite easy to understand.

The variables we used for analyses are presented in Table 1. A priori we expect that at least proportion farmland and proportion crops should be related to intensity. Similarly, we expect that field islands, Contagion, Simpson land use diversity, field size, border area, and area of trees and hedges should represent complexity.

Statistical analyses were done in R 2.8.1 (R Development Core Team, 2008) with the procedures factanal and cor in package stats, and gls in package nlme. We ran two separate factor analyses, one on each spatial scale of measurement (1 km and 5 km), which included 11 and 8 variables respectively (Table 1). To maximise the interpretability of the factors we used the Promax rotation method at the 1 km scale. This method allows factors to deviate from orthogonal positions so as to better represent the variables in the analysis, and it often results in variables separating more clearly between factors (Abdi, 2003). Because factors are not orthogonal we also ran correlations between the resulting factors to check for relations. At the 5 km scale we used Varimax rotation, as preliminary analyses showed that it produced factors very similar to the Promax method, but Promax factors became heavily correlated.

Because we believe that there are underlying patterns in the dataset, which may be detected via combinations of variables, we decided to use factor analysis instead of repeated separate correlations of landscape variables and agricultural statistics. This method has the advantage of letting us combine variables into a set of factors, which are more or less independent depending on the rotation method used. The factors are interpreted through the loadings (correlations) they have on the original variables (Quinn and Keough, 2002). Another and similar method is the principal component analysis, PCA. However, that method does not assume underlying patterns in the dataset and instead extracts components in order to explain as much of the variation in the material as possible (Quinn and Keough, 2002; Suhr, 2003).

We use the yield of spring barley as an indicator of agricultural intensity. We do not include it in the factor analyses, but rather test how the resulting factors are related to the yield of barley. We expect that in particular the total proportion of farmland and that of crops are measures of intensity, whereas the structural indices – land use diversity and contagion – ought to be related to complexity. The same should be true for field size, border area, tree rows and hedges. For the remaining variables it is more difficult to predict in advance if they will be related to a complexity or an intensity dimension.

In order to evaluate how the factors were related to intensity we ran generalized least squares regression (GLS) models with the harvest of spring barley as the dependent variable and the factors, their two-way interactions and quadratic terms as independent

Table 2
Results of factor analysis at the 1 km scale in the form of factor loadings, eigenvalues and the variance explained by factors. Bold numbers indicate the main loading for each variable.

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Prop. farmland	**1.002**	−0.244	0.171	0.124	0.237
Prop. crops	**0.734**	−0.105	0.086	−0.219	−0.246
Crop diversity	**0.614**	0.242	0.098	0.015	−0.273
Field islands	**0.369**	0.108	−0.053	0.042	−0.059
Contagion	0.114	**−0.864**	0.036	0.006	−0.095
Land use diversity	−0.121	**0.874**	−0.055	0.053	0.117
Field size	**0.690**	−0.030	**−0.537**	0.003	0.163
Border area	0.172	−0.090	**0.939**	0.072	0.112
Trees and hedges	0.090	0.104	**0.534**	−0.074	0.092
Prop. leys	−0.035	0.043	0.088	**0.972**	−0.120
Prop. pasture	0.028	0.191	0.136	−0.115	**0.796**
Eigenvalues	2.60	1.71	1.54	1.04	0.91
% Cumulative variance explained	24	39	53	63	71

variables. We accounted for spatial autocorrelation in the data by adding a spatial spherical correlation structure (Dormann et al., 2007). The spherical correlation structure fit the data better than alternative structures. For each spatial scale, we ran all possible models with the factors, their interactions and quadratic terms, and for each scale we identified the best model based on the AIC value (Burnham and Anderson, 2002).

3. Results

Based on the variation explained by each factor, we retained factors with eigenvalues above or close to 1, resulting in five factors at 1 km and three factors at the 5 km scales respectively (Tables 2 and 3). At the 1 km scale we also tested retaining four and six factors, but since four factors explained substantially less total variation and the sixth factor had very low eigenvalue (0.76) we chose to keep five.

At both spatial scales (Tables 2 and 3), the first factor includes proportion of farmland, the proportion of annual crops per landscape, the size of fields and crop diversity. In the 1 km scale analyses, the area of field islands were not clearly bound to any factor but had its highest loading on factor 1 (this variable was not available at the 5 km scale). At the 1 km scale factor 2 contained the indices on structure and land use diversity; Contagion and Simpson land use diversity. At the 5 km scale factor 2 contained land use diversity together with proportions of pasture and leys. At the 1 km scale factor 3 represented the amount of field borders and other border habitats (stone walls, ditches, etc.), trees and hedgerows and the size of fields. At the 5 km scale factor 3 represented field borders and the proportion of leys in the landscape. To use the same set of variables as for the 5 km scale, we also ran the 1 km analysis with only field borders (i.e. no information on other semi-natural habitats). Since it resulted in the same structure of the factors (data not shown), we chose to use the more detailed dataset for further interpretations. The proportions of leys and pastures were represented by one factor each in the 1 km analysis (factors 4 and 5, respectively), while at the larger scale leys, pastures and land use diversity were combined into factor 2 and leys and field borders were combined into factor 3.

Table 3
Results of factor analysis at the 5 km scale in the form of factor loadings, eigenvalues and the variance explained by factors. Bold numbers indicate the main loading for each variable.

	Factor 1	Factor 2	Factor 3
Prop. crops	**0.814**	−0.541	0.202
Crop diversity	**0.721**	−0.046	0.253
Prop. farmland	**0.850**	−0.338	0.373
Field size	**0.952**	−0.246	−0.168
Land use diversity	−0.221	**0.741**	−0.098
Prop. pasture	−0.127	**0.813**	0.124
Prop. leys	−0.227	**0.625**	**0.566**
Border area	0.476	0.008	**0.877**
Eigenvalues	3.152	2.070	1.386
% Cumulative variance explained	39	65	83

Table 4
Correlations between factors from the factor analysis at the 1 km scale and between factors. *R* values and level of significance shown ($^{*}P > 0.05$, $^{**}P > 0.01$, $^{***}P > 0.001$).

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Factor 2	0.318***				
Factor 3	0.008	−0.297***			
Factor 4	0.070	−0.075	−0.239**		
Factor 5	0.314***	−0.184*	0.009	−0.170*	

As we have used the Promax rotation method at the 1 km scale, factors are not completely orthogonal but instead allow a cleaner split of the variables between factors, increasing interpretability. Correlations between factors were moderate (Table 4; highest R^2 value 0.10), and hence we see no problem in using the Promax rotation for the interpretability of the factors.

We tested to what extent the different factors were related to the yield of spring barley using GLS. At the 1 km scale the best GLS model showed that harvest of spring barley was strongly related to only factor 1 (Standardized regression coefficient $\beta_1 = 0.15$, $t_{134} = 4.30$, $P < 0.0005$; Fig. 2A). The second best model had a ΔAIC = 6.2, and thus fit much worse (Burnham and Anderson, 2002). At the 5 km scale the relation is even stronger, with spring barley being related to all three factors ($\beta_1 = 0.44$, $t_{132} = 6.58$, $P < 0.0005$; $\beta_2 = -0.16$, $t_{132} = 3.21$, $P < 0.002$; $\beta_3 = 0.13$, $t_{132} = 2.89$, $P < 0.004$; Fig. 2B–D). The second best model had a ΔAIC = 1.8, and was similar to the best model except it did not contain factor 3. All other models had $\Delta\text{AIC} \gg 3$.

4. Discussion

4.1. Intensity versus complexity

In this study we show that intensity and complexity are to a large extent independent landscape factors. The first factor generated by factor analysis of farmland landscape variables was related to the proportion of landscape under intense land use and to harvest data. The second and third factors contained variables connected to structure and complexity; border habitats, field size and land use diversity and configuration. Naturally, the result of a factor analysis depends on the variables included. The variables we have used are a mixture of what we believe are intensity related ones (proportion of farmland and annual crops), structural ones (field size, amount of small habitats and linear elements and diversity and configuration of land use classes) and in addition proportion pastures, leys and crop diversity. The proportion of farmland per landscape has previously been used as a descriptor of landscape complexity (e.g. Roschewitz et al., 2005). In this analysis it had the highest score on factor 1, at both scales analysed, and was strongly connected to harvest data and proportion annual crops but not to complexity metrics. A surprising result was that field size was represented by factor 1 at the 5 km scale and by almost equal scores on factors 1 and 3 at the 1 km scale. Field size is thus not related to other structural variables in a simple way, but is instead the variable connecting intensity and complexity at the 1 km scale.

Based on the reasoning above we propose that agricultural landscapes can indeed vary along more than the axis of intensity.

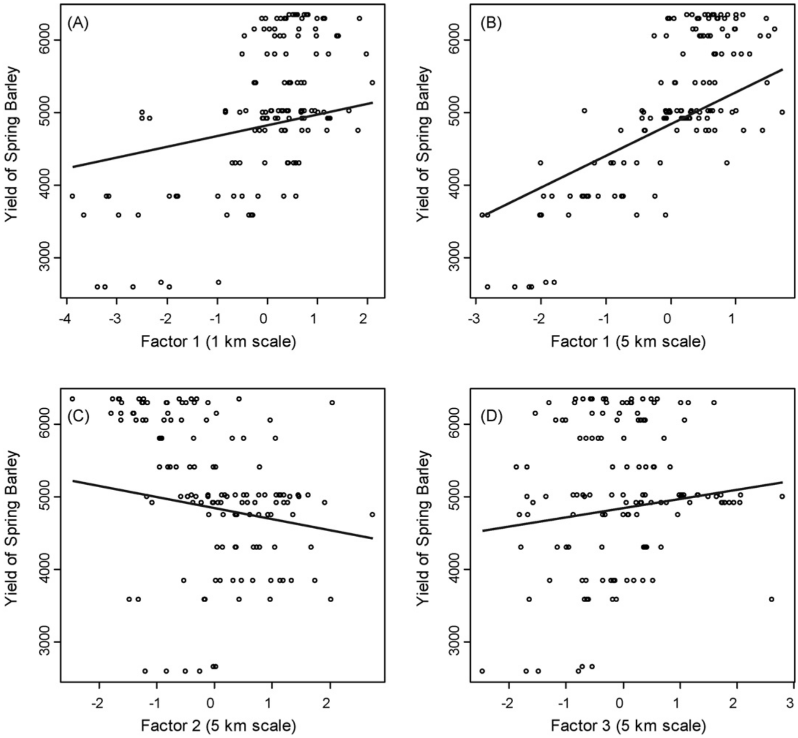

Fig. 2. The yield of spring barley (kg/ha) in relation to factors resulting from factor analysis. A is for the 1 km scale, and B, C, and D are for the 5 km scale.

This means that we cannot equate high intensity with low complexity but rather should look at these factors as two practically separate axes (see Fig. 3 for a conceptual picture), which has also been suggested by Firbank et al. (2008). We believe that the second component of landscape variation found here, complexity or structure, can be represented by the size, shape and distribution of land use units including small semi-natural habitats. Using PCA, similar results were found in central Spain (Concepción et al., 2007) and Brittany, France (Millán de la Peña et al., 2003), where the first components were interpreted as intensity related and the second ones as components of patch shape and natural vegetation or openness/connectivity respectively.

Based on the above we suggest that care should be taken to keep separate the concepts of land use intensity and landscape complexity. These are not the opposites of one another but important variation occurs in each of these dimensions independent of the other dimension.

4.2. The spatial scale of analysis

The division between land use intensity and landscape structure proved to be slightly less evident at the larger spatial scale, where proportion pasture and leys were represented together with structural variables in factors 2 and 3. This follows the reasoning by Purtauf et al. (2005), that general land use data are more closely correlated at larger spatial scales and are thus harder to split into separate axes and also that they tend to dominate over management related data. At this larger scale the

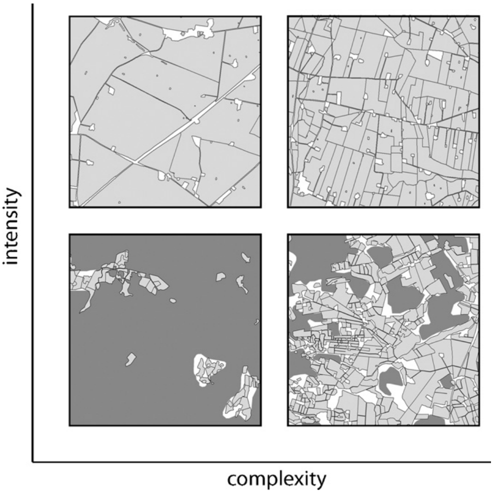

Fig. 3. A conceptual graph of how two of the factors from the analysis, representing intensity and complexity, can be visualised. As an example, four landscapes from the study area are placed in the graph to depict the landscape types indicated at the four positions respectively. Medium grey represents farmland and dark grey represents forest.

different components of structure are not as tightly connected, but are split between all three factors; factor 1 field size, factor 2 land use diversity and factor 3 field borders. The 1 km analysis gave a cleaner split of variables over factors and thus captured the variation in the dataset used here well, but it should be noted that field size was split between factors 2 and 3. The smaller scale makes possible a more detailed description of structure and complexity via variables built on field surveys and aerial photographs. Because of the labour intensity of field surveys and of digitising maps and aerial photographs, we do not have detailed information on small semi-natural habitats at the 5 km scale. We thus have to rely on field borders as a proxy. Despite this, field border was quite well separated from intensity (factor 1), even though that factor included field size. The agricultural landscape follows some large scale general patterns of intensity and land use, but there are many local exceptions leading to an uncoupling of these general patters, detectable at smaller spatial scales. If a study concerns organisms dependent on resources within 1 km one should be cautious about characterising the landscape by variables gathered at a larger scale. One should also be aware that any classification of a landscape made at a large spatial scale can be misleading on a local scale.

4.3. Indicators of farmland intensity and complexity

One aim of this study was to find general indicators of land use intensity and complexity. An already popular one, the proportion farmland in the landscape, was here represented in the first factor together with proportion of annual crops. Factor 1 was also highly correlated with the yield of spring barley, which indicates management intensity. We believe that both the proportion of total farmland per landscape and the proportion of annual crops are good indicators of land use intensity. These variables are also consistent over both spatial scales. The size of fields on the other hand, is not a robust measure of intensity since it was represented in both the intensity and structure related factors. This indicates that field size can either be regarded as a measure of intensity or a structurally related one. This would mean that using only field size as a landscape descriptor includes information on both intensity and complexity. The amount of field borders is a much better indicator of complexity. However, indices on land use diversity and structure (Simpson land use diversity and Contagion) were separated from small habitats and field borders and may be considered to be a different aspect of landscape complexity.

4.4. Landscape type and farming systems

From our results we can identify not only the intensity and complexity of landscapes, but also the landscapes shaped by different farming systems. The intensity factor was positively related to the proportion of annual crops. However, there are landscapes where pasture and leys are more dominating than annual crops. It is interesting to note that the proportion permanent pasture in the landscape was not simply the opposite of the intensity related first factor, something found in a PCA at a 10 km × 10 km scale study in Britain (Siriwardena et al., 2001). Instead, proportion pasture was a factor of its own, or in combination with leys and land use diversity depending on the spatial scale of analysis. This means that a landscape rich in pastures is not simply the opposite of an intensely farmed one, but an altogether different landscape type and direction of farming. The same is true for landscapes dominated by leys, which is mainly for cattle and dairy production. A similar result was found in Brittany, France, with one principal component describing the intensity of farming and another describing the openness of the landscape (Millán de la Peña et al., 2003). In that case the openness was also associated with maize used for milk production. This also follows the suggestion of Firbank et al. (2008), that agricultural landscapes can be described from crop management, structure and large scale land use. High production of annual crops (here represented by spring barley) was weakly positively associated with factor 3 representing complexity at the 5 km scale, while a high proportion of leys in the landscape was positively associated with field borders. This indicates that presence of border habitats is related to the direction of farming, in this case cattle and dairy, and could be interpreted such that intensification has different effects on the original landscape structure, depending on the farming system (Millán de la Peña et al., 2003). Recent studies in Sweden and England (Rundlöf and Smith, 2006; Gabriel et al., 2009) suggests that landscapes with a lower potential for high production farming are associated with a higher proportion of organic farming which is associated with low intensity management practices. The characteristics of the landscape thus influences the direction of farming (e.g. specialisation in plant or animal production) which in turn has an effect on further transformations of landscape structure and intensity of management.

Of course, it could be argued that pasture and leys might indicate intensity of beef or dairy production, i.e. a different kind of intensity than measured by yield of barley. To an extent, this could be true for leys, which are required for high dairy production. However, pastures as defined here are permanent, semi-natural habitats which are practically unfertilised. They are mostly not very productive and would in many cases probably be forested if it was not for the agri-environment schemes. It should also be noted that the yield of barley is estimated per hectare if it is grown, and not as the sum over an area. Thus, low barley yield mostly indicates low productivity of the land. At the 5 km scale, factor 2 that contained both leys and pasture was negatively associated with barley yield, which indicates this fact. In contrast, factor 3 that contained leys, but not pasture, was positively associated with barley yield. This probably indicates areas of high dairy production that does not rely on pastures.

Historically, cattle husbandry and the creation of pastures seem to follow different local patterns than do crop production. Pastures were often found on stony, too wet or otherwise unproductive land not suitable for crop production (Emanuelsson et al., 1985). Today some of these old pastures are still grazed although a substantial part of them were planted with trees during the 19th and 20th centuries. During the same period dry and stony meadows were transformed into pastures while moist meadows were drained and turned into leys or crop fields (Emanuelsson et al., 1985).

Scania has a mixed geology, with different soil textures ranging from sand to clay. Most common is glacial soil with clayey till dominating in the southwest and sandy till in the northeast. In the most productive areas of Scania the naturally fertile soils and the early introduction of artificial fertilisers made animal husbandry, pastures and meadows unprofitable in relation to cereal crop production and today these areas almost completely lack meadows and most also lack pastures (Emanuelsson et al., 1985). Areas still rich in pastures are mostly those that lie on soils of fairly low fertility. This is similar to the results of Gabriel et al. (2009).

The diversity of crops was positively related to intensity (factor 1) and to field size at both spatial scales, i.e. the larger the proportion of farmed land, fields and harvests are, the higher was crop diversity. This does not follow the general impression of a more complex landscape also hosting a diverse array of crops. The reason for this could be that also where fields and farms are smaller, today's farmers use the same common crops as in intensely farmed areas and the only pattern visible is the one where more farmland within the investigated area makes more different crops possible.

Our study is conducted in a rather small area with highly variable agriculture, which partly reflects the variable natural conditions. Our conclusions, that farming intensity and complexity are independent, are in line with several other recent studies (Millán de la Peña et al., 2003; Concepción et al., 2007; Firbank et al., 2008) and we expect them to be quite general. However, this deserves to be verified by studies from other parts of the world and across larger geographic and geological gradients.

4.5. Summary and conclusions

From the factor analyses we concluded that there were indeed several different and unrelated components to be extracted from landscape and agricultural data. We suggest that the most important ones be interpreted as farming intensity and landscape complexity, and also farming direction. Intensity can be represented by harvest data or proportion of farmland or annual crops; the latter being easy to calculate with access to spatially explicit agricultural statistics. Complexity can be well represented by land use diversity and amount of field borders, and small semi-natural habitats. To describe complexity we have used detailed information (at the level of that available from aerial photographs) but more easily available data, e.g. the length of field borders, is also valuable.

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References

Abdi, H., 2003. Factor rotations in factor analyses. In: Lewis-Beck, M., Bryman, A., Futing, T. (Eds.), Encyclopedia of Social Sciences Research Methods. Sage, Thousand Oaks, CA.

Baessler, C., Klotz, S., 2006. Effects of changes in agricultural land-use on landscape structure and arable weed vegetation over the last 50 years. Agric. Ecosyst. Environ. 115, 43–50.

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

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel declines in pollinator and insect-pollinated plants in Britain and the Netherlands. Science 313, 351–354.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Verlag, New York.

Concepción, E.D., Díaz, M., Baquero, R.A., 2007. Effects of landscape complexity on the ecological effectiveness of agri-environment schemes. Landscape Ecol. 23, 135–148.

Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird population. Proc. R. Soc. Lond. B 268, 25–29.

Dormann, C.F., McPherson, J.M., Araujo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kuhn, I., Ohlemuller, R., Peres-Neto, P.R., Reineking, B., Schroder, B., Schurr, F.M., Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30, 609–628.

Emanuelsson, U., Bergendorff, C., Carlsson, B., Lewan, N., Nordell, O., 1985. Det skånska kulturlandskapet. Bokförlaget Signum, Lund, Sweden.

Fitzpatrick, U., Murray, T.E., Paxton, R.J., Breen, J., Cotton, D., Santorum, V., Brown, M.J.F., 2007. Rarity and decline in bumblebees—a test of causes and correlates in the Irish fauna. Biol. Conserv. 136, 185–194.

Firbank, L.G., Petit, S., Smart, S., Blain, A., Fuller, R.J., 2008. Assessing the impacts of agricultural intensification on biodiversity: a British perspective. Phil. Trans. R. Soc. B 363, 777–787.

Gabriel, D., Carver, S.J., Durham, H., Kunin, W.E., Palmer, R.C., Sait, S.M., Stagl, S., Benton, T.G., 2009. The spatial aggregation of organic farming in England and its underlying environmental correlates. J. Appl. Ecol. 46, 323–333.

Herzog, F., 2005. Agri-environment schemes as landscape experiments. Agric. Ecosyst. Environ. 108, 175–177.

Jeanneret, Ph., Schüpbach, B., Luka, H., 2003. Quantifying the impact of landscape and habitat features on biodiversity in cultivated landscapes. Agric. Ecosyst. Environ. 98, 311–320.

Kleijn, D., Kohler, F., Baldi, A., Batary, P., Concepcion, E.D., Clough, Y., Diaz, M., Gabriel, D., Holzschuh, A., Knop, E., Kovacs, A., Marshall, E.J.P., Tscharntke, T., Verhulst, J., 2009. On the relationship between farmland biodiversity and land-use intensity in Europe. Proc. R. Soc. Lond. B 276, 903–909.

Kerr, J.T., Cichlar, J., 2003. Land use and cover with intensity of agriculture for Canada from satellite census data. Glob. Ecol. Biogeogr. 12, 161–172.

Lindström, Å., Svensson, S., 2005. Övervakning av fåglarnas populationsutveckling—årsrapport för 2004. Ekologiska Institutionen, Lunds Universitet, Lund.

Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Publishing, Oxford, UK.

McGarigal, K., Cushman, S.A., Neel, M.C., Ene, E., 2002. FRAGSTATS, Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following website: www.umass.edu/landeco/research/fragstats/fragstats.html.

Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H., Nowakowski, M., 2002. The effect of arable field margin composition on invertebrate biodiversity. Biol. Conserv. 106, 259–271.

Millán de la Peña, N., Butet, A., Delettre, Y., Morant, P., Burel, F., 2003. Landscape context and carabid beetles (Coleoptera, Carabidae) communities of hedgerows in western France. Agric. Ecosyst. Environ. 94, 59–72.

Purtauf, T., Thies, C., Ekschmitt, K., Wolters, V., Dauber, J., 2005. Scaling properties of multivariate landscape structure. Ecol. Indic. 5, 295–304.

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

Quinn, G., Keough, M., 2002. Factor analysis. In: Experimental Design and Data Analysis for Biologists, Cambridge University Press, Cambridge, UK, pp. 458–459.

R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Roschewitz, I., Thies, C., Tscharntke, T., 2005. Are landscape complexity and farm specialisation related to land-use intensity of annual crop fields? Agric. Ecosyst. Environ. 105, 87–99.

Rundlöf, M., Smith, H.G., 2006. The effect of organic farming on butterfly diversity depends on landscape context. J. Appl. Ecol. 43, 1121–1127.

Rundlöf, M., Bengtsson, J., Smith, H.G., 2008. Local and landscape effects of organic farming on butterfly species richness and abundance. J. Appl. Ecol. 45, 813–820.

Sandkvist, M., Pärt, T., Wretenberg, J., Söderström, B., 2005. Häckfåglar i jordbrukslandskapet. Länsstyrelsen i Skåne Län.

Schweiger, O., Maelfait, J.P., van Wingerden, W., Hendrickx, F., Billeter, R., Speelmans, M., Augenstein, I., Aukema, B., Aviron, S., Bailey, D., Bukacek, R., Burel, F., Diekötter, J., Dirksen, M., Frenzel, M., Herzog, F., Liira, J., Roubalova, M., Bugter, R., 2005. Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. J. Appl. Ecol. 42, 1129–1139.

Shrubb, M., 2003. Birds, Scythes and Combines: A History of Birds and Agricultural Change. Cambridge University Press, New York, NY, USA, pp. 1–371.

Siriwardena, G.M., Baillie, S.R., Crick, H.Q.P., Wilson, J.D., 2001. Changes in agricultural land-use and breeding performance of some granivorous farmland passerines in Britain. Agric. Ecosyst. Environ. 84, 191–206.

Steffan-Dewenter, I., 2002. Landscape context affects trap-nesting bees, wasps and their natural enemies. Ecol. Entomol. 27, 631–637.

Suhr, D., 2003. Principal component analysis vs. exploratory factor analysis. SUGI 30, Statistics and Data Analysis, pp. 203–230.

Svensson, S., 2001. Övervakning av jordbrukslandskapets fåglar i Skåne, manual för fältarbetet. Ekologiska institutionen, Lunds Universitet, Lund, 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.

Turner, M.G., Gardner, R.H., O'Neill, R.V., 2001. Landscape Ecology in Theory and Practice: Pattern and Process. Springer Science + Business Media, LLC, New York, NY, USA.

Vepsäläinen, V., 2007. Farmland birds and habitat heterogeneity in an intensely cultivated boreal agricultural landscape. Academic dissertation, Faculty of Biosciences University of Helsinki, Finland.

Wretenberg, J., Lindström, Å., Svensson, S., Pärt, T., 2007. Linking agricultural policies to population trends of Swedish farmland birds in different agricultural regions. J. Appl. Ecol. 44, 933–941.

II

Seasonal persistence of bumblebee populations is affected by landscape context

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ABSTRACT

1. Large scale reductions in the abundance and diversity of bumblebees in Western Europe, North America and China have been attributed to agricultural intensification as well as landscape scale losses and fragmentation of natural and semi-natural, flower-rich grasslands. However, it has been suggested that mass flowering crops could subsidise bumblebee populations.
2. In southern Sweden, we surveyed bumblebee communities and their foraging resources in agricultural landscapes of contrasting complexity, defined by size of arable fields and amount of permanent grazed pastures.
3. We showed that, after the flowering of oilseed rape (*Brassic napus*), simplified landscapes contained substantially less herbaceous flower resources and a lower proportion of perennials, compared to complex ones.
4. The seasonal pattern of bumblebee abundance differed between landscape types. Initially bumblebee abundance was equal in both landscape types. However, by late July there was a sharp decline in simple landscapes while abundances instead continued to increase in complex landscapes. This suggests that despite a good start, a large proportion of bumblebee colonies may fail to reproduce in simple landscapes.
5. 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 wild 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 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 *B. napus*.
6. The initially high abundances of workers in simple landscapes, as well as the fact that also many of the regionally rarer species persist in these landscapes, suggests that there may be an inflow of queens from nearby complex landscapes. If so, further simplification or abandonment of complex landscapes may threaten bumblebee populations also in simple landscapes were they still persist.

KEYWORDS: *Bombus;* agriculture; mass flowering crops; pollinator; permanent grassland

1. INTRODUCTION

Pollinating insects have decreased dramatically in Western Europe, North America and Asia since the 1950's (Potts et al. 2010). This is also true for bumblebees (*Bombus spp.*), which are important pollinators of wild plants and crops (Cederberg, Pettersson & Nilsson 2006;Winfree 2010;Winfree et al. 2008). The 20th century has seen a massive intensification of agricultural practices (Stoate et al. 2001;Stoate et al. 2009). This has left much of Western Europe with only fragments of natural or semi-natural habitats and simplified landscapes (Benton, Vickery & Wilson 2003;Tscharntke et al. 2005) In Europe, the combined decrease in bumblebee abundance and species distribution has been suggested to be related to such agricultural intensification and the concomitant loss of food plants (reviewed by Goulson, Lye & Darvill 2008;Potts et al. 2010;Williams & 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 particular negative effects on bumblebees since these habitats provide both nesting habitat and foraging resources (Fitzpatrick et al. 2007;Goulson, Lye & Darvill 2008;Hendricks et al. 2007). Remaining permanent grasslands can still act as a source of bumblebees to the surrounding landscape (Öckinger & Smith 2007) and to farmland fields (Morandin et al. 2007).

A large plant species pool may result in a high probability that bumblebees find forage during their whole colony cycle. Agricultural intensification has influenced plant diversity negatively, both within crop fields and in field borders (Baessler & Klotz 2006;Gabriel, Thies & Tscharntke 2005;Ma 2008;Rundlöf, Edlund & Smith 2010). Perennial plants are preferred by bumblebees (Fussell & Corbet 1992;Goulson et al. 2005;Potts et al. 2009) but have declined more than annuals in simplified landscapes (Smart et al. 2006). Forage quality may therefore also have declined. Bumblebee populations have been suggested to benefit from Mass Flowering Crops (MFCs); in North Western Europe predominantly oilseed rape, *Brassica napus*. The overwhelming, but short term flush of resources (approximately three to four weeks) offered by *B. napus* occur in early May to early June, i.e. in Scandinavia during an early stage of the bumblebees' colony cycle and may aid colonies during establishment and early growth (Knight et al. 2009;Westphal, Steffan-Dewenter & Tscharntke 2006b). However, it has been questioned if it also boosts reproduction (Herrmann et al. 2007;Westphal, Steffan-Dewenter & Tscharntke 2009).

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, Ward & Chittka 2006;Schmid-Hempel & Schmid-Hempel 1998). To our knowledge, there have been no previous studies exploring the spatial and temporal dynamics of total bumblebee communities in differently simplified agricultural landscape and related this to the total availability of flower resources. Many studies have focused on surveys of bumblebee density in one or a few particular habitats, such as semi-natural or flower enriched habitats (Heard et al. 2007;Herrmann et al. 2007;Kells, Holland & Goulson 2001;Pywell et al. 2006). However, if landscape comparisons are made from such surveys they may underestimate the total difference in abundance between landscapes since bumblebee workers can be expected to aggregate into such habitats. The degree of aggregation may also depend on 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 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 effects of differences in landscape structure and amount of permanent grasslands on bumblebees and their resource flowers, we performed surveys in two landscape classes: *complex*, with small agricultural fields, mixed farming and a high proportion permanent grasslands and *simple*, with large fields, mainly crop production and practically lacking permanent grasslands. During June and July 2006, we surveyed bumblebees and their flower resources in common farmland habitats; edges and non-crop border zones and border zones of crop fields, leys and permanent pastures We hypothesised to find an overall higher abundance and richness of bumblebees in complex landscapes. We further expected that total bumblebee abundance is higher in complex landscapes, but that because of aggregation this difference is less pronounced regarding habitat specific densities.

2. METHODS

2.1 Landscape design

The study was carried out in the province of Skåne in southernmost Sweden (approx. 56°N, 13°30'E, figure 1a), a region dominated by agriculture but with a large variation in land use intensity and landscape complexity (Persson et al. 2010). To select study landscapes we used 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 uses on farmland (pasture, fallow, tree plantations etc.). Based on the amount of permanent, grazed pastures and the size of farmland fields, we selected ten circular landscapes (radius 3km). Five landscape were characterised as simple and without permanent pasture (< 1% pasture) and five as complex and with permanent pasture (>9% pasture), (figure 1b). Data was processed in ArcGis 9.2 (ERSI, Redlands, CA).

The amount of pastures in the landscape is related to other landscape scale variables (Persson et al. 2010). Complex landscapes therefore also had a lower proportion of annual crops, more leys and less oilseed rape (*B. napus*) than simple landscapes (table 1). According to the classification used here pastures are permanent, non-fertilized, semi-natural grasslands used exclusively for grazing. In contrast, leys are rotational crops where grass mixed with clover (*Trifolium repens* or *T. pratense*) is cultivated for grazing, hay or silage production. Typically, a field is used as ley for two to five years in sequence. There were no significant differences between landscape classes of three other potential bumblebee foraging habitats: fallow, *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

Bumblebee surveys

From each circular landscape we selected six 500m × 500m cells along the north-south axis for the bumblebee survey (figure 1b). During field visits we identified two 100 × 2m transects of each of the following habitats: (1) non-flowering crop field, (2) ley field, (3) pasture. Following the methodology of Rundlöf, Nilson & Smith (2008), transects were placed in the field/ley/pasture margin such that 1m covered the field/ley/pasture, and 1m covered its non-crop border zone. In simple landscape it was naturally not possible to sample pastures in all cells.

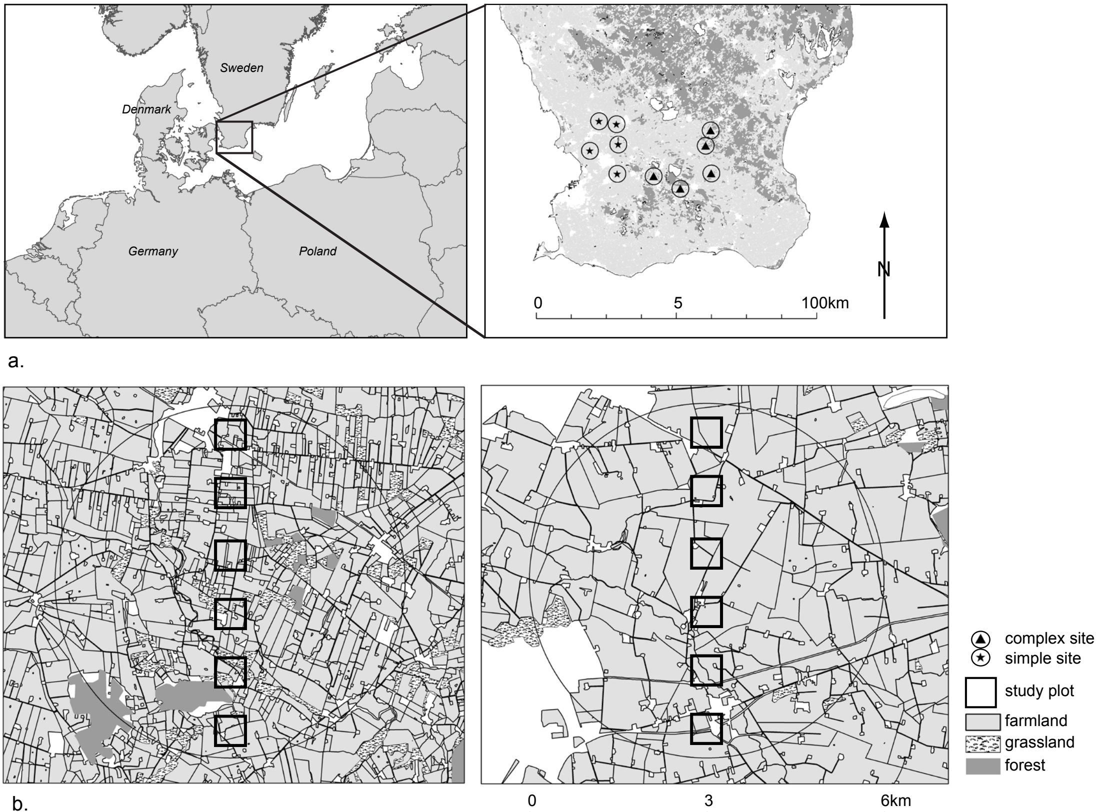

Figure 1: (a) The study region and the ten landscape sites used (radius 3 km) out of which five were located in simple and five in complex landscapes, respectively. (b) Example of a typical complex (left) and simple (right) landscape and the bumblebee inventory setup with six 500× 500m grid-cells per site. For differences between landscape classes see table 1. Data originate from the IACS data base (the Swedish Board of Agriculture) and were processed in ArcGis 9.2.

Bumblebees (*Bombus spp.*) were recorded using transect walks adopted from the standard line transects method developed for butterfly surveys (Pollard 1977;Rundlöf, Nilsson & Smith 2008). We did not discriminate between workers, queens or males. We counted all bumblebees seen within a 1m by 200m zone on each side of transects, i.e. one zone lying within the crops/leys/pastures and the other side being the 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 & Corbet (1987) and Holmström (2002). In case of uncertainty, the bumblebee was noted as the most common species. The species of the visited flower was also noted. Because of the difficulty of separating *B. lucorum* and *B. terrestris* in the field (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.

Flower surveys

We surveyed flowering plants in twelve 500m × 500m cells per circular landscape (six along the north-south, and six along east-west axis) at the start of the study in mid June. We surveyed five habitat-types: pasture, ley, crop field, road verge, non-crop field border. Two 0.25m^2-sqares of each of habitat were randomly selected within each of the twelve 500m × 500m cells. i.e. in total 30m^2 was surveyed in each circular landscape. Plant taxonomy followed Mossberg et al. (1992). To make flower resources more comparable between plant species, they were noted in units based on equivalents of flower heads; for *Asteraceae* and *Dipsaceae* the number

Table1: Land-cover in simple and complex landscapes within a 3km radius. Differences analysed with t-tests; when dfs deviate from 1,8 tests we allowed for heterogeneous variances since that decreased the AIC-value. Significant differences are typed in bold.

Landscape Class	**Complex** (n=5)		**Simple** (n=5)		**Test of difference between groups**	
Landscape Variables	mean	std	mean	std	Fdf	P
Fieldsize (ha)	6.08	4.37	21.52	7.32	$16.39_{1,8}$	**0.0037**
Pasture (ha)	487.43	178.29	17.61	10.38	$34.60_{1,4.0}$	**0.0041**
Brassica napus fields (ha)	48.16	62.80	208.58	42.29	$22.44_{1,8}$	**0.0015**
Leys (ha)	797.86	158.85	72.27	33.03	$100.00_{1,4.4}$	**0.004**
Annual crops (ha)	605.55	370.71	2325.76	60.45	$104.87_{1,4.2}$	**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	$15.52_{1,4.0}$	**0.017**
Field borders (ha)	25.87	11.03	5.68	6.32	$12.61_{1,8}$	**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

of flower heads, for *Fabaceae* the numbers of racemes and for *Campanulaceae*, *Lamiaceae* and *Scrophulariaceae* flower stalks.

Land-cover data

To describe landscapes and also to be able to quantify flower resources and bumblebees, we gathered data on land-cover on farmland fields from IACS, and processed this in ArcGis 9.2. To estimate the amount of linear non-crop habitats we noted the quantity (length and width) of all border habitats during field surveys in twelve 500m × 500m cells per circular landscape (same cells as the flower survey).

2.3 Calculations and statistical methods

Statistics

All statistical analyses were done in SAS 9.2 for Windows (SAS Institute Inc., Cary, NC). In one case we used a General Linear Model (SAS Proc GLM), 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, we used random factors nested at several levels, see sections below. Fixed effects were tested using F-tests with the degrees of freedom being estimated using the Kenward-Roger method. When covariance estimations of random factors were occasionally non-significantly negative we used the Nobound option, since the Kenward-Roger method otherwise give 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 or were used for further calculations, standard errors were however calculated from data aggregated at the level they were tested at, using SAS Proc Means.. When log(density) was used as response variable, we first added the smallest non-zero value to all values to avoid zeros.

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

Response variable	Basic model	Fdf	P	Interactions	Fdf	P
N.o. species per landscape	landscape class	$<0.001_{1,17}$	0.96	landscape class × survey round	$2.12_{2,15}$	0.15
	survey round	$4.27_{2,17}$	**0.031**			
	log (Area)	$3.64_{1,17}$	**0.0073**			
Habitat specific density per landscape	landscape class	$1.16_{1,7.4}$	0.31	**landscape class × survey round**	$7.46_{2,16}$	**0.0051**
	survey round	$18.21_{2,17.4}$	**<0.0001**	**habitat type × survey round**	$2.93_{10,78.6}$	**0.0036**
	habitat type			landscape class × habitat type	$0.69_{5,39.0}$	0.63
				landscape × survey r. × habitat	$1.17_{9,68.9}$	0.33
Total n.o. bumblebees per landscape	landscape class	$23.85_{1,8}$	**0.0012**	**landscape class × survey round**	$5.84_{2,16}$	**0.013**
	survey round	$6.59_{2,16}$	**0.0082**			
Total amount of flowers per habitat	**landscape class**	$11.03_{1,8.3}$	**0.010**	landscape class × habitat type	$1.87_{3,24}$	0.17
	habitat type	$0.24_{3,27}$	0.87			
Flower density per habitat and plant type	landscape class	$4.76_{1,8.2}$	0.060	landscape class × habitat type	$0.81_{1,2.0}$	0.37
	habitat type	$7.99_{1,36.2}$	**<0.0001**	**landscape class × plant type**	$6.26_{5,43.0}$	**0.0002**
	plant type	$1.74_{1,43.0}$	0.19			

Bumblebee habitat specific density

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

Bumblebee species richness

We summed the total number of species detected and the area surveyed per landscape and survey round and analysed data using a Generalised Linear Mixed Model (SAS Proc Glimmix). The fixed part of the model was: N species=landscape class, survey round, surveyed area, landscape class × survey round. Random factor was landscape.

Estimation and analysis of total numbers of bumblebees

To estimate total abundances of bumblebees per landscape we used data on habitat-specific and landscape specific densities of bumblebees predicted from the model described above, and multiplied with the area of each habitat type per landscape. Habitat data was attained from the landscape survey and IACS data. We used mean values of bumblebee density over crop, field and pasture borders to multiply with the total area of non-crop linear elements (field borders, road verges, borders of open ditches). However during field visits we noted that the structure and flora in borders to open ditches differed between landscape classes such that those in complex landscapes resemble other non-crop borders, while in complex landscapes they were often several meters wide, grassy protective zones of small water courses. Because of this they constitute a large part of all non-crop habitats in those landscapes but contribute few flower resources. Ditch borders had on average 78% of the flower density in other borders of complex and 16% in simple landscapes. We assumed that the number of bumblebees found in a habitat is positively related to the amount of flower resources (e.g. Bäckman & Tiainen 2002;Kleijn & van Langevelde 2006;Pywell et al. 2005) and therefore corrected for the lower resource value of ditch borders by multiplying ditch area with 0.78 and 0.16 for complex and simple sites, respectively.

We analysed total bumblebee abundance (Linear Mixed Model) with the following model: log n.o. bumblebees per landscape = survey round, landscape class, survey-round × landscape class, with random factor landscape.

Estimation and analysis of total amount of resource flowers

From our flower survey, we calculated the density per habitat type per landscape of all species considered nectar and/or pollen resources for bumblebees (Fussell & Corbet 1992;Rundlöf, Nilsson & Smith 2008; Appendix table A3). As for total bumblebee numbers, density was then multiplied with the total area of each habitat per site, giving us 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 class, habitat type, landscape class × habitat type, and with random factors landscape and habitat type × landscape.

Analysis of resource quality and flower visitation frequencies

Perennial flowers are preferred by bumblebees (Fussell & Corbet 1992), so to test for qualitative differences in the flora between landscape classes, plants were divided into perennials vs. annuals and biennials. We used a Mixed Model with log(flowerdensity+1) as dependent and the fixed factors landscape class, habitat type, plant type, landscape class × plant type, habitat type × plant type and plant type × habitat type × landscape class. The random structure included landscape and habitat type × landscape.

From the data on flower visitation frequencies we calculated the Shannon diversity index of visited flower species per landscape, all three survey rounds combined, and used a General Linear Model; Diversity = landscape class, to detect potential differences between landscape classes.

Analysis of bumblebee abundance in relation to resources

We performed Pearson correlations (SAS Proc Corr) between total bumblebee abundance per landscape and survey round and the amount of four potential resources or resource habitats: oilseed rape, ley fields, permanent pastures and total flower abundance.

3. RESULTS

Out of a total of 1560 bumblebee individuals 1007 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), *B. lapidarius* (206), *B. ruderarius* (184) and *B. 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 *B. lucourum* pooled, Appendix table A1). There was a significant difference in species richness between survey rounds (table 2), with the 1st survey round being poorer (3.0±0.7, mean±sem) than the following rounds (2nd survey 2: 6.1±0.5; 3rd survey: 5.9±0.9).

3.2 Bumblebee habitat specific density

We detected seasonally dependent effects of both landscape context and habitat type on the density of bumblebees (table 2, figure 2a,c). There was no difference in density between landscape classes during survey round 1 or 2 (simple main effect: $F_{1,19.8}=1.96$, P=0.18; $F_{1,15.9}=1.47$, P=0.24)), but during survey round 3 our model predicted on average approximately a threefold higher density in complex landscapes ($F_{1,15.5}=8.11$, P=0.012; figure 2a).

The abundance of bumblebees in border habitats, and to some degree crop fields, also changed over time, while this was not the case in leys and pastures (table 2, figure 2c), as verified by the significant simple main effects for these habitat types (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; crop field $F_{2,88.7}$=6.85, P=0.0017). This pattern was the same irrespective of landscape class (non-significant interactions habitat type × survey-round × landscape class; table 2).

3.3 Total number of bumblebees

The total number of bumblebees within a landscape depended on both survey round and landscape class (significant interaction survey round × landscape class, table 2, figure 2b). This was because of significantly more bumblebees in complex landscapes during the 3rd survey round (simple main effect $F_{1,24}$=31.60, P<0.0001), but no significant difference between landscape classes during the 1st and 2nd surveys ($F_{1,24}$=2.05, P=0.16; $F_{1,24}$=2.17, P=0.15, respectively). This resulted in that complex landscapes held ca. 30 times more bumblebees than simple ones at the 3rd survey in late July, (figure 2b).

3.4 Flower resources

Total number of flowers

Complex landscapes held more wild resource flowers from pastures, leys, road verges, and field borders than did simple landscapes. There were on average (mean±stdev) 17.9±16.9 flower units (log-scale) in complex sites and 14.4±13.2 in simple landscapes; i.e. approximately 30 times more resources in complex sites. Non-flowering crop fields were surveyed but contributed no

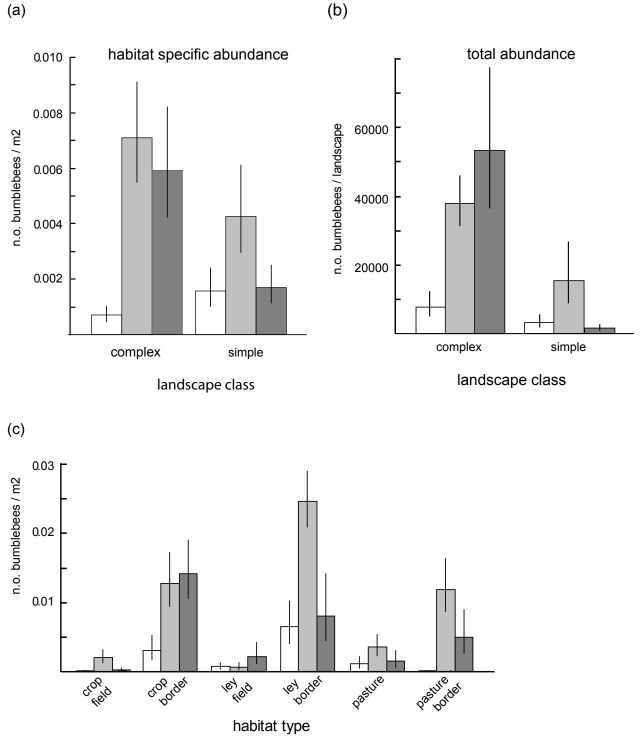

Figure 2: Bumblebee abundance over time. Open bars: 1st survey, light grey: 2nd survey, dark grey: 3rd survey. (a) Habitat specific density (mean±sem) of bumblebees in the two landscape classes surveyed; complex and simple, back-transformed from log-transformed data. (b) Total numbers (mean±sem) of bumblebees per landscape class, estimated from habitat specific densities and total area of each habitat per landscape. The difference between landscape classes in the 3rd survey-round is statistically significant. (c) Mean density ± SEM of bumblebees in the habitats surveyed; back-transformed from log-transformed data. The increased density over time seen in all border habitats is statistically significant. During the first round no bumblebees were found in borders of pastures or crop fields.

resource flowers at any site. Habitats not included were flowering crops (other than clover leys), fallows, flowering trees and bushes and private gardens. However, except for oilseed rape, which had almost ceased to flower at the time of this survey, the amount of these are either similar between landscape classes (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).

Quality of flower resources

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). The relative density of perennials was higher in pastures, leys, road verges and field borders (simple main effects of habitat, pasture: $F_{1,43}$=25.00, P<0.0001; ley: $F_{1,43}$=12.45, P=0.0010; road verge: $F_{1,43}$=13.13, P=0.0008; field border: F1,43=5.81, P=0.020), while fallows showed the opposite pattern; more annuals/biennials than perennials ($F_{1,43}$=9.10, P=0.0043). There was no significant difference between the relative density of the two plant types in crop fields ($F_{1,43}$=0.07,P=0.79), but densities of flowers were very low in this habitat.

Flower visitation frequency

Bumblebees were recorded foraging on 38 different plant species and a total of 885 flower visits were recorded (Appendix, table A2). There was a significantly higher diversity among visited flowers in complex compared to simple sites (Shannon diversity index, complex: 2.09±0.18, simple: 1.43±0.12; $F_{1,8}$=8.6, P=0.019).

3.5 Relation of bumblebees numbers to potential resources

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). Naturally, area of pasture, ley and total amount of flowers were also all positively correlated to each other and negatively correlated to area of oilseed rape (data not shown, but see table 1 for land-cover data).

4. DISCUSSION

In this study we show that the relationship between bumblebee abundance and landscape complexity has a strong seasonal component. Patterns of abundance interacted with both time and landscape context such that, despite initially equal density and total abundance in both landscape classes, bumblebee numbers decreased sharply in simple landscapes in late July, whereas they continued to increase in complex landscapes. We also show that the late season (but not early season) bumblebee abundance was positively related to the area of leys, pastures and total flower resources in the landscapes. The initially equal bumblebee densities in the two landscape types, in spite of a low availability of herbaceous wild flower resources in the simple landscapes, indicates that nest establishment and early season growth in simple landscapes is subsidised by other resources, possibly oilseed rape or flowering trees and shrubs. However only in more complex landscapes with higher availability of flower resources (i.e. wild flowers and possibly leys), was colony growth sustained until the mid/late of the season.

Bumblebee queens establish colonies in early spring and the ability to reproduce depends on the build-up of a force of workers to provision the brood (e.g. Benton 2006;Schmid-Hempel & Schmid-Hempel 1998). The ability of a colony to attain resources from the surrounding depends on several factors; e.g. the number of workers, their foraging ranges (Westphal, Steffan-Dewenter & Tscharntke 2006a), size (Goulson et al. 2002) and foraging efficiency in different habitats (Heinrich 1979;Peat, Tucker & Goulson 2005). Thus, reproductive success by the end of the season will depend on the resource availability during the whole season and the spatial distribution of these resources.

It has previously been suggested that MFCs lead to an early build up of large colonies (Herrmann et al. 2007;Westphal, Steffan-Dewenter & Tscharntke 2009), colonies which later can not find enough forage but are attracted to the few patches of flowers available in non-crop habitats (Heard et al. 2007). We could not detect any positive effect of oilseed rape on bumblebee abundance, in part since this study (with two contrasting landscape classes) was not designed for that purpose. However, we believe that the lack of landscape differences in density and total abundances during June and early July can indeed have been caused by colony growth subsidised by the higher availability of oilseed rape in simple landscapes, while complex landscapes instead offered more wild flower resources. Complex landscapes contained ca. 30 times more herbaceous flowers and also a larger proportion of perennials. At the end of July, ca 6 weeks after the end of *B. napus* flowering, that was also the approximate relation in bumblebee numbers between the two landscape classes (figure 2b). It is therefore logic to conclude that the lack of resources following MFCs limited continued growth of colonies in simple landscapes. Since colony size has been shown to be positively related to production of young queens and males (Ings, Ward & Chittka 2006;Westphal, Steffan-Dewenter & Tscharntke 2009), the pattern found here thus indicates an overall lower reproduction in simple landscapes. Furthermore, since we did not discriminate between workers, males and queens, a part of the large difference in total abundance may indeed be attributed to a higher production of sexual offspring in complex landscapes. This has also been found in a later study in this same area (Persson, Rundlöf & Smith 2011, Ch. III this thesis).

Interestingly the total number of species found did not differ significantly between landscape classes. Out of the 17 social bumblebee species present in the province of Scania, out of which four are considered very rare and one regionally extinct (ArtdataBanken 2010;Holmström 2007), we encountered nine in our five simple landscapes and eleven in our five complex landscapes. This result is supported by other studies in the same region using similar landscape classifications (Rundlöf, Nilsson & Smith 2008;Persson & Smith 2011, Ch. III this thesis). The crucial question for persistence of bumblebee populations in simplified landscapes is if colonies have enough resources to complete reproduction, i.e. if the population crash detected here occurs before or after new queens and males are produced. Indeed, Westphal et al. (2009) suggested that larger colonies but not more sexual offspring per colony was produced by bumblebees in response to high abundances of MFCs. The fact that early total abundances did not differ between landscape classes and that a similar total species richness was found in both classes, therefore either suggest that colonies of simple and MFC-rich landscapes have a higher growth rate during May and June or that there is an annual inflow of queens to simple landscapes from more complex areas. The latter would imply source-sink population dynamics (Dias 1996; Pulliam 1988) where simple landscapes act as sinks, at least for a subset of the species. Quite possibly a combination of these scenarios could be the case, at least for species with an ability to efficiently utilise abundant MFC resources (Westphal, Steffan-Dewenter & Tscharntke 2006a) and with queens prone to disperse. Considering their large size and that they are not yet tied to a nest, queens are thought to have far better dispersal abilities than workers and may travel several kilometres after hibernation (Lepais et al. 2010). If dispersal mainly takes place in spring, the availability of fields of flowering oilseed rape and possibly also spring flowering trees and shrubs, 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 than in complex landscapes, or that winter survival and colony establishment is higher in simple landscapes.

It is known that bumblebees prefer to forage on perennials (e.g. Fussell & 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, Mänd & Williams 2002). In addition to more flowers, complex landscapes generally contained a higher proportion of perennial flowers, i.e. both more and higher quality forage for bumblebees. Furthermore, the flower visits recorded were significantly more diverse in complex than in simple landscapes and flower visitation frequencies (Appendix, table A3) indicated that bumblebees in complex landscapes visited a whole array of perennial flowers not visited (or even available) in simple landscapes. Apart from lack of flowers, this may also contribute to the low abundance in simple landscapes since low pollen and protein diversity in forage has been shown to negatively affect the immune response at the colony level for the honeybee, *Apis mellifera* (Alaux et al. 2010).

In this setup, the difference between landscape classes during the last survey in mid July was much more pronounced when total numbers instead of habitat specific densities per landscape were considered. For example, habitat specific densities in the 3rd survey round were only a little more than threefold higher in complex compared to simple landscapes while estimated total abundance was 30-fold higher. Thus, the use of habitat specific densities underestimates landscape differences in abundance, especially when measured in “good” habitats situated in otherwise impoverished landscapes (Heard et al 2007). It may therefore be important to estimate total numbers when translating abundances of mobile pollinators such as bumblebees into pollination services, not the least since total numbers is likely to be more important than densities within particular habitats (Klein et al. 2007;Rader et al. 2009).

There is an east-west gradient which coincides with the landscape classification such that the simple sites have a more westerly position than the complex ones (figure 1a). Since spring and summer temperatures are somewhat higher in western compared to inland landscapes (SMHI 2010), this could results in that bumblebee activity in simple landscapes started approximately half a week to a week earlier. The high early abundance of bumblebees in simple landscapes may thus in part be caused by earlier emergence of queens and establishment of colonies. In combination with the more abundant MFC resources, colonies in simple landscapes may therefore have reached a stage of more rapid growth by the first survey in mid June, compared to those complex landscapes. However, we also tested for effects of day number on density during the 3rd survey-round and this was non-significant (data not shown). Therefore the crash during the 3rd round can not be explained solely by a few days earlier colony establishment, onset of daughter queen production and degeneration, Instead it is likely that colonies, because of more abundant flower resources, lived longer and grew large later in the season in complex landscapes.

In conclusion, we show that contrary to expectations, both simple and complex agricultural landscapes of southern Sweden hosted initially high abundances of bumblebees, but that a peak season crash of populations appeared in simple, intensively managed landscapes. We explain this crash with the lack of wild flower resources resulting from fewer and poorer flower-rich habitats such as non-crop border zones and permanent grasslands. On the other hand, we found a relatively high bumblebee species richness also in simple landscapes. The initially high abundance and species richness could indicate an in-flow from source populations inhabiting more complex areas. Thus, actions to avoid simplification or abandonment of complex landscapes may therefore benefit bumblebees also in adjacent more simplified landscapes. Furthermore, 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, even 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.

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6. REFERENCES

Alaux,C., Ducloz, F., Crauser, D. & Le Conte, Y. (2010) Diet effects on honeybee immunocompetence. Biology Letters.

ArtdataBanken. (2010) Rödlistan -Sök arter. http://snotra.artdata.slu.se/artfakta/GetSpecies.aspx?SearchType=Advanced. Accessed 2010-12-01

Bäckman,J.P. & Tiainen, J. (2002) Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera: Bombus and Psithyrus). Agriculture, Ecosystems & Environment 89, 53-68.

Baessler,C. & Klotz, S. (2006) Effects of changes in agricultural land-use on landscape structure and arable weed vegetation over the last 50 years. Agriculture Ecosystems & Environment 115, 43-50.

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

Benton,T.G., Vickery, J. A. & Wilson, J. D. (2003) Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology & Evolution 18, 182-188.

Cederberg,B., Pettersson, M. W. & Nilsson, L. A. (2006) ArtDatabanken, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Fitzpatrick,U., Murray, T. E., Paxton, R. J., Breen, J., Cotton, D., Santorum, V. & Brown, M. J. F. (2007) Rarity and decline in bumblebees - A test of causes and correlates in the Irish fauna. Biological Conservation 136, 185-194.

Fussell,M. & Corbet, S. A. (1992) Flower Usage by Bumble-Bees: A Basis for Forage Plant Management. The Journal of Applied Ecology 29, 451-465.

Gabriel,D., Thies, C. & Tscharntke, T. (2005) Local diversity of arable weeds increases with landscape complexity. Perspectives in Plant Ecology, Evolution and Systematics 7, 85-93.

Goulson,D., Lye, G. C. & Darvill, B. (2008) Decline and Conservation of Bumble Bees. Annual Review of Entomology 53, 191-208.

Goulson,D., Hanley, M. E., Darvill, B., Ellis, J. & Knight, M. (2005) Causes of rarity in bumblebees. Biological Conservation 122, 1-8.

Goulson,D., Peat, J., Stout, J. C., Tucker, J., Darvill, B., Derwent, L. C. & Hughes, W. O. (2002) Can alloethism in workers of the bumblebee, Bombus terrestris, be explained in terms of foraging efficiency? Animal Behaviour 64, 123-130.

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. Biology Letters 3, 638-641.

Heinrich,B. (1979) Bumblebee economics. Harvard University Press, Cambridge.

Hendricks,F., Maelfait, J., Van Wingerd, W., Schweiger, O., Speelmans, M., Aviron, S., Augenstein, I., Billeter, R., Bayley, D., Bukacek, R., Burel, F., Diekötter, T., Dirksen, J., Herzog, F., Liira, J., Roubalova, M., Vandomme & Bugter, R. (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. Journal of Applied Ecology 44, 340-351.

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. Molecular Ecology 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. Landscape and Urban Planning 31, 21-37.

Ings,T.C., Ward, N. L. & Chittka, L. (2006) Can commercially imported bumble bees out-compete their native conspecifics? Journal of Applied Ecology 43, 940-948.

Kells,A.R., Holland, J. M. & Goulson, D. (2001) The value of uncropped field margins for foraging bumblebees. Journal of Insect Conservation 5, 283-291.

Kleijn,D. & van Langevelde, F. (2006) Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. Basic and Applied Ecology 7, 201-214.

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. Proceedings of the Royal Society B: Biological Sciences 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 Conservation and Diversity 2, 116-124.

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. Molecular Ecology 19, 819-831.

Ma,M. (2008) Multi-scale responses of plant species diversity in semi-natural buffer strips to agricultural landscapes. Applied Vegetation Science 11, 269-278.

Mänd,M., Mänd, R. & Williams, I. H. (2002) Bumblebees in the agricultural landscape of Estonia. Agriculture, Ecosystems & Environment 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 and Applied Ecology 8, 117-124.

Öckinger,E. & Smith, H. G. (2007) Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. Journal of Applied Ecology 44, 50-59.

Peat,J., Tucker, J. & Goulson, D. (2005) Does intraspecific size variation in bumblebees allow colonies to efficiently exploit different flowers? Ecological Entomology 30, 176-181.

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. Agriculture Ecosystems & Environment 136, 169-176.

Pollard,E. (1977) A method for assessing changes in butterfly abundance. Biological Conservation 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. Journal of Applied Ecology 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. Trends in Ecology & Evolution 25, 345-353.

Prys-Jones,O.E. & Corbet, S. A. (1987) Naturalist's Handbooks 6. Bumblebees. Cambridge University Press.

Pywell,R., Warman, E., Carvell, C., Sparks, T., Dicks, L., V, Bennett, D., Wright, A., Critchley, C. & Sherwood, A. (2005) Providing foraging resources for bumblebees in intensively farmed landscapes. Biological Conservation 121, 479-494.

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. Biological Conservation 129, 192-206.

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. Journal of Applied Ecology 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. Biological Conservation 141, 417-426.

Schmid-Hempel,R. & Schmid-Hempel, P. (1998) Colony performance and immunocompetence of a social insect, Bombus terrestris, in poor and variable environments. Functional Ecology 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. Journal of Applied Ecology 43, 1128-1137.

Stoate,C., Baldi, A., Beja, P., Boatman, N., Herzon, I., van Doorn, A., de Snoo, G., Rakosy, L. & Ramwell, C. (2009) Ecological impacts of early 21st century agricultural change in Europe - A review. Journal of Environmental Management 91, 22-46.

Stoate,C., Boatman, N. D., Borralho, R. J., Carvalho, C. R., Snoo, G. R. & Eden, P. (2001) Ecological impacts of arable intensification in Europe. Journal of Environmental Management 63, 337-365.

Svensson,B. (2002) Foraging and Nesting ecology of bumblebees (Bombus spp.) in agricultural landscapes in Sweden. Department of Ecology and Crop Production Science.

Tscharntke,T., Klein, A. M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. Ecology Letters 8, 857-874.

Westphal,C., Steffan-Dewenter, I. & Tscharntke, T. (2009) Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. Journal of Applied Ecology 46, 187-193.

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. Ecological Entomology 31, 389-394.

Williams,P.H. & Osborne, J. (2009) Bumblebee vulnerability and conservation world-wide. Apidologie 40, 367-387.

Winfree,R. (2010) The conservation and restoration of wild bees. Annals of the New York Academy of Sciences 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. Journal of Applied Ecology 45, 793-802.

APPENDIX

Table A1. Number of bumblebees of different species observed per landscape class and the total area surveyed during the three rounds of the survey. All individuals not determined to species are here denoted *Bombus spp.*

Survey round	**1**		**2**		**3**		
Landscape class	complex	simple	complex	simple	complex	simple	Total
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. soroëensis	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)	27950	16950	32700	18000	31750	18150	

APPENDIX

Table A2. Plants included as foraging resources for bumblebees in this study.

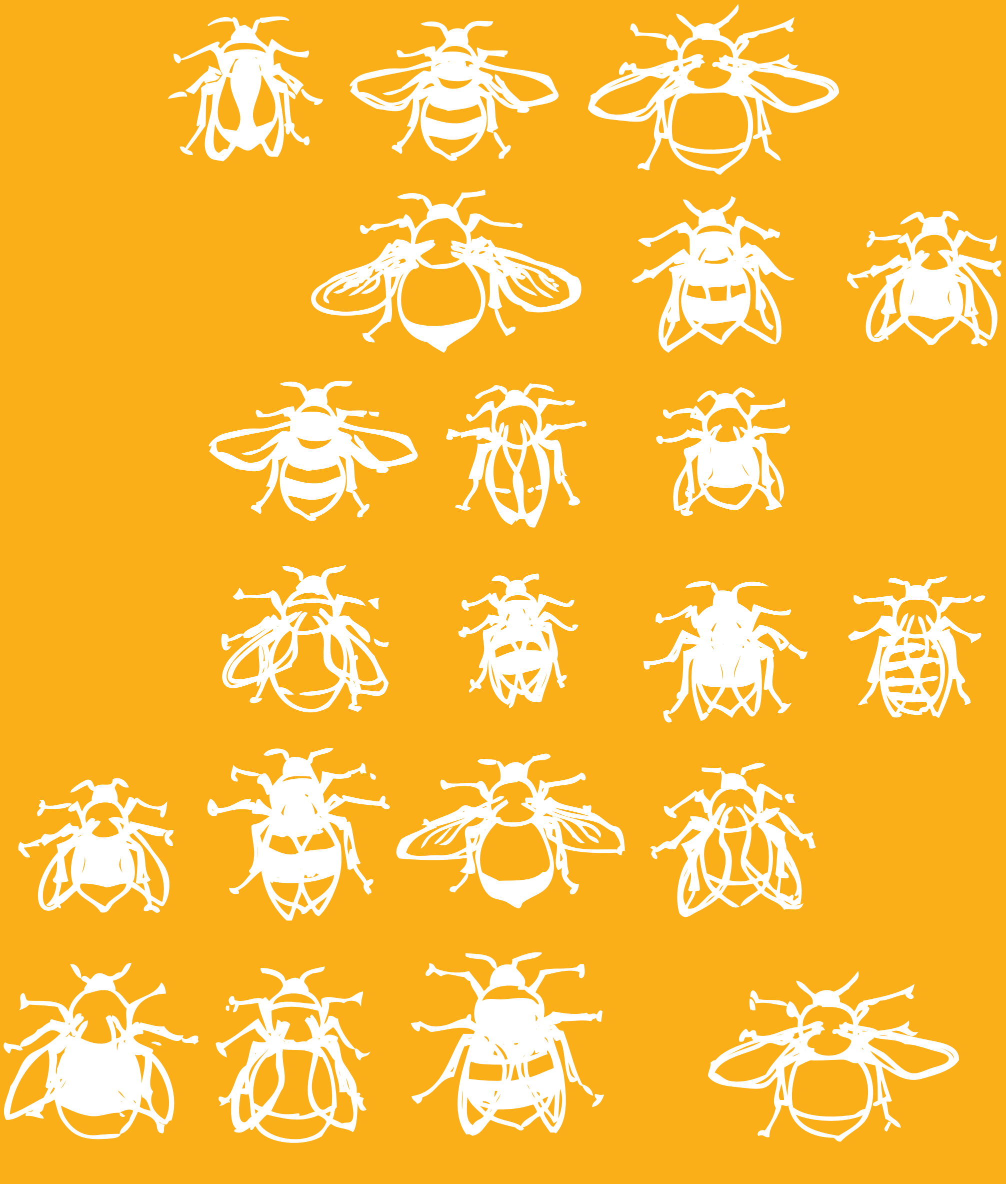
Achillea ptarmica
Anchusa arvensis
Anchusa officinalis
Anthyllis vulneraria
Aquilegia vulgaris
Armeria maritima
Barbarea vulgaris
Bunias orientalis
Butomus umbellatus
Campanula spp.
Cardamine pratensis
Centarurea scabiosa
Centaurea cyanea
Centaurea jacea
Chamomilla spp.
Cirsium spp.
Convolvulus arvensis
Crepis spp.
Echuim vulgare
Epilobium spp.
Eupatorium cannabinum
Filipendula ulmaria
Fragaria spp.
Galeopsis spp.
Geum urbanum
Geum vulgare
Helichrysum arenarium
Hypericum spp.
Impatiens spp.
Jasione montana
Knautia arvensis
Lamium spp.
Lathyrus linifolius
Lathyrus pratensis
Leontodon autumnalis
Leucanthemum vulgare
Linaria vulgaris
Lotus corniculatus
Lychnis flos-cuculi
Lysimachia spp.
Matricaria perforata
Medicago spp.
Melilotus spp.
Oonis campestris
Oonis repens
Papaver spp.
Potentilla spp
Prunella vulgaris
Ranunculus spp.
Rhinanthus spp.
Rosa spp.
Rubus spp
Sedum spp.
Senecio vulgaris
Silene latifolia
Silene vulgaris
Sinapis spp
Sonchus spp.
Symphytum spp.
Taraxacum spp.
Trifolim hybridum
Trifolium pratense
Trifolium repens
Trollius europaeus
Tropogon spp.
Vicia cracca
Vicia hirsuta
Viola arvensis

APPENDIX

Table A3. Flower visits by bumblebees recorded during the three survey-rounds in complex and simple landscapes respectively. Frequently visited plants (>4% of visits) and their visitation frequencies are in bold.

Survey round	**1**		**2**		**3**		**TOTAL**	
Landscape class	complex	simple	complex	simple	complex	simple	complex	simple
Plant species								
Brassica rapa	0	1	0	1	0	0	0	2
Lamium album	1	45	2	22	0	1	3	68
Filipendula ulmaria	0	0	10	0	1	0	11	0
Epilobium angustifolia	0	0	1	0	16	5	17	5
Knautia arvensis	0	0	0	0	0	2	0	2
Leontodon autumnalis	0	0	3	1	0	0	3	1
Symphytum spp.	14	0	4	0	0	0	18	0
Echuim vulgare	4	0	10	7	27	0	41	7
Hypericum spp.	0	0	20	2	32	3	52	5
Cichorium intybus	0	0	0	0	0	4	0	4
Cirsium arvense	0	0	1	9	6	0	7	9
Vicia cracca	1	0	19	5	11	1	31	6
Centaurea cyanea	0	0	5	11	6	5	11	16
Galeopsis speciosa	0	0	21	22	11	0	32	22
Anthyllis vulneraria	0	0	0	1	0	0	0	1
Stellaria graminea	0	0	0	0	0	0	0	0
Galeopsis spp.	1	0	7	0	25	0	33	0
Lathyrus pratensis	0	0	7	0	1	0	8	0
Helichrysum arenarium	0	0	0	0	9	0	9	0
Rubus idaea	12	0	31	0	0	0	43	0
Armeria maritima	0	0	2	0	0	0	2	0
Taraxacum spp.	0	0	0	2	0	0	0	2
Rhinanthus minor	0	0	5	0	0	0	5	0
Myosotis spp.	0	0	0	1	0	0	0	1
Anchusa officinalis	0	0	3	1	36	0	39	1
Cirsium palustre	0	0	2	0	8	0	10	0
Aegopodium podagraria	0	0	7	0	0	0	7	0
Trifolium pratense	4	0	42	2	83	4	129	6
Trifolium repens	1	2	64	10	39	2	104	14
Papaver spp.	0	0	1	7	0	0	1	7
Achillea millefolium	0	0	0	0	0	0	0	0
Rosa spp.	0	0	2	1	2	0	4	1
Campanula spp	0	0	0	0	6	0	6	0
Cetarurea scabiosa	0	0	2	9	31	19	33	28
Pentaglottis sempervirens	0	0	4	0	0	0	4	0
Stachys palustris	0	0	0	0	3	0	3	0
Arctium spp.	0	0	0	0	0	9	0	9
Viola arvensis	0	0	2	0	0	0	2	0

III



Bumblebees show trait-dependent tolerance to structural simplification of agricultural landscapes

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ABSTRACT

1. In spite of large-scale losses of bumblebees attributed to agricultural intensification, some species still remain common also in areas with intense agriculture and simplified landscape structure. It has been suggested that certain morphological, ecological and life-history traits make these species more tolerant to the landscape changes imposed by contemporary agriculture.

2. To investigate this, we surveyed bumblebees in flower-rich non-crop habitats in landscapes of contrasting structure: "complex" landscapes composed of small crop-fields and "simple" ones composed of larger fields and therefore with less non-crop field borders. We compared habitat and landscape variation in abundance of bumblebees with different traits.

3. Colony cycle length, coefficient of variation of proboscis length and three interrelated traits, queen emergence, colony size and nesting habitat, interacted with landscape class to explain bumblebee abundances. We suggest that those traits, alone or in combination, affect the vulnerability of bumblebees to landscape simplifications such that early queen emergence, below ground nesting and a large colony in combination with a short colony cycle and low variation in proboscis length increase the chances of successful reproduction also in simple landscapes.

4. The composition of trait groups differed between the surveyed habitat types. This most likely reflects differences in the flora of the surveyed habitats and that bumblebee workers prefer to forage from those flowers that fit their morphological requirements, e.g. regarding size and corolla depth.

5. We suggest that bumblebees can be described by their traits in two different ways; one group of traits connected to worker morphology and physiology acting on the individual workers' choice of plants and foraging efficiency in different habitats, and a second group describing how colonies utilise resource in the wider landscape over space and time.

6. Synthesis and applications. Remedies to the ongoing loss of bumblebees from farmland landscapes must include actions to increase the fit of resources to the less successful groups, both at the level of the individual worker and at level of the colony. Thus, to aid declining bumblebee species, preferred flowers must be available throughout the season and within a distance allowing detection and utilisation also by colonies with few workers.

KEYWORDS

Bombus; clover leys; diet breadth; garden; foraging; life-history traits; nesting; phenology; social insects

1. INTRODUCTION

Several recent studies, meta-analyses and reviews have highlighted the decline of pollinating insects in general and of bees in particular from regions dominated by agriculture (Biesmeijer et al. 2006;Cameron et al. 2011;Carre et al. 2009;Goulson, Lye & Darvill 2008a;Kosior et al. 2007;Potts et al. 2010;Roulston & Goodell 2010;Williams et al. 2010;Williams & Osborne 2009;Winfree 2010). The dependence of both wild plants and crops on insect pollinators for plant reproduction, fruit and seed set point to the urgency of reversing this decline (Kearns, Inouye & Waser 1998;Klein et al. 2007;Ricketts et al. 2008). Generally, the reasons for the negative trends of pollinators has been assumed to be large-scale intensification of land-use and management of agricultural landscapes, causing losses of natural and semi-natural habitats and their associated food plants (e.g. reviewed by Goulson, Lye & Darvill 2008a;Williams & Osborne 2009;Winfree 2010).

Bumblebees have indeed experienced large scale declines in response to agricultural intensification, but some species still remain common even in areas with intense agriculture and simplified landscape structure (Goulson, Lye & Darvill 2008a;Kosior et al. 2007;Williams 1982). The reason for this is not well understood, but several different morphological, ecological and life-history traits have been proposed to affect persistence in intensively farmed landscapes. Below we outline these, as well as put forward the degree of intra-specific variation in individual-based traits as an additional, but so far largely overlooked, factor which might modify bumblebee responses to landscape simplifications.

Suggested traits include worker body size (Westphal et al. (2006)), colony size (Rundlöf, Nilsson & Smith 2008;Westphal, Steffan-Dewenter & Tscharntke 2006), phenology of the queen and colony (Fitzpatrick et al. 2007;Williams, Colla & Xie 2009), nesting habitat (Williams et al. 2010) and diet breadth (Bommarco et al. 2010;Goulson, Lye & Darvill 2008b;Kleijn & Raemakers 2008;Williams et al. 2010). Furthermore the ability and propensity for dispersal of queens (Darvill et al. 2010), the range of the climatic niche and the proximity to the range edge (Williams, Colla & Xie 2009;Williams, Araujo & Rasmont 2007) may affect sensitivity to habitat disturbance and fragmentation.

Thorax width is strongly (non-linearly) related to flight capacity and foraging ranges of bees in general (Gathmann & Tscharntke 2002;Greenleaf et al. 2007). It could thus inform about the spatial scale at which a bumblebee worker can attain resources from the surrounding landscape when foraging (Darvill, Knight & Goulson 2004;Westphal, Steffan-Dewenter & Tscharntke 2006). In situations where resources are scarce and fragmented, larger foraging ranges could positively influence the rate of nectar and pollen influx to the colony, and therefore also the fitness of the colony.

Proboscis (or tongue) length is strongly negatively correlated with diet breadth in pollen plants (Goulson, Lye & Darvill 2008b). Tongue length thus indirectly informs us of the degree of food plant specialization. Long tongue also indicates a preference for pollen from the *Fabaceae* family (Goulson, Lye & Darvill 2008b). Consequently the loss of unimproved grasslands and pastures rich in *Fabaceae* may have been more severe for long tongued species.

Intra-specific variation in individual-based traits may be as important as mean values. Previous studies have used mean values of thorax width or wingspan, as proxies for flight ability and foraging range of bees in general (Greenleaf et al. 2007) and for bumblebees (Westphal, Steffan-Dewenter & Tscharntke 2006). However, in reality there is a large and well documented intra-specific variation in forager size among bumblebees (Brian 1952;Goulson et al. 2002;Inoue & Yokoyama 2006;Peat, Tucker & Goulson 2005). Variation in size within a colony would increase variation also in correlated factors such as flight speed and the ability to transport nectar (Goulson et al. 2002), foraging distance (Greenleaf et al. 2007;Westphal, Steffan-Dewenter & Tscharntke 2006), the efficiency of handling flowers of different morphology (Peat, Tucker & Goulson 2005) and the ambient temperature range where activity is possible (Heinrich 1979, p. 97). In analogy with variation in body size, intra-specific variation in proboscis length could be more important than mean length itself in determining diet breadth of a species. Since other groups of bees (honeybees and stingless bees) do not show the same degree of variation in size (Waddington, Herbst & Roubik 1986), the question has been raised whether this variation is adaptive, e.g. allowing efficient feeding from a larger range of flowers per colony, or a result from constraints laid upon equal feeding and caring for all larval cells, which determines the size of adults (Peat, Tucker & Goulson 2005).

Colony size (i.e. the number of workers) may inform us of the degree to which a colony can cover the resources available in the surrounding landscape. Colony size has been associated with foraging range, such that bumblebee species with larger colonies also have larger foraging ranges (Westphal et al. 2006). Large colonies in combination with a large foraging range may result in a better ability to utilize spatio-temporally scattered resources (Rundlöf, Nilsson & Smith 2008), for example by enhancing the ability to find and exploit abundant resources available for a short time period such as mass-flowering crops (Westphal, Steffan-Dewenter & Tscharntke 2006)

Queen emergence time determines when colonies are founded and when the first worker generation appears. The timing of queen emergence to the availability of floral resources is therefore critical. Different strategies exist; from emergence in early spring to late emergence at the start of summer (Benton 2006;Goulson, Lye & Darvill 2008a;Löken 1973). The peaks in resource availability have most likely changed from those under which the phenological strategies evolved, making formerly successful strategies less so in contemporary agricultural landscapes. Under the assumption that suitable nesting habitats may be limiting in these landscapes, emergence time may also affect populations via competition for nest sites, with early species having an advantage (Goulson, Lye & Darvill 2008a;McFrederick & LeBuhn 2006).

Colony cycle length, i.e. the length of the reproductive cycle of a colony, signifies the time from colony establishment till new queens leave the nest. In analogy with the reasoning above concerning queen emergence, colony cycle length regulates the period during which a colony will gather resources to build up a workforce and provision for male and queen larvae. A longer cycle may therefore result in a longer period of vulnerability to resource limitations (Benton 2006;Williams, Colla & Xie 2009). However, it may also allow for an extended period of resource acquisition and make possible a slow growth based on relatively low, but constant resource.

The role of *nesting habitat* availability has not been as well studied as that of foraging habitats, in part because of the difficulty in finding bumblebee nests (but see Osborne et al. 2008;Williams et al. 2010). Generally the loss of non-crop habitats and the management (summertime cutting, pesticide spraying or drift from bordering fields) of the remaining ones have most likely reduced the amount and lowered the quality of nesting habitats in current agricultural landscapes. Among bumblebees, above-ground nesters generally construct their nest in habitats of tall, tussocky and withered grass. This group may therefore be more sensitive to loss of field margins and cutting of road verges and other non-crop habitats (Fussell & Corbet 1992a). Below-ground nesters on the other hand, are not as dependent on vegetation structures and their nests are not as subjected to physical harm by vegetation cutting, although they will be sensitive to destruction by tilling (Roulston & Goodell 2010).

The mechanisms behind trait effects on sustenance in simplified landscapes presumably act via both habitat and forage plants preferences (Goulson et al. 2005), as well as the ability to reach and efficiently exploit preferred habitats and plants (Rundlöf, Nilsson & Smith 2008;Westphal, Steffan-Dewenter & Tscharntke 2006). Bumblebee traits may modify habitat preferences according to morphological (Goulson, Lye & Darvill 2008b) and phenological fit of worker bee and colony to flowering plants. Forage plant and habitat preferences in combination with landscape effects may therefore inform us about the mechanisms behind population declines, as well as possible measures to mitigate these. It is thus interesting how traits interact with both local habitat and landscape structure to determine the abundance of bumblebees.

We investigated the effects of individual- and colony-based traits (table 1) on bumblebee abundances in agricultural landscapes. The number of males was used as a proxy for reproductive output. We performed separate analyses for workers and males. We divided bumblebees into trait-categories to investigate if the trait-composition of bumblebee workers and males differed between landscape classes and also if the composition of workers differed between habitats.

2. MATERIALS AND METHODS

2.1 Landscape selection

The study was carried out in southernmost Sweden in the province of Skåne (figure 1), which is dominated by agriculture but shows a large variation in land-use intensity and landscape complexity (Persson et al. 2010). Using ArcGis 9.2 (ESRI, Redlands, CA) we selected six *simple* and six *complex* non-overlapping circular landscapes (radius 2km) based on digital information from the Integrated Administration and Control System (IACS; a yearly updated database on all registered farmland fields in Sweden from the Swedish Board of Agriculture). To vary the amount and distribution of non-crop field border, an important foraging habitat in intensively farmed landscapes (Persson & Smith 2011, Ch. II this thesis), we selected *simple* landscapes with large (mean > 40ha) or *complex* landscapes with small (< 15ha) fields, but with less than 200ha of permanent pastures (figure 1). Comparisons of land-use between the landscape classes (SAS Proc GLM, proportions arcsin-square-root transformed) showed that complex landscapes, as expected, had smaller fields than did simple ones, but also differed because of correlated differences in other landscape variables (table 2). Complex landscapes thus had a higher proportion of leys (predominantly clover or grass and clover mixtures), a lower proportion of annual crops and slightly more forest (incl. woodlots and shrubs) than did simple ones. Although we aimed to select landscapes with little permanent pasture, complex landscapes contained slightly more pasture than simple ones (table 2). It should be noted that according to the classification we have used, semi-natural pastures and leys are quite different. Pastures are permanent grasslands used exclusively for grazing. In contrast, leys are rotational crops where grass, sometimes mixed with clover, is cultivated for grazing or hay or silage production. Typically, a field is used as ley for at least two and sometimes up to five years in sequence.

2.2 Selection of survey sites

In order to allow statistical analyses of sufficient power, we collected a dataset containing as many bumblebees from as many species as possible, in each landscape. We therefore surveyed only flower-rich habitats where bees may come to forage. In these landscapes such habitats mainly consisted of non-crop field borders, leys, fallows and domestic gardens. During field visits we

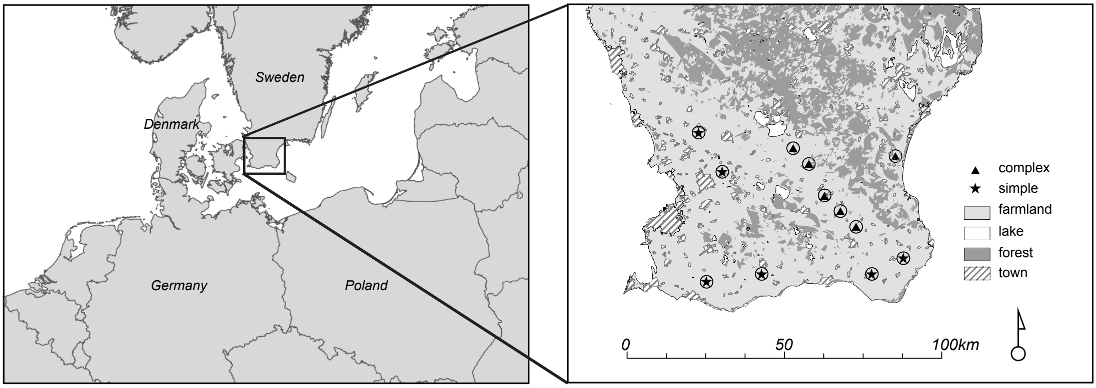

Figure 1. The position of landscapes used for the study. Circles around landscape symbols delimit a 2km radius, within which 16 sites were selected for bumblebee sampling.

selected in total 16 survey sites per landscape: 4 gardens and 12 sites of flower-rich fallows, semi-natural habitats, borders of crop fields and leys. We aimed at selecting sites with an even spread within landscapes and between habitat types, but in simple landscapes borders of pastures were under-represented.

2.3 Bumblebee inventory

All bumblebees found during a 10min survey of 100m^2 of each survey site were collected by hand netting and preserved in 70% ethanol. We sampled bumblebees on days with predominantly clear skies, temperatures above 15°C and no strong winds. We carried out 3 survey rounds from 25 June to 31 August 2008. Bumblebees were determined to species and caste in the lab following Löken (1973), Prŷs-Jones and Corbet (1987) and Holmström (2007). We used the number of collected males as a proxy for production of sexual individuals. Parasitic bumblebee species (former *Psityris spp.*) do not have a worker caste but instead depend on the host workforce and the reproductive output of these species is therefore linked to the performance of their host colony (Benton 2006). We therefore added parasitic males to the number of males from their respective host species. Thorax width, the inter-tegular distance (ITD) of each individual was measured using digital callipers (table 1).

2.4 Flower inventory

We counted the total number of potential resource plant species flowering and estimated the total amount of resources available to bumblebees at the time of each survey. To make resources comparable between plant species and also easier to count, they were noted in units based number of flower heads or equivalents. For *Asteraceae* and *Dipsaceae* the number of flower

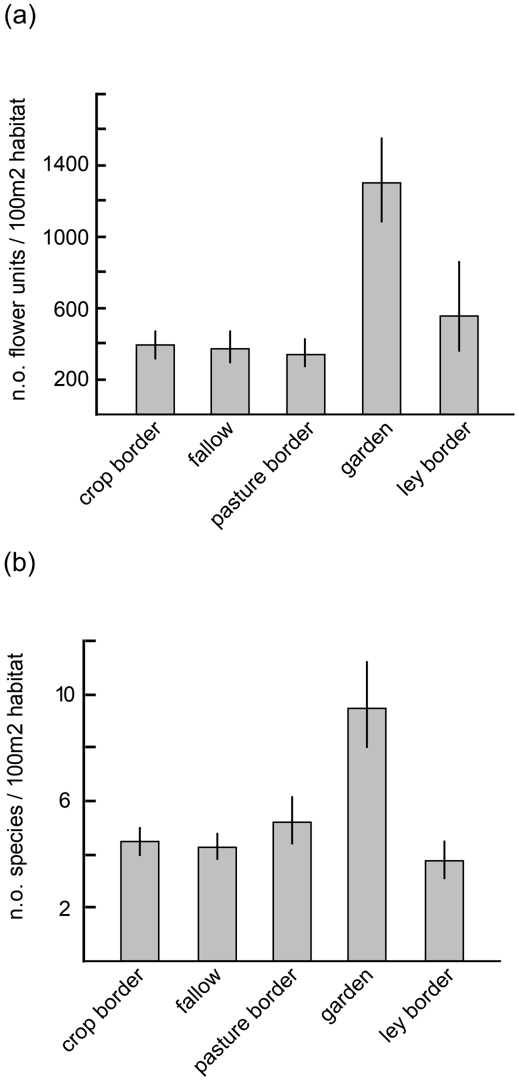

Figure 2: Resources for bumblebees in the surveyed habitats; (a) mean abundance of flower heads or equivalents, (b) mean flowering plant species richness. See text for details on statistical differences. Error bars show SEM.

heads was counted, for *Fabaceae* the numbers of racemes, and for *Campanulaceae*, *Lamiaceae* and *Scrophulariaceae* flower stalks.

The (log-transformed) number of flower units differed significantly between habitats (linear mixed model, SAS Proc Mixed, with landscape identity as random factor, $F_{4,38.4}$=5.10, P=0.0021) such that gardens held more flowers than ley borders while borders of crop fields and pastures and fallows all held lower but similar numbers (figure 2a). There was no significant difference in flower abundance between landscape classes ($F_{1,9.6}$=0.84, P=0.38). Species richness (log-transformed) of flowering plants per 100m^2 survey site depended on both habitat ($F_{4.37.5}$=16.06, P<0.0001) and landscape type ($F_{1,10}$ =5.13, P=0.047), with no significant interaction between the two factors ($F_{4,33.4}$=1.82, P=0.15). This was because sites in complex landscapes were richer (mean 6.4 species, 95% CI: 5.4-7.6) compared to sites in simple landscapes (mean 4.1, CI 3.2-5.2). Also gardens had higher species richness compared to the other habitats (figure 2b). Based on these patterns, we divided habitats into (1) gardens, (2) ley borders and (3) "other" habitats, for the analyses of bumblebee abundances below.

2.5 Division into trait groups

We used our own measurements of thorax width and tongue length, whereas measures of proboscis length (glossa and prementum) were obtained from bumblebees sampled during a concurrent study in the same region using a similar design (Rundlöf, M. unpubl.), (table 1). Information on colony traits (class variables)

Table 1: The classifications of bumblebee species into trait-groups and the sample size of workers and males. Thorax width and proboscis lengths are also given in mm and sample size for proboscis length measurements are notes within brackets. Males of parasitic bumblebee species (former Psityris spp.) were analysed together with their host species and their sample sizes are noted within brackets. The sample size for calculations of proboscis length and its CV are given in brackets. Denotations of naming authorities: F. Fabricius, K. Kirby, L. Linneus, M. Müller, S. Scopoli. *Classifications based on Benton (2006) and Löken (1973).

Bombus species	N workers	N males (*Psityris*)	Queen emergence *	Colony cycle *	Nesting habitat*	Colony size*	Thorax width	Thorax width class	CV×100 Thorax width	CV Thorax class	Proboscis length (N)	Proboscis length class	CV×100 Proboscis length	CV Proboscis class
B. hortorum L.	156	131	late	short	below	medium	4.47	large	11.62	3	10.55 (31)	long	16.87	2
B. hypnorum L.	47	22	early	long	above	medium	4.12	small	10.39	2	5.73 (16)	short	6.00	1
B. lapidarius L.	754	322 (111)	early	short	below	large	4.07	small	8.68	1	6.07 (31)	short	5.69	1
B. lucorum L.	21	24 (5)	early	medium	below	large	4.20	small	12.09	3	5.82 (29)	short	12.38	2
B. terrestris L.	563	784 (55)	early	medium	below	large	4.61	large	9.76	2	6.99 (31)	medium	10.18	1
B. muscorum L.	2	1	late	short	above	small								
B. pascourum S.	151	38 (1)	early	long	above	medium	4.07	small	9.93	2	7.13 (30)	medium	13.72	2
B. pratorum L.	16	14 (5)	early	short	above	small	3.71	small	7.10	1	5.91 (12)	short	6.03	1
B. ruderarius M.	22	8	late	short	above	small	4.69	large	10.28	2	6.90 (26)	medium	8.84	1
B. soroensis F.	28	5	late	long	below	medium	4.01	small	7.56	1	5.62 (29)	short	7.42	1
B. subt'aneus L.	42	9	late	short	below	medium	4.78	large	12.96	3	8.60 (30)	long	12.03	2
B. sylvarum L.	239	78	late	long	above	small	4.05	small	8.61	1	6.84 (20)	medium	15.95	2
B. jonellus K.	1	0	late	medium	above	small								

was collected from Löken (1973) who compiled data on Scandinavian bumblebee populations and Benton (2006) basing information on British populations. Since there may be climatic differences between these sources affecting phenological traits as well as large differences between northern and southern Scandinavia, we combined these sources of information (see table 1). Colony cycle length was estimated from Löken's (1973) data on first dates of queen sightings and last sightings of workers. When workers stop activity is when the life of the colony ends, although new queens and males are still active. For some species (*B. terrestris* and *B. lucorum*) where Löken noted very late queen emergence and Benton assigned them to the early group, our personal experience shows that an earlier start is the case in our study region. We calculated the percentage coefficient of variation ($CV=100 \times \sigma/\mu$) of thorax width and proboscis length of each species with at least 16 workers sampled, thus leaving out *B. muscorum* and *B. jonellus* because of too few individuals.

2.6 Statistical methods

Statistical analyses were carried out in SAS 9.2 for Windows (SAS Institute Inc., Cary, NC). To aid interpretations of any trait effects on bumblebee abundances, we analysed if the different traits that we used as predictors were interrelated. We used Pearson correlations (SAS Proc Corr) for continuous traits. For class variables we used different tests depending on the number of classes (2 × 2: Fisher Exact test, SAS Proc Freq; 2 × n, Cochran-Armitage test for trend, SAS Proc Freq; 3 × 4: Jonckheere-Terpstra test, SAS Proc Freq).

We analysed the abundance of bumblebee workers and males (including parasitic species) separately. Analyses can potentially be made of the trait-composition of bumblebee communities in different landscapes or of the differential response to landscapes by individual species in relation to their traits. Since the abundance of many species is quite low when dividing the material by landscape type, habitat and survey round, we instead performed analyses of trait groups. Thus, our results focus on the community composition of bumblebees in relation to traits and the results we find will therefore most likely be driven by abundances of the more common species. To analyse trait composition in different landscapes and habitats we used the number of bumblebees per 100m^2 site and per trait class as the response variable and tested for differences using

Variable	**Complex** (mean±std)	**Simple** (mean±std)	**F** (1, 10)	**P**
Field size (ha)	9.49±2.82	53.11±8.71	136.19	<0.0001
Prop. farmland	0.81±0.085	0.90±0.026	7.61	0.020
Prop. pasture	0.090±0.044	0.022±0.031	11.24	0.0073
Prop. leys	0.28±0.094	0.054±0.0072	53.16	<0.0001
Prop. annual crop	0.61±0.12	0.91±0.036	41.87	<0.0001
Prop. forest	0.080±0.062	0.010±0.023	6.57	0.028

Table 2. Data on differences in field size and land-use between the two landscape classes studies. Pasture, leys and annual crops are presented as the proportion of total farmland

generalised mixed models assuming Poisson error (SAS Proc Glimmix). We accounted for the dependence of observations within circular landscapes and within the same habitat type in a particular landscape using landscape identity and habitat nested within landscape identity, as well as their interaction with the trait factor, as random effects. We accounted for the uneven sampling of habitat types by using the $\log_{10}$ number of survey sites per habitat type as an offset. Day number and amount of potential resource flowers per survey site were used as covariates. Fixed effects were tested using F-tests with the degrees of freedom estimated using the Kenward-Roger method. When covariance estimations of random factors were non-significantly negative we used the Nobound option, since the Kenward-Roger method otherwise give inflated denominator degrees of freedom. We first fitted a model without traits to check for pure landscape or habitat effects (Williams et al. 2010) and then added traits to the models together with possible interaction between factors. When a significant interaction between trait and landscape class or trait and habitat occurred, we used simple main effects (SAS option Slice) over trait to reveal the reasons for the interactions. For clarity, only significant simple main effects are reported. Full models were reduced by backward selection to include only significant factors; when interactions were retained so were their component factors.

3. RESULTS

3.1 Interrelations of traits

Coefficient of variation (CV) of thorax width and proboscis length, was positively related

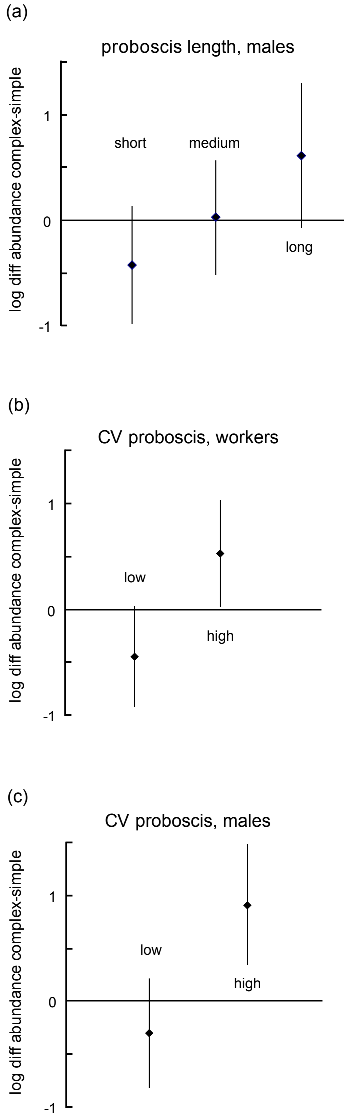

Figure 3: Landscape effects of traits on male and worker abundances. Graphs show difference in mean abundance between complex and simple landscapes for (a) effect of proboscis length on male abundance, (b) effect of CV of proboscis length on worker abundance, (c) effect of CV proboscis length on male abundance. Error bars show 95% CI. Landscape effects were detected where the difference was statistical significantly separated from zero.

to the means of the trait (r_{12}=0.83, P=0.0007; r_{12}=0.76, P=0.0040 respectively). Colony size was significantly associated to nesting habitat (Z_{13}=2.23, P=0.026), such that larger colonies also indicated below ground nesting species. Queen emergence was significantly related to tongue length (Z_{12}=-2.00, P=0.046), such that earlier species had shorter and later species had longer tongues. Queen emergence was also significantly related to colony size (Z_{13}=2.11, P=0.035), such that early species create larger colonies than do later nesting ones. No other combinations of traits were correlated (P>0.09).

3.2 Interacting effects of landscape and traits on bumblebee abundance

When pooling bumblebees irrespective of trait and testing for effects of season, habitat type and its interactions, we did not find any difference between the landscape classes in bumblebee abundance of flower-rich patches, either for workers ($F_{1,9}$=1.10, P=0.32) or for males ($F_{1,8.84}$=0.38, P=0.55).

Community composition with respect to *thorax width* did not differ between landscapes since neither the abundance of workers, nor that of males was significantly related to the interaction between thorax width and landscape class (table 3). For thorax CV class the same held true for the abundance of workers, whereas the abundance of males was marginally non-significant related to the landscape class × trait class interaction (table 3), because of a non-significant tendency

Table 3: Statistical results for effects of trait × landscape class and trait × habitat type interactions, tested with Generalised mixed model (see Methods for details). Significant results in bold. Habitat × trait interactions were also included in models of male abundances, but since the foraging of males does not affect colony growth we chose not discuss those results further.

Trait analysed	**Caste**	**Landscape interaction**		**Habitat type interaction**	
		Fdf	P	Fdf	P
Thorax width	workers	$0.02_{1,11.7}$	0.88	$9.68_{2,21.9}$	0.0010
	males	$0.17_{1,10.0}$	0.69		
CV thorax width	workers	$1.90_{2,21.3}$	0.17	$12.58_{4,41.2}$	<0.0001
	males	$2.28_{2,21.0}$	0.058		
Proboscis length	workers	$2.25_{2,21.1}$	0.13	$5.84_{4.46.1}$	0.0007
	males	$3.29_{2,18.5}$	0.060		
CV prob. length	workers	$22.87_{1,6.6}$	0.0024	$2.18_{2,22.5}$	0.14
	males	$26.78_{1,33.5}$	<0.0001		
Colony size	workers	$9.61_{2.18.0}$	0.0014	$11.32_{4,42.6}$	<0.0001
	males	$13.60_{2,32.5}$	<0.0001		
Queen emerge.	workers	$9.51_{1,7.2}$	0.017	$1.67_{2,20.1}$	0.21
	males	$11.02_{1,10.2}$	0.0076		
Colony cycle l.	workers	$5.89_{2,17.5}$	0.011	$7.79_{4,37.0}$	0.0001
	males	$14.18_{2,25.2}$	<0.0001		
Nesting habitat	workers	$12.89_{1,8.4}$	0.0066	$5.18_{2,19.7}$	0.016
	males	$21.51_{1,13.4}$	0.0004		

for higher abundance of the most variable trait class (class 3) in complex compared to simple landscapes (simple main effects: $F_{1,47.5}=3.12$, $P=0.084$), while the less variable classes (class 1 and 2) did not differ between landscape classes.

Community composition with respect to *proboscis length* did not differ for workers (tab. 3), whereas the community composition of males marginally non-significantly differed between landscape classes (table 3), because of a tendency for more long tongued males in complex landscapes (simple main effects: $F_{1,56.6}=3.25$, $P=0.077$, figure 3a). The composition of proboscis CV classes differed between landscapes for both workers and males (table 3), because of a relatively higher abundance of the more variable classes in complex landscapes. For worker, class 2 (high variation) was more abundant in complex landscapes ($F_{1,16.5}=4.79$,

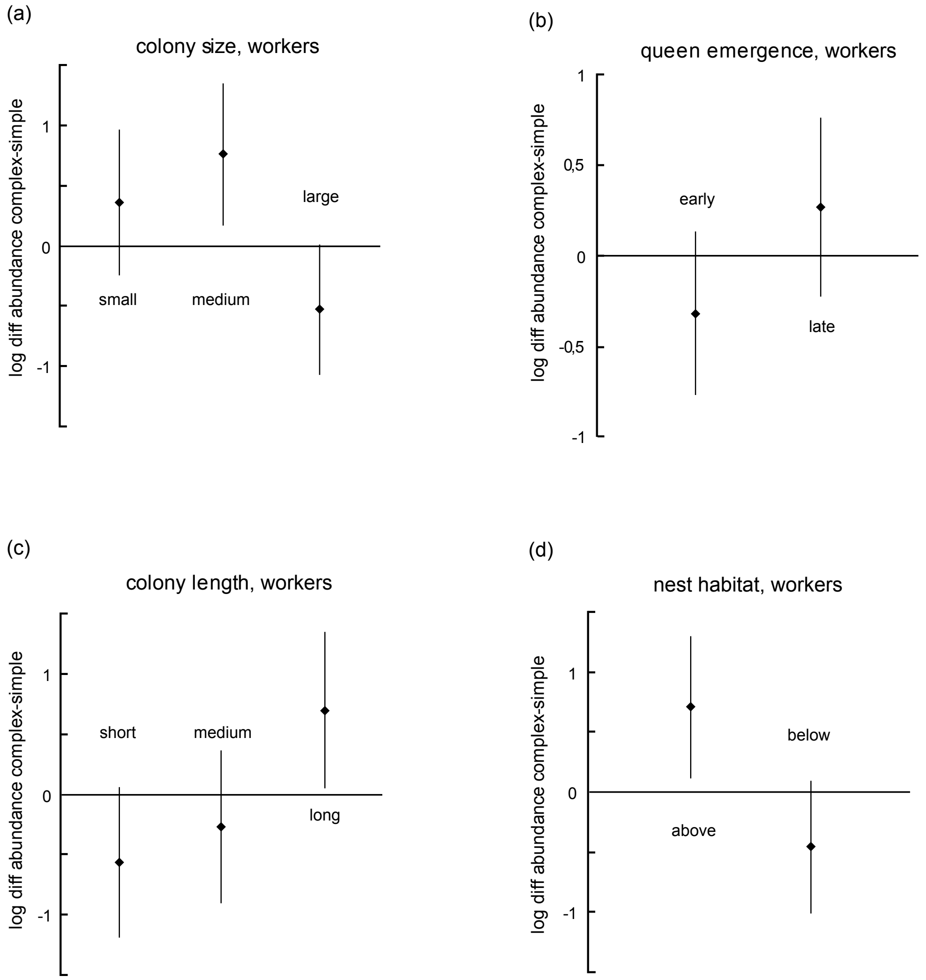

Figure 4: Landscape effects of colony colony-based traits on worker abundances. Graphs show difference in mean abundance between complex and simple landscapes for (a) effect of colony size, (b) effect of queen emergence time (c) colony cycle length, (d) effect of nesting habitat. Error bars show 95% CI. Landscape effects were detected where the difference was statistical significantly separated from zero.

P=0.043) and class 1 (low variation) showed a near-significant tendency to be more abundant in simple ($F_{1,11.2}$=4.37, P=0.060, figure 3b). For males class 2 was more abundant in complex landscapes ($F_{1,20.0}$=11.28, P=0.0031), while class 1 showed no landscape difference (fig. 3c).

Community composition with respect to *colony size* differed between landscapes for both workers and males (table 3) because both workers and males from medium colonies were less abundant in simple compared to complex landscapes (workers: $F_{1,24.1}$=7.02, P=0.014, figure 4a; males: $F_{1,38.1}$=12.92, P=0.0009, figure 5a), as were males from small colonies ($F_{1,71.1}$=11.88, P=0.0010; figure 3a). The large colony group was however unaffected by landscape class.

Community composition of both workers and males with respect to *queen emergence* classes differed between landscape types (tablke 3). For workers the reason was that the relative proportion of early to late emergence groups was higher in simple landscapes (figure 4b). However,

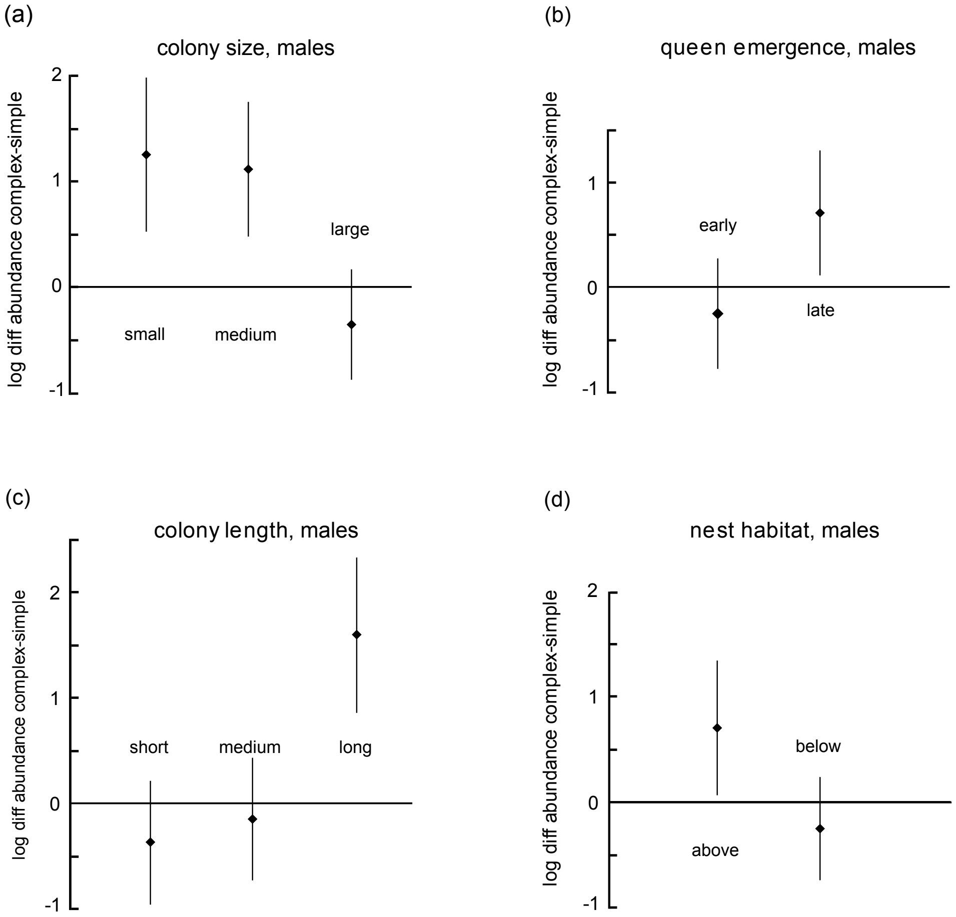

Figure 5: Landscape effects of colony colony-based traits on male abundances. Graphs show difference in mean abundance between complex and simple landscapes for (a) effect of colony size, (b) effect of queen emergence time, (c) effect of colony cycle length, (d) effect of nesting habitat. Error bars show 95% CI. Landscape effects were detected where the difference was statistical significantly separated from zero.

neither the early nor the late group showed significant simple main effect when slicing over trait. For males the interaction was caused by the abundance of late emerging species being lower in simple landscapes compared to complex ones ($F_{1,23.4}$=6.12, P=0.020, figyre 5b), while early species did not differ between landscape classes.

Community composition in relation to *colony cycle length* differed significantly between landscapes for both workers and males (table 3). For both workers ($F_{1,25.7}$=64.87, P=0.037, figure 4c) and males ($F_{1,56.5}$=19.13, P<0.0001, figure 5c) this was because those of the long colony cycle group were more common in complex than in simple landscapes, while abundances of short or medium cycled groups did not differ between landscapes.

Community composition in relation to *nesting habitat* differed significantly between landscape types for both workers and males (table 3). For

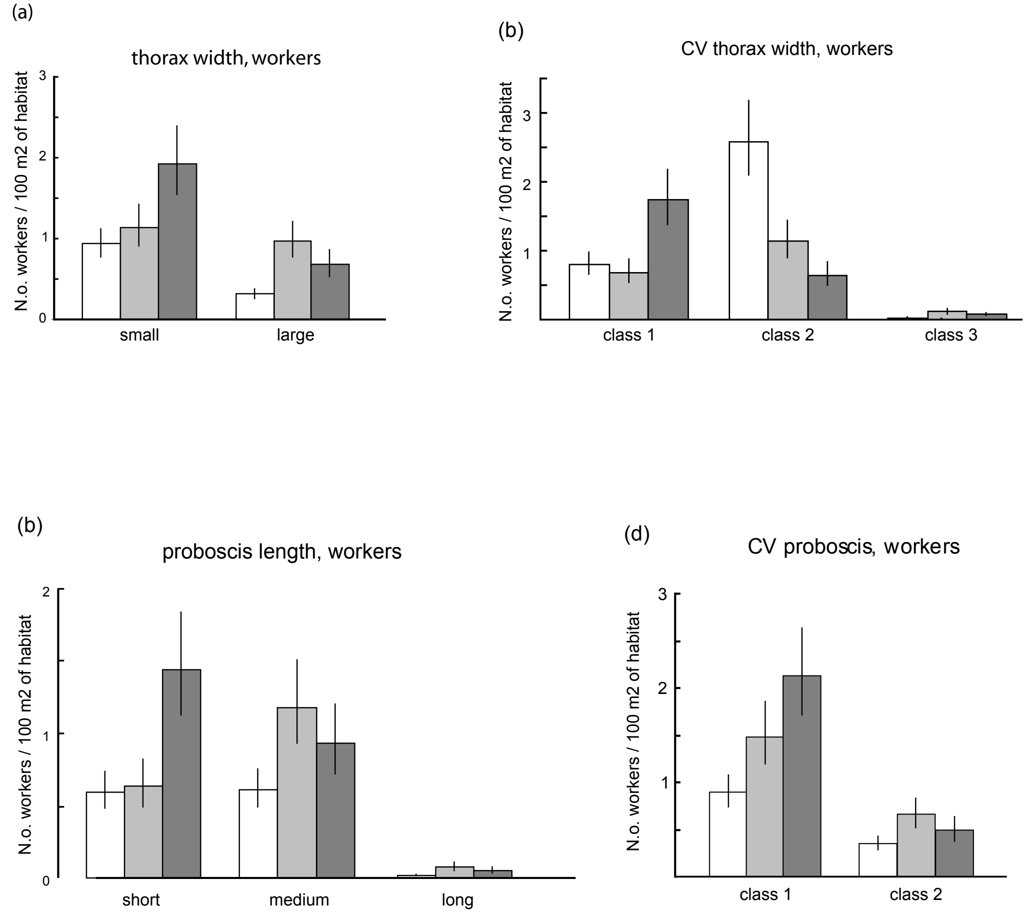

Figure 6: Mean habitat specific abundances of workers in the surveyed habitats, depending on individual-based traits; (a) thorax width, (b) CV of thorax width, (c) proboscis length, (d) CV of proboscis length. White bars: crop and pasture borders and fallows, grey: gardens, dark grey: clover ley borders. Means (least square means) and error bars (SEM) are from model results, see Methods for details.

both workers ($F_{1,18.1}$=6.17, P=0.023, figure 4d) and males ($F_{1,53.4}$=21.65, P<0.0001, figure 5d), higher abundances of above-ground nesting workers were found in complex compared to simple landscapes, while below-ground nesters were not significantly affected by landscape class.

3.3 Interacting effects of habitat selection and traits on bumblebee abundance

Habitat × trait interactions were included, when statistically significant, in all models of both worker and male abundances. Since however, the foraging of males does not affect colony growth we chose not discuss those results further here, but instead focus on trait dependent effects on foraging of workers.

Community composition with respect to *thorax width* differed between habitats (table 3) such that workers of the trait class "small" were more abundant in ley borders than in any other habitat ($F_{2,44..5}$=3.48, P=0.040), while "large" workers were more abundant in gardens than in any other habitat ($F_{2,54.8}$=7.97, P=0.0009, figure 6a). In addition community composition with respect to thorax CV class differed between habitats (tab. 3) because workers with a low CV (class 1) were more abundant in ley borders ($F_{2,37.9}$=5.16, P=0.011), while those with medium CV (class 2) were most abundant in "other" habitats ($F_{2,44.3}$=6.68, P=0.0029) and high CV workers (class 3) were most abundant in gardens ($F_{2,101.8}$=8.45 P=0.0004, figure 6b).

Community composition with respect to *proboscis length* differed between habitat types (tab. 3). Workers with a short proboscis were more abundant in ley borders ($F_{2,43.1}$=4.48, P=0.013), while those with the longest proboscis were more common in gardens and ley borders ($F_{2,113.4}$=7.54, P=0.00080; figure 6c). Worker proboscis CV class did not show a significant interaction with habitat differed between habitats (table 3). However, graphical inspection of the results and simple main effects indicated that the trait group with the low variation (class 1) was most abundant in ley borders ($F_{2,37.0}$=4.62, P=0.016), while high variation workers (class 2) did not show any significant difference between habitats (figure 6d).

Community composition with respect to *colony size class* differed between habitat types (table 3) because workers from the large colony class were more common in ley borders and gardens ($F_{2,32.2}$=4.99, P=0.0013), while workers from medium sized colonies were more abundant in gardens ($F_{2,57.6}$=8.48, P=0.0006, figure 7a).

Community composition with respect to *queen emergence* did not differ between habitats (table 3).

Community composition with respect to the *length of the colony cycle* varied between habitat types (tab. 3), because the abundance of workers belonging to species with a short cycle was relatively higher in ley borders ($F_{2,36.2}$=6.00, P=0.0056), while the abundance of those from medium cycled species were relatively higher in gardens and ley borders ($F_{2,45.9}$=7.02, P=0.0022, figure 7b).

Community composition with respect to

nesting habitat type differed between foraging habitats (table 3), because workers belonging to below-ground nesting species were relatively more abundant in gardens and ley borders ($F_{2,29.5}$=5.94, P=0.0068, figure 7c).

4. DISCUSSION

We found that, when controlling for habitat, the composition of bumblebee trait groups differed between “simple” and “complex” landscapes. Since there were inter-relations between some of the investigated traits, these results must be interpreted together. Of the traits that were clearly related to landscape differences in abundance, all were colony-based: CV of proboscis length, colony cycle length, the three interrelated traits queen emergence, colony size, and nesting habitat. We interpret these findings such that those traits, alone or in combination, affect the vulnerability of bumblebees to landscape simplification resulting from agricultural intensification. We also found that the composition of trait groups differed between the surveyed habitat types. We suggest that individual-based traits (worker thorax width and tongue length) affect plant preferences and thus foraging habitat choices, with correlated responses regarding variability. Colony-based traits may affect habitat choice indirectly; colony size via the ability to detect and utilise resource hot-spots and phonological traits via the fit in timing between colony and flowering phenological of habitats.

4.1 Landscape effects

We found significant interacting effects of bumblebee traits and landscape type. This was

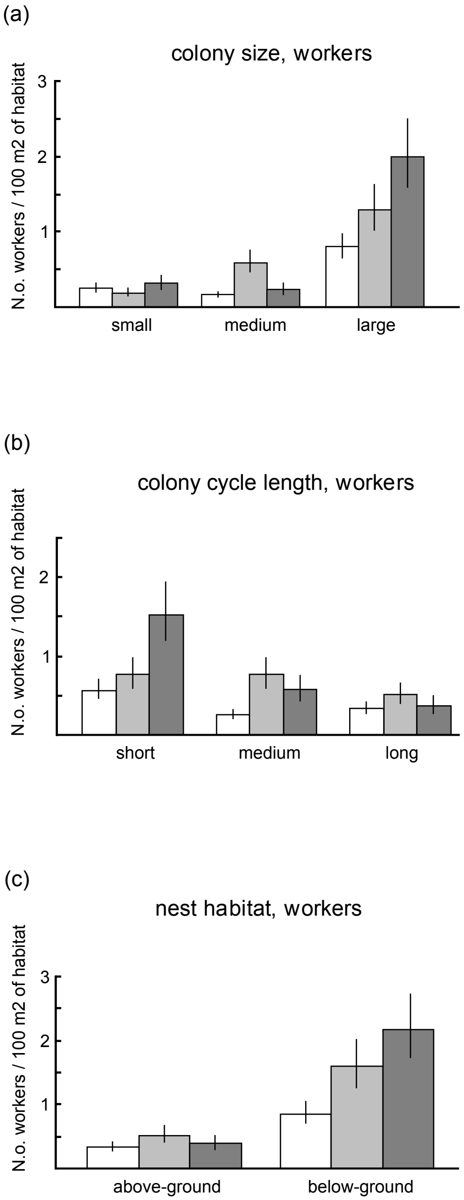

Figure 7: Mean habitat specific abundances of workers in the surveyed habitats, depending on colony-based traits; (a) colony size, (b) colony cycle length, (c) nesting habitat. White bars: crop and pasture borders and fallows, grey: gardens, dark grey: clover ley borders. Means (least square means) and error bars (SEM) are from model results, see text for details.

because workers and males of either small or medium sized, late founded colonies, using above-ground nest sites or requiring a long time to complete their reproductive cycle were found in lower numbers in simple compared to in complex landscapes, whereas either early or below-ground nesting species with a large colony or a short cycle were equally common or more common in both landscapes classes (fig. 3-5). This study thus supports some previous suggestions regarding traits which make bees in general, and bumblebees in particular, vulnerable to landscape changes and habitat disturbances; queen emergence (Fitzpatrick et al. 2007; Goulson, Lye & Darvill 2008a), colony size (Rundlöf, Nilsson & Smith 2008), diet breadth (Goulson, Lye & Darvill 2008b), nesting habitat (Williams et al. 2010), colony cycle length (Williams, Colla & Xie 2009).

It has been hypothesized that a longer colony reproductive cycle may render a species more vulnerable to habitat loss and degradation (Benton 2006), especially in combination with a late queen emergence and proximity to climatic niche-edge (Williams, Colla & Xie 2009). However, to our knowledge it has not previously been shown that this traits actually affect vulnerability to landscape and land-use changes. Here we show that the relative abundance of bumblebees with a longer cycle is indeed lower in simple compared to complex landscapes, why this group is likely more vulnerable to landscape simplifications. We believe this is caused by the extended period over which the colony must cater for its brood, and that loss of forage and large variability in resource availability therefore has a more negative effect on this group than on short cycled species.

The significant inter-relations between colony size and nesting habitat, queen emergence and colony size and queen emergence and tongue length means that effects of these traits must be interpreted together since one may drive the apparent landscape effect detected in the other. For example, if colonies of early emerging queens benefit from early mass flowering crops in simple landscapes, this may incidentally result in landscape-dependence also of the traits nesting habitat and colony size. However, it is possible that there are co-adapted clusters of traits related to seasonal foraging strategies. Bumblebees evolved in the temperate and alpine regions of the world (Hines 2008), which are among other things characterised by large variations in food supply due to flowering phenology of plants and frequent changes in weather conditions, resulting in periods of several days when foraging is not be possible (Couvillon & Dornhaus 2010). It may be that early colonies (founded in March-April and with peaks in June in Scandinavia) need a large workforce in order to reduce the risk of a highly variable food influx-rate to the colony, caused by the combination of a high risk of wet and cold weather spells and low food availability in spring and early summer. In addition, the larger area used for foraging by a large colony may increase its ability to integrate spatially and temporally scattered resources. Because of more abundant and predictable resources and a more benign weather, a smaller work force may have been optimal for later founded colonies (founded in May-June, with peaks in late July and August in Scandinavia). Regarding the relation between queen emergence and proboscis length; a shorter tongue for early species would make sense if shallow and easily accessible flowers (e.g. *Prunus, Malus, Acer, Salix, Sorbus*) was an essential resource for this group. Later, during high summer a more varied flora is potentially found, possibly also containing a larger proportion of flowers with deep corollas. A possible reason for the interrelation between colony size and nesting habitat could be that below-ground nests are better protected against cold and rain, and that within-colony temperatures may be better regulated in below-ground burrows compared to surface nests. This may allow for faster, more efficient growth of larvae and thus the possibility to build-up a larger colony (Heinrich 1979, p. 65). It could also be that surface-nests remain smaller since they may be less well protected against predators, e.g. badgers and foxes, than are below-ground nests, and a large colony may run a higher risk of detection from a potential predator.

Whatever the reason is for trait inter-relations and correlation, recent landscape changes may have influenced the relative competitiveness of these combinations of colony-based traits, favouring the "large, early and below-ground" colony strategy, especially in combination with a short reproductive cycle. A large part of early flower resources are composed of trees and bushes and large stands of a few common "nitrophilic" or ruderal plants such as white dead nettle, *Lamium album* (Goodwin 1995;Lye et al. 2009;Persson & Smith 2011, Ch. II this thesis). Agricultural intensification may further have had a more negative effect on the abundance of mid to late summer flora compared to early flowering plants. Late flowering habitats e.g. hay meadows, legume-based fodder crops and un-cropped habitats have largely been lost from modern farmland (Fitzpatrick et al. 2007;Goulson, Lye & Darvill 2008a;Stoate et al. 2001). Trees and bushes most certainly have also been lost to a high degree, but those remaining may still provide the necessary resources for the critical phases of colony growth in early season. Furthermore, the increased farming of winter-sown oilseed rape (*Brassica napus*) may aid early, large colonies with a short cycle, since it would take a large work force already by mid May to efficiently localise and exploit this abundant but ephemeral resource (Westphal, Steffan-Dewenter & Tscharntke 2006). It may thus not only be the decrease of forage *per se* but the spatial and temporal match (or mis-match) between colony cycle, foraging ranges and resources, which result in today's patterns of bumblebee abundance; a few relatively successful species, but many more facing serious declines. If the match is good it enables population sustenance (and perhaps also growth) even in simplified landscapes. Early species also have the advantage of already having a relatively large colony when the later species emerge. This gives them a competitive advantage, especially when resources are scarce and scattered, which is indeed the case in simple landscapes after the flowering of trees and bushes and oilseed rape (Persson & Smith 2011, Ch. II this thesis).

Furthermore, preferred nesting habitats of many above-ground nesters; tall tussocky and withered grass (Fussell & Corbet 1992a;Svensson, Lagerlöf & Svensson 2000), have decreased in concordance with loss of permanent grasslands and linear non-crop habitats (Banaszak 1992). This was mirrored in our landscape design of small or large fields, and above-ground nesters were also more abundant in complex landscapes. The management of field borders and road verges could further increase vulnerability of this group if the few remaining habitats are cut during summer, which would lead to disturbance or destruction of nests (Goulson 2003). Below-ground nesters may be less subjected to nest habitat limitations and destruction, although tilling of fields may damage nests (Roulston & Goodell 2010) and availability of old rodent-nests, which are preferred by both surface and below-ground nesters, have likely decreased more in simple than in complex landscapes (Goulson, Lye & Darvill 2008a).

We did not find any landscape effects of the individual-based trait worker thorax width and the related CV thorax width. Thorax width is assumed to represent foraging ranges of bees in general (Greenleaf et al. 2007;Westphal, Steffan-Dewenter & Tscharntke 2006). However, it could be that the colony-based traits and the spatially and temporally extended foraging which sociality infers, over-ride any effects of forager size (Bommarco et al. 2010). Thorax width may therefore not reflect the spatial patterns of foraging of the whole colony. For example, behaviour may modify the pure physical ability to forage at a certain distance. This was found for workers of *B. pascuorum,* which increased their foraging distance at the end of the season (Goulson et al. 2010). Furthermore, all bumblebee species are large relative to most other wild bees and the number of workers per colony, which indicate how meticulously the search for forage is within flight range, may be a better indicator of the spatial scale of efficient resource acquisition.

Although negatively related to colony size, the tendencies for males of species with a long and highly variable proboscis to be more abundant in complex landscapes may indicate a morphological mis-match of this group to the flora of simplified farmland landscapes. Mean tongue length and CV of tongue length were positively related. This means that, although larger variation in tongue length may lead to a more varied within-colony diet, these bumblebees are still confined to flowers with deeper corollas. If deeper flowers vary more in depth than shallow ones, then larger variation in tongue length might also be an adaptation to track variations in flower morphology. Tongue length has further been shown to negatively correlate with diversity of preferred pollen plants and indicate preferences for the *Fabaceae* family (Goulson et al. 2005;Goulson, Lye & Darvill 2008b). The analysis of species richness of flowering plants showed that sites in complex landscapes held on average 2.3 species more than did sites in simple ones, despite the fact that we had selected the “best” bumblebee foraging sites we could find. Our results thus indirectly corroborate those of Goulson et al. (2008b) and Bommarco et al. (2010); that bee species with narrow diets are more vulnerable to habitat loss.

There were no simple landscape effects when analysing the material without traits. Nor were there any landscape and day number interactions to indicate an earlier collapse of colonies in simple landscapes. Both patterns have been seen in previous studies in the same area (Rundlöf, Nilsson & Smith 2008;Persson & Smith 2011, Ch. II this thesis). However, this study surveyed only habitats rich in potential forage plants, and it has been shown that rich habitats indeed attract more bumblebees when the surrounding landscape is otherwise poor (Heard et al. 2007;Persson & Smith 2011, Ch. II this thesis). An aggregation of bees into the surveyed habitats therefore most likely masked both pure and seasonal landscape effects. The results found here are similar for workers and males except in one respect. In some cases, the abundance of workers of the most common trait group was more abundant in simple compared to in complex landscapes (colony size, CV tongue length and nearly so for colony cycle), while this was not so for males. We believe that the reason for this is an increased aggregation of workers from these groups into the resource rich habitats surveyed. Because of a landscape wide lack of resources, the higher habitat specific density of some groups of workers in simple landscapes may not reflect the level of reproduction. This explains why male abundance for these groups was indeed similar in both landscapes. Since males are not provisioning for the colony, they are not expected to aggregate into resource rich habitats to the same extent as workers, which aim to maximize their foraging efficiency. Instead, males provision only for themselves (mainly with nectar) and use their time and energy to patrol a territory in search of a mate (Goulson 2003). They could thus be less prone to visit resource hot-spots and instead choose areas with a high chance to detect a queen. However, the ability to actually obtain a similar reproductive output in both landscape classes may indeed be caused by the ability of the work force of certain trait groups to find and meticulously utilize the few available resources in simple landscapes, i.e. to aggregate.

We did not include information on climatic niches or distributional ranges (Williams 1982;Williams, Colla & Xie 2009;Williams, Araujo & Rasmont 2007) as we do not have access to this type of data for our study region at this time. But it would be very interesting to do so and to be able to analyse this in combination with the traits found to affect sustenance here.

4.2 Habitat preferences

All traits except queen emergence amd CV proboscis length showed significant interactions with foraging habitat type, to explain the abundances of bumblebees. Traits thus modify habitat preferences of bumblebees. Most likely this occurs via the composition of pollen and nectar-producing plants characteristic of the different habitats, and in the case of individual-based traits (thorax width, tongue length) this is quite intuitive and has been shown in previous studies (e.g. Goulson, Lye & Darvill 2008b;Peat, Tucker & Goulson 2005). Intra-specific variation in size and tongue length further affects the range of flower species where foraging is efficient (Peat, Tucker & Goulson 2005). We found both more resource flower units and a higher species richness of flowering plants in gardens compared to other habitats. Ley borders were relatively species poor, but contained more flower units than did “other” habitats (borders of crop fields, pastures and fallows). Subsequently we found most workers of small species with short tongues and possibly also with low intra-specific variation foraging in ley borders and “other” habitats, with a high proportion of white clover and annual and biennial plants readily visited by short tongued bumblebees (Fussell & Corbet 1992b). Large species with long tongues and a large variation on the other hand, were more often found in gardens than in leys or other habitats. In gardens human preferences may result in a large variety of ornamental plants, often with more complex flower morphology and a deeper corolla which could fit the morphology of large, long tounged bees.

Regarding colony-based traits and habitat preferences, queen emergence did not show any significant interaction with habitat at all. The groups with medium and large colonies were more abundant in gardens and ley borders than in “other” habitats. This indicates a higher ability for large colonies to detect and utilize resource hot-spots, e.g. gardens or flowering clover ley borders. This is possible if a larger colony indeed searches and forages over a large area than a small colony. In contrast, small colony workers were equally common in all habitats, possibly because fewer workers decrease the chances of detecting hot-spots. Below-ground species were also more commonly found in gardens and ley borders. This could however be caused by the inter-relation between colony size and nesting habitat. The group with a long reproductive cycle was equally common in all habitats, possibly because of a need to utilize a broader variety of resources and habitats over their extended cycle, compared to shorter cycled species.

4.3 Conclusions

We suggest that bumblebees can be described by their traits in two different ways. First, one group of traits connected to worker morphology and physiology which acts on the individual workers’ choice of plants and efficiency in different foraging habitats. Second, another group of traits describe how colonies utilise resource in the surrounding landscape over space and time. Any remedy to the ongoing loss of bumblebees from farmland landscapes must therefore include actions to increase the fit of resources to the less successful groups, both at the level of the individual worker and at level of the colony. Recreating flower-rich field margins may not have an effect on bumblebee population numbers if it does not also contain flowers of the “correct” morphology and phenology, or if the spatial scale of implementation does not allow also for small colonies to find and utilise them. Our results adds more evidence to the suggestions that an early species which completes its life cycle in a short time period, nests underground or produces a large colony, has a better ability to reproduce in simplified agricultural landscapes. Our results also indicate that the addition of linear non-crop elements like grassy field borders could indeed benefit the more vulnerable species, as long as they also contain a variety of nectar and pollen plants throughout the season. Leaving (margins of) white clover leys to flower may also have positive effects for short tongued, small and low variation species, since those were found more abundant in borders of leys compared to other habitats and to other trait groups.

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6. REFERENCES

Banaszak,J. (1992) Strategy for conservation of wild bees in an agricultural landscape. Agriculture, Ecosystems & Environment 40, 179-192.

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

Biesmeijer,J.C., Roberts, S. P. M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J. & Kunin, W. E. (2006) Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. Science 313, 351-354.

Bommarco,R., Biesmeijer, J. C., Meyer, B., Potts, S. G., Poyry, J., Roberts, S. P., Steffan-Dewenter, I. & Ockinger, E. (2010) Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. Proceedings of the Royal Society Biological Sciences Series B 277, 2075-2082.

Brian,A. (1952) Division of labour and foraging in Bombus agrorum Fabricius. Journal of Animal Ecology 21, 223-240.

Cameron,S.A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F. & Griswold, T. L. (2011) Patterns of widespread decline in North American bumble bees. Proceedings of the National Academy of Sciences.

Carre,G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K., Potts, S. G., Roberts, S. P., Rodet, G., Settele, J., Steffan-Dewenter, I., Szentgyorgyi, H., Tscheulin, T., Westphal, C., Woyciechowski, M. & Vaissiere, B. E. (2009) Landscape context and habitat type as drivers of bee diversity in European annual crops. Agriculture Ecosystems & Environment 133, 40-47.

Couvillon,M. & Dornhaus, A. (2010) Small worker bumble bees (Bombus impatiens) are hardier against starvation than their larger sisters. Insectes Sociaux 57, 193-197.

Darvill,B., Knight, M. & Goulson, D. (2004) Use of genetic markers to quantify bumblebee foraging range and nest density. Oikos 107, 471-478.

Darvill,B., O'Connor, S., Lye, G., Waters, J., Lepais, O. & Goulson, D. (2010) Cryptic differences in dispersal lead to differential sensitivity to habitat fragmentation in two bumblebee species. Molecular Ecology 19, 53-63.

Fitzpatrick,U., Murray, T. E., Paxton, R. J., Breen, J., Cotton, D., Santorum, V. & Brown, M. J. F. (2007) Rarity and decline in bumblebees - A test of causes and correlates in the Irish fauna. Biological Conservation 136, 185-194.

Fussell,M. & Corbet, S. A. (1992a) The Nesting Places of Some British Bumble Bees. Journal of Apicultural Research 31, 32-41.

Fussell,M. & Corbet, S. A. (1992b) Flower Usage by Bumble-Bees: A Basis for Forage Plant Management. The Journal of Applied Ecology 29, 451-465.

Gathmann,A. & Tscharntke, T. (2002) Foraging ranges of solitary bees. Journal of Animal Ecology 71, 757-764.

Goodwin,S. (1995) Seasonal phenology and abundance of early-, mid- and long-season bumble bees in southern England, 1985-1989. Journal of Apicultural Research 34, 79-87.

Goulson,D., Lye, G. C. & Darvill, B. (2008a) Decline and Conservation of Bumble Bees. Annual Review of Entomology 53, 191-208.

Goulson,D. (2003) Bumblebees: Their behaviour and ecology. Oxford University Press, Oxford, UK.

Goulson,D., Hanley, M. E., Darvill, B., Ellis, J. & Knight, M. (2005) Causes of rarity in bumblebees. Biological Conservation 122, 1-8.

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. Journal of Applied Ecology 47, 1207-1215.

Goulson,D., Lye, G. C. & Darvill, B. (2008b) Diet breadth, coexistence and rarity in bumblebees. Biodiversity and Conservation 17, 3269-3288.

Goulson,D., Peat, J., Stout, J. C., Tucker, J., Darvill, B., Derwent, L. C. & Hughes, W. O. (2002) Can alloethism in workers of the bumblebee, Bombus terrestris, be explained in terms of foraging efficiency? Animal Behaviour 64, 123-130.

Greenleaf,S., Williams, N., Winfree, R. & Kremen, C. (2007) Bee foraging ranges and their relationship to body size. Oecologia 153, 589-596.

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. Biology Letters 3, 638-641.

Heinrich,B. (1979) Bumblebee economics. Harvard University Press, Cambridge.

Hines,H.M. (2008) Historical Biogeography, Divergence Times, and Diversification Patterns of Bumble Bees (Hymenoptera: Apidae: Bombus). Systematic Biology 57, 58-75.

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

Inoue,M.N. & Yokoyama, J. (2006) Morphological variation in relation to flower use in bumblebees. Entomological Science 9, 147-159.

Kearns,C.A., Inouye, D. W. & Waser, N. M. (1998) Endangered Mutualisms: The Conservation of Plant-Pollinator Interactions. Annual Review of Ecology and Systematics 29, 83-112.

Kleijn,D. & Raemakers, I. (2008) A retrospective analysis of pollen host plant use by stable and declining bumble bee species. Ecology 89, 1811-1823.

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. Proceedings of the Royal Society B: Biological Sciences 274, 303-313.

Kosior,A., Celary, W., Olejniczak, P., Fijal, J., Krol, W., Solarz, W. & Plonka, P. (2007) The decline of the bumble bees and cuckoo bees (Hymenoptera : Apidae : Bombini) of Western and Central Europe. Oryx 41, 79-88.

Löken, A. (1973) Studies on Scandinavian Bumble Bees (Hymenoptera, Apidae). Norwegian Journal of Entomology 20, 1-218.

Lye,G., Park, K., Osborne, J., Holland, J. & Goulson, D. (2009) Assessing the value of Rural Stewardship schemes for providing foraging resources and nesting habitat for bumblebee queens (Hymenoptera: Apidae). Biological Conservation 142, 2023-2032.

McFrederick,Q.S. & LeBuhn, G. (2006) Are urban parks refuges for bumble bees Bombus spp. (Hymenoptera: Apidae)? Biological Conservation 129, 372-382.

Osborne,J.L., Martin, A. P., Shortall, C. R., Tod, A. D., Goulson, D., Knight, M., Hale, R. J. & Sanderson, R. A. (2008) Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. Journal of Applied Ecology 45, 784-792.

Peat,J., Tucker, J. & Goulson, D. (2005) Does intraspecific size variation in bumblebees allow colonies to efficiently exploit different flowers? Ecological Entomology 30, 176-181.

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. Agriculture Ecosystems & Environment 136, 169-176.

Potts,S.G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W. E. (2010) Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution 25, 345-353.

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

Ricketts,T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S. S., Klein, A. M., Mayfield, M. M., Morandin, L. A., Ochieng, A. & Viana, B. F. (2008) Landscape effects on crop pollination services: are there general patterns? Ecology Letters 11, 499-515.

Roulston,T.H. & Goodell, K. (2010) The Role of Resources and Risks in Regulating Wild Bee Populations. Annual Review of Entomology 56, 293-312.

Rundlöf,M., Nilsson, H. & Smith, H. G. (2008) Interacting effects of farming practice and landscape context on bumblebees. Biological Conservation 141, 417-426.

Stoate,C., Boatman, N. D., Borralho, R. J., Carvalho, C. R., Snoo, G. R. & Eden, P. (2001) Ecological impacts of arable intensification in Europe. Journal of Environmental Management 63, 337-365.

Svensson,B., Lagerlöf, J. & Svensson, G. (2000) Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. Agriculture, Ecosystems & Environment 77, 247-255.

Waddington,K.D., Herbst, L. H. & Roubik, D. W. (1986) Relationship Between Recruitment Systems of Stingless Bees and Within-Nest Worker Size Variation. Journal of the Kansas Entomological Society 59, 95-102.

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

Williams,N.M., Crone, E. E., Roulston, T. H., Minckley, R. L., Packer, L. & Potts, S. G. (2010) Ecological and life-history traits predict bee species responses to environmental disturbances. Biological Conservation 143, 2280-2291.

Williams,P.H. (1982) The Distribution and Decline of British Bumble Bees Bombus. Journal of Apicultural Research 21, 236-245.

Williams,P.H. & Osborne, J. (2009) Bumblebee vulnerability and conservation world-wide. Apidologie 40, 367-387.

Williams,P., Colla, S. & Xie, Z. (2009) Bumblebee Vulnerability: Common Correlates of Winners and Losers across Three Continents. Conservation Biology 23, 931-940.

Williams,P.H., Araujo, M. B. & Rasmont, P. (2007) Can vulnerability among British bumblebee (Bombus) species be explained by niche position and breadth? Biological Conservation 138, 493-505.

Winfree,R. (2010) The conservation and restoration of wild bees. Annals of the New York Academy of Sciences 1195, 169-197.

IV

Bumblebee colonies produce larger workers in complex landscapes

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ABSTRACT

The negative effect of agricultural intensification on bumblebee populations is thought to partly be caused by loss of food plants, for example because of increased field size and concomitant loss of non-crop field borders and their nectar and pollen plants. Earlier studies have focused on how loss of foraging resources affects colony growth and thereby abundance of workers and sexual reproduction. By comparing bumblebees in agricultural landscapes of different complexity in Southern Sweden, we here demonstrate that also the adult size of bumblebee workers is significantly related to the availability of foraging resources. This effect was independent of both species identity and foraging habitat type. This suggests a shortage of flower resources in landscapes of lower complexity which may also affect the reproductive success of colonies negatively.

KEYWORDS: *Bombus*; worker size; landscape ecology; agriculture; MFC

1. INTRODUCTION

It is widely recognised that pollinating insects have been negatively affected by agricultural intensification, loss and fragmentation of natural and semi-natural habitats e.g. (Kearns, Inouye, & Waser (1998), Biesmeijer, Roberts, Reemer, Ohlemuller, Edwards et al. (2006), Potts, Biesmeijer, Kremen, Neumann, Schweiger et al. (2010)). Several studies have focused on losses of bumblebees from regions with intensive agriculture (Kosior, Celary, Olejniczak, Fijal, Krol et al. (2007), Goulson, Lye, & Darvill (2008), Williams & Osborne (2009), Grixti, Wong, Cameron, & Favret (2009), Cameron, Lozier, Strange, Koch, Cordes et al. (2011)). However, responses of bumblebees to landscape changes imposed by agriculture differ among studies and between species, e.g. in the spatial scale of resource acquisition (Westphal, Steffan-Dewenter, & Tscharntke (2006), Goulson, Lepais, O'Connor, Osborne, Sanderson et al. (2010)) and in the effects of mass flowering crops (MFCs) (Herrmann, Westphal, Moritz, & Steffan-Dewenter (2007), Westphal, Steffan-Dewenter, & Tscharntke (2009), Knight, Osborne, Sanderson, Hale, Martin et al. (2009), Goulson et al. (2010)). Also some species do remain common even in very simplified regions (Williams (1982), Goulson et al. (2008), Williams, Colla, & Xie (2009)). These differences may reflect both species specific responses and specific qualities of the study landscapes. Such variability of responses, together with the great importance of bumblebees as pollinators of crops and wild plants throughout much of the world (Goulson (2003), Cederberg, Pettersson, & Nilsson (2006), Winfree, Williams, Gaines, Ascher, & Kremen (2008)), calls for continued research on the mechanisms underlying their responses to past and present landscape changes.

Bumblebees are social insects, constructing colonies of worker bees (all full sisters) around one reproducing queen, and the colony is thus the reproductive unit (Goulson (2003)). This drastically reduces the effective population size in comparison to census counts of worker bees. The existence of a nest also makes bumblebees central place foragers; their fitness being dependent on the distance between the nest and the resources necessary for survival and reproduction (Goulson (2003)). Bumblebees thus constitute both an important and interesting group to study in the light of the ongoing pollinator declines and intensification of agricultural landscapes.

The effect of large scale landscape intensification and simplification on bumblebee populations is considered to in part act via loss of food plants (Benton, Vickery, & Wilson (2003), Carvell, Roy, Smart, Pywell, Preston et al. (2006)). The ability of a bumblebee colony to attain sufficient resources for reproduction depends on several aspects of the individual worker and the colony. The foraging range, which is positively (non linearly) related to forager body size of bees in general (Greenleaf, Williams, Winfree, & Kremen (2007)) and possibly also positively correlated with colony size in bumblebees (Westphal et al. (2006)), may affect the ability to utilise fragmented resources. The size of workers may also affect the rate of energy influx to the colony since larger workers have been found to be more efficient nectar foragers in *Bombus terrestris*

(Spaethe & Weidenmueller (2002), Goulson, Peat, Stout, Tucker, Darvill et al. (2002)), and this could also be so for other species. Larger foragers may also carry out a larger proportion of pollen collection (Brian (1952)), although this was not confirmed in a later study (Goulson et al. (2002)). A larger colony is presumably better able to meticulously scan for and utilise resources in the surrounding, compared to a colony of fewer workers. Larger workers and colonies may thus increase the ability to cope with a high variation in food plant availability, which is significant for structurally simplified agricultural landscapes. There are inter-specific differences in mean size of workers and size of the worker caste (Löken (1973), Benton (2006)), and this has also been suggested as a cause behind differences in population responses to land-use intensification and habitat fragmentation (Westphal et al. (2006), Rundlöf, Nilsson, & Smith (2008)).

The size of adult worker bees is determined by the amount of food they are fed as larvae (Schmid-Hempel & Schmid-Hempel (1998), Goulson (2003)). The number of sexual offspring produced by a colony is related to the amount of food that the colony can harvest to build up a large worker caste in order to maintain the high rates of provisioning needed, especially during queen development (Goulson (2003)). Smaller and fewer workers and fewer males in response to food shortage has been demonstrated in a lab environment (Schmid-Hempel & Schmid-Hempel 1998). In a field study competition from managed honeybees, *Apis mellifera*, resulted in decreased mean body size of co-occurring bumblebees (Goulson & Sparrow (2009)). Smaller foragers may in turn result in a decreased influx of food, further reducing the size and number of the work force and adding to the already hampered performance of the colony. Quite plausibly this also affects the reproductive output negatively. One way of identifying landscapes where resource are in short supply could be to compare size of worker bees. This would also allow for detection of inter-specific differences in ability of resource acquisition depending on the surrounding landscape.

Our aim was to investigate if the amount and spatial segregation of flower-rich non-crop habitats (i.e. a component of landscape structure), affects the mean size of bumblebee workers. Resources within a distance of 250m up to 3000m have been shown to affect bumblebee densities and this indicates an ability to forage within this distance from the colony (Westphal et al. (2006), Knight et al. (2009)). Studies using other techniques have come to similar conclusions (Walther-Hellwig & Frankl (2000), Darvill, Knight, & Goulson (2004), Knight, Martin, Bishop, Osborne, Hale et al. (2005), Osborne et al. (2008)). However, as long as forage is available, a large part of the work force is presumed to forage much closer to the nest (Walther-Hellwig et al. (2000), Wolf & Moritz (2008)). A separation of resources and nest by a few hundred meters could thus constitute a distance that not all species or workers easily overcome, although there are of course inter-specific differences in foraging ranges (e.g. Walther-Hellwig et al. (2000), Darvill et al. (2004), Knight et al. (2005), Westphal et al. (2006)). We therefore performed our study in contrasting landscapes where resources were separated by different mean distances, i.e. landscapes with differently sized agricultural fields. This variation in field size will inevitably also affect the amount of resources potentially found in field borders, since the perimeter to area ratio will change.

Based on the reasoning above we hypothesise to find smaller workers in landscapes of simplified structure. We also hypothesise to find differences between species in the response to landscape structure, such that the still common species will not respond to landscape simplifications by producing smaller workers.

2. METHODS

Landscape selection: The study was carried out in southernmost Sweden in the province of Skåne (approx. 56°N, 13°30'E, figure 1). This region is dominated by agriculture but also shows a large variation in land-use intensity and landscape complexity (Persson, Olsson, Rundlöf, & Smith (2010)). We used digital information from the Integrated Administration and Control System (IACS), a yearly updated database on all registered farmland fields in Sweden (Swedish Board of Agriculture), to select two classes of landscapes. As we were interested in the effect of the amount and distribution of non-crop field margins on bumblebees, we selected circular landscapes (radius 2km) with either large (mean > 40ha) or small (< 15ha) fields, but with less than 200ha of permanent pastures, which may affect bumblebees positively (Morandin, Winston, Abbott, & Franklin (2007), Öckinger & Smith (2007)). We also aimed at minimizing the amount of forest and larger woodlots within the landscapes. Data was processed in ArcGis 9.2 (ESRI) and six landscapes of each class were selected. Landscapes composed of large blocks of fields are here after called "simple" and those of small blocks are called "complex" (figure 1).

We used landscapes of 2km radius since this size should suffice to describe the landscape encountered by central-place foraging bumblebees. The circular landscapes were also well positioned within larger "simple"

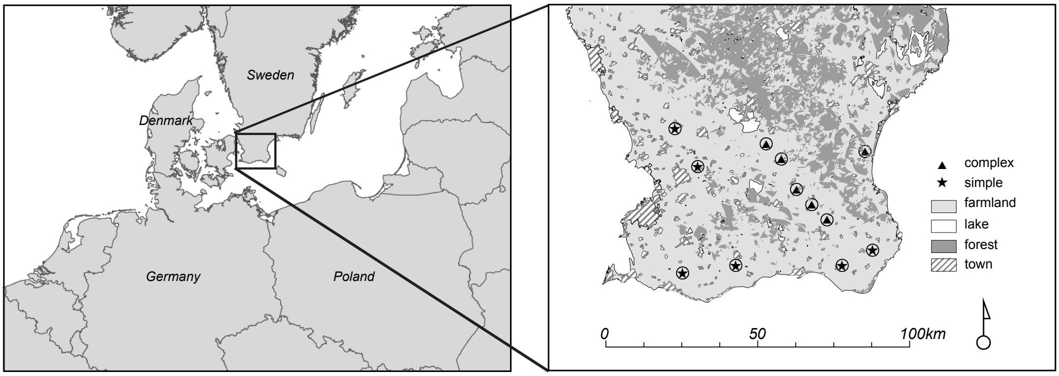

Figure 1. The position of landscapes used for the study. Circles around landscape symbols delimit a 2km radius.

or "complex" landscapes (not shown). All circular landscapes are at least 3km apart such that, regarding foraging bumblebees, we can consider them independent. However, because of the geography of our study region, simple and complex landscapes cannot be completely interspersed, potentially resulting in spatial auto-correlation (figure 1). We handed this by maximizing interspersion, within the constraints of landscape variation and reasonable driving distances, and tested for spatial autocorrelation when analysing results.

Selection of survey sites: In order to allow statistical analyses of sufficient power we collected a dataset where we detected as many bumblebees from as many species as possible in each landscape. We did this by surveying only flower-rich habitats where bees may come to forage. In our landscapes such habitats mainly consisted of non-crop field borders, leys, fallows and domestic gardens. From each circular landscape (n=12) we therefore selected 4 gardens and 12 other survey sites consisting of fallows, semi-natural habitats or flower rich borders of crop fields and leys during field visits, i.e. in total 16 survey sites per circular landscape (table 1). In addition we placed 4 sets of pan-traps in each circular landscape (3 plastic cups , 6cm deep, ø 15cm; one white, one blue, one yellow, sprayed with the corresponding fluorescent colour (Sparvar, Leuchtfarbe), filled with 50% propylene glycol), (table 1). Pan-traps were placed directly on the ground at a "safe" distance from physical harm by agricultural activities, within or bordering to one of the habitat types mentioned above. We aimed at an even spread of survey habitats and pan-traps over each circular landscape.

Bumblebee collection: All bumblebees found during a 10min survey of 100m^2 of each survey site were collected by hand netting and preserved in 70% ethanol. Sites were sampled 3 times, from 25 June to 31 August 2008. Pan-traps were emptied in connection to each survey round (table 1). No queens were collected to avoid affecting population persistence, but we could not avoid accidental collection of some queens in the pan-traps. Bumblebees were determined to species and caste in the lab following Löken (1973), Prŷs-Jones & Corbet (1987) and Holmström (2007). The thorax width of each individual was measured using digital callipers.

Statistics: Statistical analyses were carried out in SAS 9.2 for Windows (SAS Institute Inc., Cary, NC) using General Linear Models (SAS

Table 1: Sampling set-up of the study. Two landscape classes, complex and simple, of 6 circular landscapes each were sample according to this set-up.

Survey sites per circular landscape (n=12)	**Sampling methods**
12 non-crop habitats (100m^2)	Hand-netting (10min), 3 times
4 domestic gardens (100m^2)	Hand-netting (10min), 3 times
4 sets of pan-traps in non-crop habitats	Left in field for 3 periods of 16.4±4.3 days

proc GLM) and Linear Mixed Models (SAS Proc Mixed). Where proportions were used to describe land-use they were arcsin-square-root transformed before statistical testing to normalise data and avoid the variance to be associated with the mean. Land use data was analysed with GLMs at the level of each landscape, with landscape class as the explaining factor. For the bumblebee data analyses were made at the level of an individual bumblebee. Since workers from the same landscape are not independent estimates of the effect of landscape structure and even may be sisters (Darvill et al. (2004)), we use a Mixed Model (SAS Proc Mixed) and accounted for non-independence at the landscape level via the random structure. We used individual thorax width as the response variable and landscape class, species and habitat type as fixed factors. We assigned landscape, landscape × habitat type and landscape × species as random factors. Degrees of freedom were estimated using the Kenward-Rogers method. We used the Nobound option since covariance estimation of one random factor was non-significantly negative and the Kenward-Rogers method otherwise give inflated denominator degrees of freedom. To account for possible effects of differences in sampling date between landscapes we also ran the model including date of each sample. Date alone did however not have a significant effect, nor did it interact with landscape class and we therefore dropped it from the model. We tested for spatial auto-correlation by including a spherical spatial covariance structure. However, this covariance was not significant (z=0.58, P=0.28) and inclusion of it did not affect results qualitatively and was therefore not included. We present model least square means (lsm) while standard errors (sem) were calculated from data aggregated at the level they were tested at, using SAS Proc Means.

3. RESULTS

Landscapes: Since landscapes were selected based on mean block size they consequently differed such that complex landscapes had significantly smaller fields. Landscapes also differed because of correlated differences in other landscape variables. Complex landscapes had a higher proportion of leys and consequently, less annual crops than simple landscapes (table 2). Although we aimed to only select landscapes with little permanent pasture and forest, complex landscapes contained slightly but significantly more pasture and forest than did simple ones. It should be noted that according to our classification pastures are

Variable	**Complex** (mean±std)	**Simple** (mean±std)	**F** (1, 10)	**P**
Field size (ha)	9.49±2.82	53.11±8.71	136.19	<0.0001
Prop. farmland	0.81±0.085	0.90±0.026	7.61	0.020
Prop. pasture	0.090±0.044	0.022±0.031	11.24	0.0073
Prop. leys	0.28±0.094	0.054±0.0072	53.16	<0.0001
Prop. annual crop	0.61±0.12	0.91±0.036	41.87	<0.0001
Prop. forest	0.080±0.062	0.010±0.023	6.57	0.028

Table 2: Data on differences in land-use and land-cover between the two landscape classes studied. Pasture, leys and annual crops are given as proportions of land classified as farmland.

permanent, unfertilised, semi-natural grasslands used exclusively for grazing. In contrast, leys are rotational crops where grass mixed with clover (*Trifolium repens* or *T. pratense*) is cultivated for grazing, hay or silage production. Leys are typically included in the crop rotation and a field is used for ley at least two and sometimes up to five years in sequence.

Bumblebees: In total 2033 worker bees from 11 species were included in the analysis. The most common species were *B. lapidarius* (754), *B. terrestris* (563), *B. sylvarum* (239), *B hortorum* (156) and *B. pascourum* (151). Since in simple landscapes only 5 individuals of *B. pratorum* were sampled and from only 2 landscapes, we also ran the model excluding *B. pratorum*. However this only changed the results marginally and in favour of larger bees in complex landscapes. We therefore only present the results based on all species.

We found that worker bees were significantly larger, on average 2%, in complex compared to simple landscapes (lsm±sem (mm) complex 4.28±0.059, simple 4.19±0.049, effect size 1.61; $F_{1,9.7}$= 6.60, P=0.019, figure 2). Species, naturally, differed in size ($F_{10,96.7}$=40.04, P<0.0001, figure 2). There were also significant differences in size of workers caught foraging in different habitat types ($F_{4,28.2}$=3.67, P=0.016). Workers caught in gardens and adjacent to leys were larger (4.29±0.022 and 4.31±0.026 respectively) than those caught in or adjacent to pasture (4.18±0.037), crop fields (4.23±0.017) and fallow (4.18±0.027). We did not find any significant interactions between landscape class and either species or habitat type, indicating that the pattern of difference between landscapes was general.

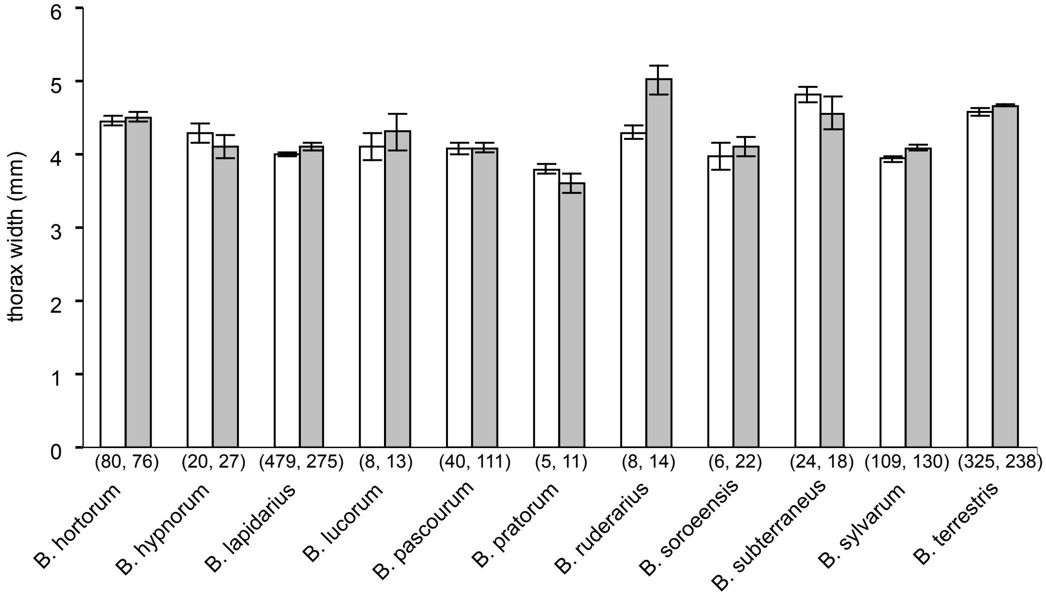

Figure 2: Mean thorax width±sem of bumblebee species collected in simple (white bars) and complex landscapes (grey bars). Sample size is given for simple and complex landscapes separately, within brackets under each species' bar. Individuals caught in complex landscapes were significantly larger that those caught in simple ones and mean size differed between species, see text.

4. DISCUSSION

We found that bumblebee workers were larger in more complex landscapes, independent of species identity. Hence, the five most common species, which have been considered to be able to cope with intensively managed, simple landscapes (Kosior et al. (2007), Goulson et al. (2008)), were similarly negatively affected by the simplified landscape structure. This effect on worker size could be because food availability, as modified by the presence of non-crop field borders, leys, pastures and forest edges, affects the growth of larvae and final size of bumblebee workers. Production of smaller individuals and fewer sexual in response to low food availability has been documented for *B. terrestris* in a lab environment (Schmid-Hempel & Schmid-Hempel (1998)). Smaller bumblebee workers of several species have also been found when they are sympatric with honey bees, which was suggested to indicate competition for food (Goulson et al. (2009)). Alternatively, it has been suggested that production of smaller workers is an adaptive response to starvation, since smaller bumblebees survive longer during low colony nectar intake rates (Couvillon & Dornhaus (2010)). This could mean that colonies in simple landscapes adjust to food scarcity by producing more, smaller and hardier workers rather than fewer, larger and more energy demanding ones. As we do not have information on landscape specific colony sizes we can unfortunately not evaluate this hypothesis. However, it still implies that the colonies sampled in simple landscapes experience a shortage of resources.

Landscape complexity is the mix of habitat types within an area, i.e. the number of land-cover classes and their distribution and configuration (Turner & O'Neill (2001), Vepsäläinen (2007)) and field size is one component of complexity (Vepsäläinen (2007)). In the current experimental design we studied bumblebees in landscapes of contrasting complexity, based on size of agricultural fields and with correlated differences in land-use (Persson et al. (2010)). Thus, food shortage for bumblebees is inevitable coupled with longer foraging trips, since flower-rich habitats (e.g. field margins, leys and possibly forest edges) are both fewer and farther apart in simple landscapes. We can therefore not separate the two effects of forage abundance and foraging distance. However, a lab study (Persson et al. (2010)) found no effect on worker size in response to temporal variation in food supply, a situation which may resemble a structurally simple landscape but with ample food. Bumblebees evolved in the temperate and alpine regions of the world (Hines (2008)), which are largely characterised by large variations in food supply due to flowering phenology of plants and frequent changes in weather conditions, resulting in periods of several days when foraging may not be possible (Couvillon & Dornhaus (2010)). They should thus be adapted to cope with variation in intake rates, as long as there is an ample food supply (over the whole season) to compensate for periods short in food influx. The detection of smaller workers in simplified landscapes therefore suggests that forage resources are indeed in short supply, and that there may therefore also be a constraint on queen (and male) production. Since smaller workers are less efficient in gathering nectar

(Spaethe et al. (2002), Goulson et al. (2002)), the whole colony is expected to suffer from lowered energy influx and end up in a downward spiral, further decreasing the size and efficiency of its potential work force and its reproductive output. Interestingly, other studies have suggested that mass flowering crops (MFCs) early in the season may boost bumblebee worker numbers but not reproduction (Herrmann et al. (2007), Westphal et al. (2009)). In the region studied here, oilseed rape is widely grown. It is thus possible that colonies have been initiated and grown large in response to oilseed rape early in the season. However, in simple landscapes these colonies would later all compete for the few available resources in non-crop habitats and, as a consequence, are unable to keep up the size of their workers.

It is known that bumblebees to prefer to forage on flowers which fit their morphology (Peat, Tucker, & Goulson (2005)), such that a smaller worker would presumably chose smaller flower heads than larger ones would. We found that bumblebees caught in gardens and in margins of leys were larger than those caught elsewhere. Larger bees thus appear to be attracted to the flowers of those habitats. A plausible reason for this is that larger bumblebees also have a longer proboscis (Peat et al. (2005)) which makes them able to attain nectar from deeper flowers. The leys in this study contained grass and either white or red clover, both important nectar and pollen plants. Both species produce flowers that are deeper than many of the disc-shaped annual or biennial flowers growing in fallows, ruderal habitats and in margins of crop fields and may therefore attract slightly larger foragers. Gardens often present a variety of ornamental flowers and herbs varying in shape and corolla depth. The shape of many of the common garden plants known to attract pollinators (e.g. *Nepeta spp., Thymus spp., Origanum spp., Menta spp., Lavandula, Salvia*) (Fussell & Corbet (1992)) indicate that they also require bees with longer proboscis for efficient nectar foraging.

An alternative explanation to our results may be that the flower compositions of simple and complex landscapes differ such that smaller bees are better apt to utilise that of simple landscapes, while larger bees are better foragers in complex landscapes. In that case, smaller workers would be an adaptive response to the available flora. Data from a previous study in this same region indeed show that the proportion of annual to perennial flowers is higher in simple compared to in complex landscapes (Persson & Smith (2011) Ch. II this thesis). However, the total amount of flower resources was also substantially lower in simple landscapes of this region (Persson & Smith (2011) Ch. II this thesis) and it is therefore unlikely that the smaller size of workers detected here is solely an adaptive response to flower morphology although it may contribute to the size difference detected.

There may be some concerns regarding spatial auto-correlation, since landscapes cannot be perfectly interspersed given the overall structure of landscape variation. We argue that the landscapes were separated enough to be independent considering the foraging ranges of bumblebees (e.g. Knight et al. (2005), Osborne et al. (2008), Wolf et al. (2008)),but close enough that gene-flow would be sufficient to restrict possibilities for local adaptations (Kraus, Wolf, & Moritz (2009), Lepais, Darvill, O'Connor, Osborne, Sanderson et al. (2010)). However, although the result was unaffected when accounting for spatial auto-correlation, it is clear that a correlative study cannot ascertain which aspects of landscape variation are causing the differences in the size of workers. In real landscapes characteristics are inevitably linked (Persson et al. (2010)). For example, although our design attempted to maximize differences in farmland complexity, there is a small but significant difference between the landscapes in the amount of forest. However, given that we focused on maximizing the difference in farmland complexity while minimizing variation in amount of pasture and forest, we believe that the cause for variation in worker size should primarily be sought in landscape complexity or in factors closely linked to farmland complexity.

In summary, the results presented here indicate that simple landscapes with a shortage of food are indeed hampering worker body size and thereby possibly colony development of several bumblebee species. It is therefore urgent to recreate and properly manage non-crop habitats of simplified landscapes, in order to increase the amount of suitable resource flowers for bees.

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6. REFERENCES

Benton, T. (2006). Bumblebees, London: Harper Collins

Benton, T. G., Vickery, J. A., Wilson, J. D. (2003). Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology & Evolution, 18, 182-188.

Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J., Kunin, W. E. (2006). Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. Science, 313, 351-354.

Brian, A. (1952). Division of labour and foraging in Bombus agrorum Fabricius. Journal of Animal Ecology, 21, 223-240.

Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F., Griswold, T. L. (2011). Patterns of widespread decline in North American bumble bees. Proceedings of the National Academy of Sciences.

Carvell, C., Roy, D. B., Smart, S. M., Pywell, R. F., Preston, C. D., Goulson, D. (2006). Declines in forage availability for bumblebees at a national scale. Biological Conservation, 132, 481-489.

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.

Couvillon, M., Dornhaus, A. (2010). Small worker bumble bees (Bombus impatiens) are hardier against starvation than their larger sisters. Insectes Sociaux, 57, 193-197.

Darvill, B., Knight, M., Goulson, D. (2004). Use of genetic markers to quantify bumblebee foraging range and nest density. Oikos, 107, 471-478.

Fussell, M., Corbet, S. A. (1992). Flower Usage by Bumble-Bees: A Basis for Forage Plant Management. The Journal of Applied Ecology, 29, 451-465.

Goulson, D., Lye, G. C., Darvill, B. (2008). Decline and Conservation of Bumble Bees. Annual Review of Entomology, 53, 191-208.

Goulson, D. (2003). Bumblebees: Their behaviour and ecology, Oxford, UK: Oxford University Press

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. Journal of Applied Ecology, 47, 1207-1215.

Goulson, D., Peat, J., Stout, J. C., Tucker, J., Darvill, B., Derwent, L. C., Hughes, W. O. (2002). Can alloethism in workers of the bumblebee, Bombus terrestris, be explained in terms of foraging efficiency? Animal Behaviour, 64, 123-130.

Goulson, D., Sparrow, K. (2009). Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. Journal of Insect Conservation, 13, 177-181.

Greenleaf, S., Williams, N., Winfree, R., Kremen, C. (2007). Bee foraging ranges and their relationship to body size. Oecologia, 153, 589-596.

Grixti, J. C., Wong, L. T., Cameron, S. A., Favret, C. (2009). Decline of bumble bees (Bombus) in the North American Midwest. Biological Conservation, 142, 75-84.

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. Molecular Ecology, 16, 1167-1178.

Hines, H. M. (2008). Historical Biogeography, Divergence Times, and Diversification Patterns of Bumble Bees (Hymenoptera: Apidae: Bombus). Systematic Biology, 57, 58-75.

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

Kearns, C. A., Inouye, D. W., Waser, N. M. (1998). Endangered Mutualisms: The Conservation of Plant-Pollinator Interactions. Annual Review of Ecology and Systematics, 29, 83-112.

Knight, M., Martin, A., Bishop, S., Osborne, J., Hale, R., Sanderson, A., Goulson, D. (2005). An interspecific comparison of foraging range and nest density of four bumblebee (Bombus) species. Molecular Ecology, 14, 1811-1820.

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 Conservation and Diversity, 2, 116-124.

Kosior, A., Celary, W., Olejniczak, P., Fijal, J., Krol, W., Solarz, W., Plonka, P. (2007). The decline of the bumble bees and cuckoo bees (Hymenoptera : Apidae : Bombini) of Western and Central Europe. Oryx, 41, 79-88.

Kraus, F., Wolf, S., Moritz, R. (2009). Male flight distance and population substructure in the bumblebee Bombus terrestris. Journal of Animal Ecology, 78, 247-252.

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. Molecular Ecology, 19, 819-831.

Löken, A. (1973). Studies on Scandinavian Bumble Bees (Hymenoptera, Apidae). Norwegian Journal of Entomology, 20, 1-218.

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

Öckinger, E., Smith, H. G. (2007). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. Journal of Applied Ecology, 44, 50-59.

Osborne, J. L., Martin, A. P., Carreck, N. L., Swain, J. L., Knight, M. E., Goulson, D., Hale, R. J., Sanderson, R. A. (2008). Bumblebee flight distances in relation to the forage landscape. Journal of Animal Ecology, 77, 406-415.

Peat, J., Tucker, J., Goulson, D. (2005). Does intraspecific size variation in bumblebees allow colonies to efficiently exploit different flowers? Ecological Entomology, 30, 176-181.

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. Agriculture Ecosystems & Environment, 136, 169-176.

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution, 25, 345-353.

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

Rundlöf, M., Nilsson, H., Smith, H. G. (2008). Interacting effects of farming practice and landscape context on bumblebees. Biological Conservation, 141, 417-426.

Schmid-Hempel, R., Schmid-Hempel, P. (1998). Colony performance and immunocompetence of a social insect, Bombus terrestris, in poor and variable environments. Functional Ecology, 12, 22-30.

Spaethe, J., Weidenmueller, A. (2002). Size variation and foraging rate in bumblebees (Bombus terrestris). Insectes Sociaux, 49, 142-146.

Turner, M. G., Gardner, R. H., O'Neill, R. V. (2001). Landscape Ecology in theory and practice, New York, NY: Springer Science+Business Media, LLC

Vepsäläinen, V. (2007). Farmland birds and habitat heterogeneity in an intensively cultivated boreal agricultural landscape. Faculty of Biosciences, University of Helsinki, Finland, Helsinki, Finland.

Walther-Hellwig, K., Frankl, R. (2000). Foraging habitats and foraging distances of bumblebees, Bombus spp. (Hym., Apidae), in an agricultural landscape. Journal of Applied Entomology, 124, 299-306.

Westphal, C., Steffan-Dewenter, I., Tscharntke, T. (2009). Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. Journal of Applied Ecology, 46, 187-193.

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

Williams, P. H. (1982). The Distribution and Decline of British Bumble Bees Bombus. Journal of Apicultural Research, 21, 236-245.

Williams, P. H., Osborne, J. L. (2009). Bumblebee vulnerability and conservation world-wide. Apidologie, 40, 367-387.

Williams, P., Colla, S., Xie, Z. (2009). Bumblebee Vulnerability: Common Correlates of Winners and Losers across Three Continents. Conservation Biology, 23, 931-940.

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. Journal of Applied Ecology, 45, 793-802.

Wolf, S., Moritz, R. F. (2008). Foraging distance in Bombus terrestris L. (Hymenoptera : Apidae). Apidologie, 39, 419-427.

V

Gardens benefit bees and enhance pollination in intensively managed farmland

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ABSTRACT

The recent loss of pollinating insects and out-crossing plants in agricultural landscapes has raised a concern for the maintenance of ecosystem services. Wild bees have been shown to benefit from garden habitats in urban and suburban areas. We investigated the effects of distance from garden habitats on wild bees and seed set of a wild out-crossing plant *Campanula persicifolia*, in intensively managed agricultural landscapes in southern Sweden. Bee abundance and species richness, as well as plant seed set, was higher closer to gardens (<15m) than further away (>140m). This highlights domestic gardens as a landscape wide resource for pollinators but also the lack of sufficient pollination of wild plants in contemporary agricultural landscapes.

KEYWORDS: *Apoidea*; *Bombus*; *Campanula*; pollinator; seed set; agriculture; landscape

1. INTRODUCTION

Agricultural intensification, resulting in loss and fragmentation of natural habitats, has caused large-scale losses of farmland biodiversity (e.g. Krebs et al., 1999). Widespread declines of pollinators have received particular attention because of the risk it poses to the ecosystem service they provide (Kremen et al., 2002; Steffan-Dewenter et al., 2005). In fragmented landscapes, a main threat to wild plant reproduction is pollination failure, caused either by lack of mates or of pollinators (Wilcock & Neiland, 2002). In fact, large-scale losses of pollinators have been paralleled by losses of out-crossing plant species (Biesmeijer et al., 2006; Gabriel & Tscharntke, 2007).

Semi-natural habitats are known to positively affect pollinators in the surrounding agricultural landscape (e.g. Öckinger & Smith, 2007; Ricketts et al., 2008) presumably through contributing both nest sites and forage resources. Other non-crop areas such as field margins may also be beneficial provided that they are rich in flower resources (Kleijn & van Langevelde, 2006). Linear landscape elements are also known to be important for bumblebee nesting (Osborne et al., 2007; Svensson et al., 2000). Non-crop, semi-natural areas add heterogeneity to otherwise, in many aspects, simplified agricultural landscapes (Benton et al., 2003). Another type of non-crop areas are domestic gardens situated in the countryside. In heavily cultivated surroundings, gardens can be assumed to enhance floral abundance and diversity, as well as three-dimensional structure (i.e. habitat complexity). Lately attention has been drawn to the positive impact of urban gardens and allotment gardens on pollinators (Ahrné et al., 2009; Goddard et al., 2010) and on the process of pollination (Cussans et al., 2010). Gardens often provide a continuous supply of nectar and pollen which bees can utilise (Fussel & Corbet, 1992). Suburban gardens have been shown to increase growth of experimental colonies of *Bombus terrestris* compared to rural areas (Goulson et al., 2002). In urban gardens, habitat complexity and diversity of flowering plants have been shown to be positively related to bumblebee and solitary bee diversity (Smith et al., 2006). Gardens can provide suitable habitats for bees to nest and have been shown to contain higher densities of bumblebee nests than grasslands and woodlands in arable landscapes (Osborne et al., 2008). Hence, gardens may promote pollinator abundance and species richness also in agricultural landscapes.

However, measures promoting pollinators may not necessarily benefit pollination of wild plants, because species may vary in their effectiveness as pollinators (Klein et al., 2003). Species may for example vary in rates of removal and deposition of pollen (Wilson & Thomson 1991) and also in their degree of flower constancy (Goulson 1999). Another example of a more indirect effect on pollination is large-scale cultivation of oilseed rape, *Brassica napus*. This mass flowering crop may be beneficial for some early emerging and short-tongued bumblebee species, but result in reduced abundance of long-tongued bumblebees, which are in turn important pollinators of plants with deep corollas (Diekötter et al., 2010). Thus, it is important to determine not only the effect of gardens on the general abundance of pollinators, but on different groups of pollinators and pollination *per se*. It has also been shown that the decline with distance (from natural or semi-natural habitats) of native pollinator visits to crops is steeper than the decline of pollinator richness with distance (Ricketts et al., 2008), which again highlights the importance of studies including the pollination service itself. Foraging ranges of bees are positively related to body size (Greenleaf et al., 2007). In the region of this study, bee body size coincides with sociality such that social bees (*Bombus* species and *Apis mellifera*) are larger than solitary bees.

Our aim was to investigate if gardens in landscapes highly dominated by agriculture can act as sources of pollinators and subsequently benefit pollination of wild out-crossing plants. To this end we investigated if species richness and abundance of bees were higher close to gardens than further away, if the abundance of two groups of pollinators (large social and small solitary bees) were differently affected by distance and if, because of improved pollination, plant seed set for a native out-crossing plant was higher close to gardens. We focused on bees (Hymenoptera: Apoidea) as they are an important group of pollinators (Winfree et al., 2008). Bees can benefit from gardens for both nesting and foraging but as they are central place foragers with restricted foraging ranges (Goulson, 2003) they may also be negatively affected by distance between nests and forage sites and thus indirectly allow detection of their source of origin.

2. MATERIAL AND METHODS

2.1 Study set up

The study was carried out in southernmost Sweden (approx. 56°N, 13°30'E, figure 1). We selected nine landscape sectors (squares of 2.5 × 2.5km) situated in a region largely dominated by agriculture. The percentage area of sectors under agricultural land use was on average 81.7±10.7% (mean±stdv). Of this area annual crop fields composed 91.2±5.9% and leys 5.9±5.5% (mean±stdv). The total area of permanent pastures was 1.0±1.5% (mean±stdv). Within each landscape sector two isolated domestic gardens were identified and inspected to ensure reasonable similarity with respect to

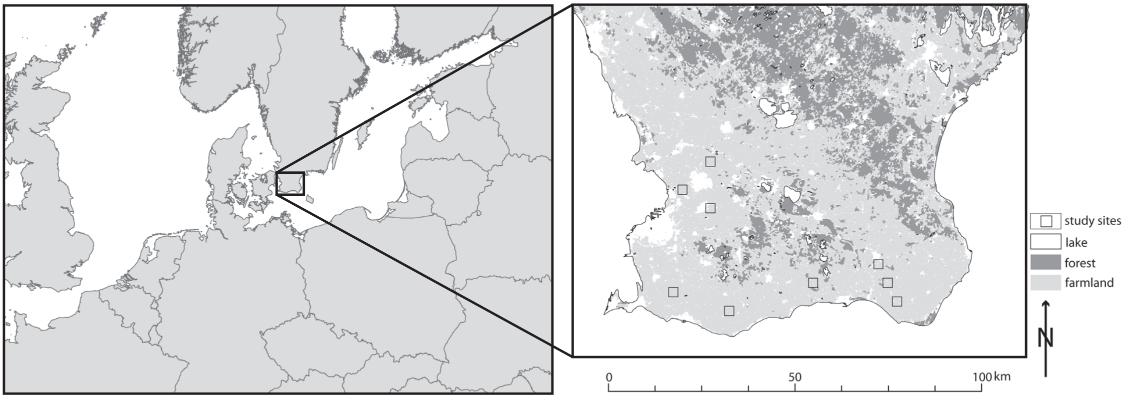

Figure 1: Map of the study region in southernmost Sweden, which is largely dominated by agriculture. The nine landscape sectors (2.5 × 2.5km quadrates) used in the study are drawn.

features important to pollinator abundance and diversity (Osborne et al., 2007; Smith et al., 2006). All gardens had an area of at least 500 m^2 and included all the following features: planted flowers, wild plants, trees, flowering bushes and sections with tall grass. The majority of gardens also included hedges and a compost heap.

Along road verges reaching out from the gardens either phytometers (plants used to estimate pollination [cf. Albrecht et al. 2007], in this case *Campanula persicifolia*) or a set of pan-traps were placed at two different distances, either "proximate" within 15m from the edge of the garden or "distant" approximately 140m away. We did not use the same garden for both phytometers and traps because of the risk of pollinator depletion due to the traps. Which of the two gardens within a landscape that received phytometers and traps respectively, was randomly selected. One landscape also had a third garden with phytometers bagged in fine mesh. These plants served as pollinator free controls and were placed in the field to ensure similar weather and wind conditions to experimental plants.

The pan-traps were sets of one yellow, one white and one blue plastic cup (6cm deep, ø 15cm) sprayed with fluorescent colours (Sparvar, Leuchtfarbe) placed directly on the ground and filled with 50% propylene glycol. Each phytometer consisted of two plants of peach-leaved bellflower, *C. persicifolia;* a wild, self-incompatible flower native to Sweden (Nyman, 1992). The plants were purchased from a local garden centre at the beginning of May 2009 and were immediately replanted in 7.5l pots with commercial garden soil. Phytometers and traps were kept in the field during three weeks, from end of June until mid July, and were visited and watered twice a week. To be able to determine in which order flowers had bloomed, we marked all flowers that had started to bloom since the last visit with coloured thread and used one colour for each visit. *C. persicifolia* was present in one of the gardens where phytometers were placed. Lack of other suitable gardens made us unable to remove this garden from the study, but we do not believe that this will lead to any bias since the study design focuses on pollination in relation to distance from gardens rather than on pollination inside gardens. Both proximate and distant phytometers should benefit from a pollen source inside the garden. Insects caught in traps were collected and stored in 70% ethanol. After the field study all plants were transferred to a greenhouse.

2.2 Data collection

All capsules from *C. persicifolia* marked in the field, except those marked at the last visit, were harvested between 30 July and 20 August when ripe (n=233). Seeds were weighed and we used the weight of each capsule's seeds as a proxy for seed set. To estimate plant size we noted total number of flowers per plant. Capsules hosting seed eating weevils (n=68) were excluded from analyses. In two landscapes plants had all flowers and capsules eaten by slugs, resulting in six complete pairs of phytometers and one with only distant plants. Cuckoo bumblebees former *Psityris spp.* (n=4) were excluded since they lack a pollen collecting worker caste (Goulson, 2003). Analyses were run with and without honey bees (n=18) since their origin is determined not only by habitat quality but by where bee keepers place hives. For some analyses we distinguished between social and solitary species to evaluate if body size has an effect on pollinator foraging distance at the distances under study. If a trap had been damaged, neither the sample from this nor other traps at that location and date were used. One location had to be excluded from the analyses because of the small amount of bees collected (in total 3 individuals). The reason was most likely dust accumulation in the traps preventing colour reflection, and since the amount of dust differed between distances the location was omitted from analyses.

2.3 Statistical analysis

To account for the pair-wise design with two distances; we used mixed models with Landscape as a random factor and the Distance from the gardens as a fixed factor. For analyses of seed set we calculated the mean value of the capsules' seed set per plant followed by mean value per distance. To test if the size of plants had any effect, we also analysed data at the plant level, including Distance nested within Landscape as a second random factor and Plant size as a covariate. To test if sequential order of inflorescences, (i.e. the order in which individual flowers bloomed on a plant), had any effect on seed set we analysed data at the capsule level including Plant nested within Distance and Landscape as a third random factor and with Order of inflorescence and Plant size as covariates. In these latter two analyses, there was a negative covariance between the seed weight in the two plants at the same Distance, possibly because of competition for pollinators, which was accounted for by the random structure in the analysis. Tests were run with and without data from capsules without seeds but not clearly attacked by weevils (n=18), which we suspected were from seed abortion or damage to the plant. Pollinator data was summarized at each Distance. For comparison of the effect of distance on social and solitary bees, the abundances of groups were summarized separately and Distance nested within Landscape included as a second random factor. Variables were log-transformed ($\log_{10}[x + 1]$) to normalize residuals.

Table 1: Total number of individuals and species per family of social and solitary bees collected in pan-traps.

Genus	No. individuals	No. species
Bombus	148	12
Apis	18	1
Andrena	40	6
Lasioglossum	23	4
Halictus	11	2
Colletes	2	1
Hylaeus	1	1
Osmia	1	1

3. RESULTS

In total, 244 bees of 28 species and 8 genera were sampled (table 1). The most abundant social bee was *Bombus terrestris* (27% of social bees) and the most abundant solitary bee was *Andrena nigroaenea* (29% of solitary bees). Abundance of bees were significantly higher proximate than distant to gardens ($F_{1,\ 7.46}$=21.02, P=0.0021). On average 23.75±6.79 (mean±SEM) bees were sampled in proximate traps and 7.25±1.42 bees in distant traps. Social and solitary bee abundance were not differently affected by distance ($F_{1,\ 21.61}$=1.19, P=0.29), and social bees were significantly more abundant in proximate traps also when excluding honey bees ($F_{1,\ 7.66}$=11.75, P=0.0096). Species richness of solitary bees was significantly higher close to gardens (3.28±0.96) than farther away (1.13 ± 0.30), ($F_{1,\ 14}$=5.79, P=0.0305). Bumblebee species richness was only marginally significantly higher in proximate traps (5.00±0.93) compared to distant traps (3.25±0.65), ($F_{1,\ 7.62}$=4.88, P=0.060).

The mean capsular seed set was significantly higher on proximate (32.55±2.67mg) compared to distant phytometers (17.78±1.83mg), ($F_{1,\ 5.01}$=12.27, P=0.017; effect size 1.95), Figure 2. The result held true both when excluding the garden containing *C. persicifolia* ($F_{1,4.23}$=9.12, P=0.037) and when excluding capsules without seeds ($F_{1,5.14}$=7.86, P=0.037). Plant size and sequential order of flowering did not explain any additional variance (P=0.52 and P=0.17 respectively). The control plants bagged in field (n=11 capsules) did not set any seeds, confirming that *C. persicifolia* is self-incompatible and dependent on animal pollination (Nyman, 1992).

4. DISCUSSION

We found evidence that gardens acted as a source of pollinating bees for a native out-crossing plant in landscapes dominated by agriculture. Both abundance and species richness of bees were higher close to gardens than further away. Furthermore, seed set of C. persicifolia was higher close to gardens, suggesting that the presence of gardens indeed enhanced pollination. Our results further strengthen the notion that modern agricultural landscapes are lacking in pollinator services. They also point to the value of other habitat types than the natural or semi-natural ones, which are commonly considered in these circumstances and most often constitute the focus of both scientific studies and management actions.

It remains to be shown to what extent our results generalize to other plant species. In a similar study of an agricultural crop, *Trifolium pratense*, we could not detect any effect of gardens on seed set because of heavy seed predation (Samnegård, 2010). Likewise, Albrecht et al. (2007) could

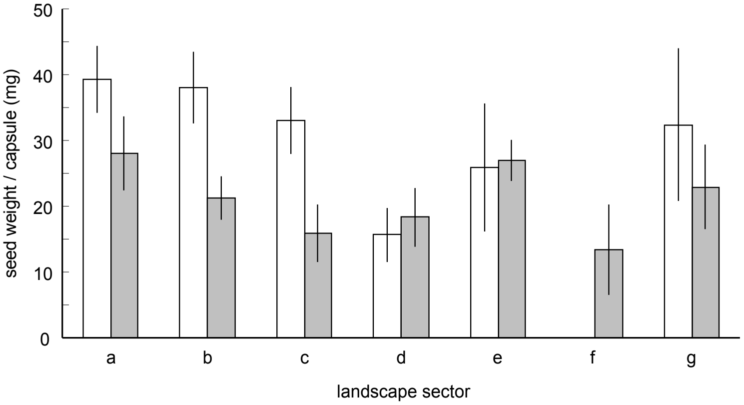

Figure 2: Mean and SEM in seed weight per capsule of *Campanula persicifolia* at proximate (white bars) and distant (grey bars) locations. The proximate location is missing from landscape f, see text.

not detect any effect of distance (<200m) from restored meadows on either decline of large sized pollinators or seed set of three insect pollinated plants species (*Rahnanus sativus*, *Hypochaeris radicata* and *Campanula glomerata*). On the other hand, small sized pollinators did show clear declines (Albrecht et al., 2007) and visitation to and seed set of *Centaurea jacea* showed a negative relation with distance from meadows (Albrecht et al., 2009). Steffan-Dewenter & Tscharntke (1999) demonstrated declines in seed set of *Sinapis arvensis* and *R. sativus* related to declines in bee visits with distance from grasslands and Cussans et al. (2010) reported on increased seed production of *Glechoma hederacea* and *Lotus corniculatus* when grown in suburban gardens compared to adjacent farmland fields. In other words, if proximity to semi-natural or other flower enriched and complex non-crop habitats indeed benefits pollination of a particular species depend on characteristics of the pollinator community involved as well as the reproductive system of the plant.

Solitary bees are known to forage close to their nests, whereas many bumblebee species cover greater distances (reviewed in Zurbuchen et al., 2010). We therefore used sociality as a proxy for body size and foraging distance; social bumblebees constituting the "large size and long distance"-group and solitary bees the "small and short"-group. However, we did not find any difference in how abundances of solitary and social bees declined with distance from gardens. Distant sites were however only 140m away from gardens, a distance which may be overcome also by many solitary bees (Zurbuchen et al., 2010). Furthermore, sample sizes of solitary and social bees separately were small, resulting in low statistical power. Another study on distance from conservation grasslands has demonstrated a difference between small and large pollinators (Albrecht et al. 2007).

The fact that distant plants had a lower seed set than proximate ones in the present as well as in other studies (e.g. Albrecht et al., 2009; Ricketts et al., 2008; Steffan-Dewenter & Tscharntke, 1999), may suggest a shortage of pollination of wild plants in intensively managed landscapes.

Table 2: Statistical models and results of the main analyses performed using Mixed Models. Statistically significant results (p<0.05) are typed in bold.

Dependent variable	**Fixed factor(s)**	**Random variable(s)**	**Fdf**	**P**
Seed set				
Seed weight/capsule, plant and distance	Distance	Landscape	$12.27_{1,5,0}$	**0.017**
Pollinators				
Total abundance/distance	Distance	Landscape	$121.02_{1,7.5}$	**0.0021**
Abundance bumblebees	Distance	Landscape	$11.75_{1,7.7}$	**0.0096**
Abundance per social class	Distance Social class Distance × Social class	Distance × Landscape	$1.19_{1,21.6}$	0.29
Solitary bee species richness	Distance	Landscape	$5.79_{1,14}$	**0.031**
Bumblebee species richness	Distance	Landscape	$4.88_{1,14}$	0.060

A shortage of pollinators can in turn, through a decrease in the pollination service they provide, affect plant community structures (Biesmeijer et al., 2006). Interestingly, organic farming has been found to benefit both pollinators (Holzschuh et al., 2008; Rundlöf et al., 2008) and insect-pollinated plants (Gabriel & Tscharnkte, 2007). Likewise, domestic gardens may promote persistence of insect-pollinated wild plants in intensively farmed landscapes because the resource rich habitats they constitute act as refuges for pollinators; habitats which have so far largely been over-looked in agricultural ecosystems (Goddard et al., 2010).

Despite the relatively low sample size, we found 12 out of the 17 species of true bumblebees potentially found in southern Sweden (Holmström, 2007). The majority of the species not found are locally extinct or extremely rare (Holmström, 2007). Thus, a quite diverse species pool may still exist even in intensively managed agricultural regions in Sweden; possibly partly because of the presence of gardens (cf. Osborne et al., 2008). This implicates that pollinator conservation in this region may actually pay off quite quickly, since at least there are remnant populations to build on.

Earlier studies on the impact of domestic gardens on pollinators have focused on urban or suburban environments (Ahrné et al., 2009; Cussans et al. 2010; Fetridge et al., 2008; Goddard et al., 2010; Goulson et al., 2002; Matteson et al., 2008; but see Osborne et al., 2008) or on pollinators in urban parks (McFredrick & LeBuhn, 2006). We have shown that gardens can contribute to the ecosystem service of pollination also in agricultural landscapes. Since gardens often include features beneficial for many bee species; e.g. a diversity of nesting substrates and continuous supply and diversity of nectar and pollen (Fussell & Corbert, 1992; Osborne et al., 2008), they may complement more "natural" habitats for pollinators in otherwise impoverished environments. However, establishing more gardens in agricultural landscapes is of course not a realistic conservation measure. Instead we propose that by making the importance of gardens known, awareness of ecosystem services can be spurred and improvements of existing gardens can be made by an interested general public. Also, acknowledging garden habitats as a resource for biodiversity not only in cities, could lead to domestic gardens being included in conservation planning situations (Goddard et al., 2010) also outside the urban environment. The position and management of gardens could for example be considered one way to increase connectedness of isolated (semi)-natural habitat fragments. The relatively high species richness of bees found in proximity to gardens also demonstrate the importance of not overlooking gardens (and other recently man-made habitats) when studying biodiversity, especially in otherwise species poor environments. Most importantly however, the lack of pollination (already 140m from gardens) found here calls for more directed measures to aid pollinators in agricultural landscapes.

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6. REFERENCES

Ahrné, K., Bengtsson, J. & Elmqvist T., 2009. Bumble Bees (Bombus spp.) along a Gradient of Increasing Urbanization. PLoS ONE, 4 (5), e5574.

Albrecht, M., Duelli, P., Müller, C., Kleijn, D. & Schmid, B., 2007. The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland. J. Appl. Ecol. 44, 813-822.

Albrecht M., Duelli P., Obrist M.K., Kleijn D. & Schmid B., 2009. Effective long-distance pollen dispersal in Centaurea jacea. PLoS ONE 4, e6751.

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

Cussans, J., Goulson, D., Sanderson, R., Goffe, L., Darvill, B. & Osborne J.L., 2010. Two bee-pollinated plant species show higher seed production when grown in gardens compared to arable farmland. PLoS ONE 5, e11753.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemueller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J. & Kunin, W.E., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science, 313, 351-354.

Diekötter, T., Kadoya, T., Peter, F., Wolters, V. & Jauker, F., 2010. Oilseed rape crops distort plant-pollinator interactions. J. Appl. Ecol., 47, 209-214.

Fetridge,E.D. Ascher,J.S. & Langellotto,G.A., 2008. The Bee Fauna of Residential Gardens in a Suburb of New York City (Hymenoptera: Apoidea) Ann. Entomol. Soc. Am., 101, 1067-1077.

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

Gabriel, D. & Tscharntke, T., 2007. Insect pollinated plants benefit from organic farming. Agric. Ecosyst. Environ., 118, 43-48.

Goddard, M.A., Dougill, A.J. & Benton, T., 2010. Scaling up from gardens: biodiversity conservation in urban environments. TREE, 25, 90-98.

Goulson, D., 1999. Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution. Perspect. Plant Ecol. Evol. Syst., 2, 185-209.

Goulson, D., Hughes, W., Derwent, L. & Stout, J., 2002. Colony growth of the bumblebee, Bombus terrestris, in improved and conventional agricultural and suburban habitats. Oecologia, 130, 267-273.

Goulson, D., 2003. Bumblebees: Their Behaviour and Ecology. Oxford, UK: Oxford University Press.

Greeleaf S.S., Williams N.M., Winfree R. & Kremen C., 2007. Bee foraging ranges and their relationship to body size. Oecologia, 153, 589-596.

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

Holzschuh, A., Steffan-Dewenter, I., Kleijn, D. & Tscharntke, T., 2008. Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. J. Appl. Ecol., 44, 41-49.

Klein, A. M., Steffan-Dewenter, I. & Tscharntke, T., 2003. Fruit set of highland coffee increases with the diversity of pollinating bees. Proc. R. Soc. London. B, Biol.Sci., 270, 955-961..

Kleijn, D. & van Langevelde, F., 2006. Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. Basic Appl. Ecol., 7, 201-214.

Krebs, J.R., Wilson, J.D., Bradbury, R.B. & Siriwardena, G.M., 1999. The second silent spring? Nature, 400, 611-612.

Kremen, C., Williams, N. & Thorp, R., 2002. Crop pollination from native bees at risk from agricultural intensification. PNAS, 99, 16 812–16 816.

Matteson,K.C., Ascher,J.S. & Langellotto,G.A.., 2008. Bee richness and abundance in New York city urban gardens. Ann. Entomol. Soc. Am., 101, 140-150.

McFrederick, Q.S. & LeBuhn, G., 2006. Are urban parks refuges for bumble bees Bombus spp. (Hymenoptera: Apidae)? Biol. Cons., 129, 372-382.

Nyman, Y., 1992. Pollination mechanisms in six Campanula species (Campanulaceae). Plant. Syst. Evol., 181, 97-108.

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

Osborne, J.L., Martin, A.P., Shortall, C.R., Todd, A.D., Goulson, D., Knight, M.E., Hale, R.J. & Sanderson, R.A., 2008. Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. J. Appl. Ecol., 45, 784-792.

Ricketts T.H., Regetz J., Steffan-Dewenter I., Cunningham S.A., Kremen C., Bogdanski A., Gemmill-Herren B., Greeleaf S.S., Klein A.M., Mayfield M.M., Morandin L.A., Ochieng A., Potts S.G. & Viana B., 2008. Ecol. Lett., 11, 499-515.

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

Samnegård, U., 2010. Gardens as sources for pollinators in intensively managed farmland in southern Sweden. MS thesis, Lund University.

Smith, R.M., Warren, P.H., Thompson, K. & Gaston K.J., 2006. Urban domestic gardens (VI): Environmental correlates of invertebrate species richness. Biodiv. Conserv., 15, 2415-2438

Steffan-Dewenter I. & Tscharntke T.,1999. Effects of habitat isolation on pollinator communities and seed set. Oecologia, 121, 432-440.

Steffan-Dewenter, I., Potts, S.G. & Packer, L., 2005. Pollinator diversity and crop pollination services are at risk. TREE, 20, 651-652.

Svensson B., Lagerlöf J. & Svensson B.G., 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. Agric. Ecosyst. Environ., 77, 247-255.

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.

Wilcock, C. & Neiland, R., 2002. Pollination failure in plants: why it happens and when it matters. Trends Plant Sci., 7, 270-277.

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.

Wilson P. & Thomson J.D., 1991. Heterogeneity among floral visitors leads to discordance between removal and deposition of pollen. Ecology, 72, 1503-1507.

Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S. & Dorn, S., 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biol. Cons., 143, 669-676.

The following is a list of **Doctoral theses** (Lund University, Sweden) from the **Department of Animal Ecology** (nos. 1-78, from no. 79 and onwards denoted by (A)) and **Theoretical Ecology** (T). (E) refers to Doctoral theses from the **Department of Chemical Ecology/Ecotoxicology** during the years 1988-1995.

1. CHARLOTTE HOLMQVIST. Problem on marine-glacial relicts on account on the genus Mysis. 6 May 1959.
2. HANS KAURI. Die Rassenbildung bei europäischen Rana-Arten und die Gültigkeit der Klimaregeln. 9 May 1959.
3. PER DALENIUS. Studies on the Oribatei (Acari) of the Torneträsk territory in Swedish Lapland. 14 May 1963.
4. INGEMAR AHLÉN. Studies on the history of distribution, taxonomy and ecology of the Red Deer in Scandinavia. 21 May 1965.
5. STAFFAN ULFSTRAND. Bentic animal communities of river Vindelälven in Swedish Lapland. 8 May 1968.
6. SAM ERLINGE. Food habits, home range and territoriality of the otter Lutra lutra L. 6 May 1969.
7. GUNNAR MARKGREN. Reproduction of moose in Sweden. 17 May 1969.
8. ARNE BERGENGREN. On genetics, evolution and history of the heath-hare, a distinct population of the arctic hare, Lepus timidus L. 17 October 1969.
9. HåKAN HALLANDER. Habitats and habitat selection in the wolf spiders Pardosa chelata (O.F. Müller) and P. pullata (Clerck). 20 March 1970.
10. ULF SCHELLER. The Pauropoda of Ceylon. 29 May 1970.
11. LEIF NILSSON. Non-breeding ecology of diving ducks in southernmost Sweden. 2 December 1970.
12. RUNE GERELL. Distributional history, food habits, diel behaviour, territoriality, and population fluctuations of the mink Mustela vison Schreber in Sweden. 30 March 1971.
13. INGRID HANSSON. Skull nematodes in mustelids. 3 June 1971.
14. STURE ABRAHAMSSON. Population ecology and relation to environmental factors of Astacus astacus Linné and Pacifastacus leniusculus Dana. 3 June 1971.
15. LENNART HANSSON. Food conditions and population dynamics of Scandinavian granivorous and herbivorous rodents. 26 November 1971.
16. SVEN-AXEL BENGTSON. Ecological segregation, reproduction and fluctuations in the size of duck populations in Iceland. 21 April 1972.
17. STEN ANDREASSON. Distribution, habitat selection, food and diel activity of Swedish freshwater sculpins (Cottus L.). 5 May 1972.
18. KERSTIN SVAHN. Coccidian blood parasites in Lacertids. 17 May 1972.
19. RUTGER ROSENBERG. Macrofaunal recovery in a Swedish fjord following the closure of a sulphite pulp mill. 13 April 1973.
20. SVEN ALMQVIST. Habitat selection and spatial distribution of spiders in coastal sand dunes. 25 May 1973.
21. TORSTEN MALMBERG. Population fluctuations and pesticide influence in the rook Corvus frugilegus L., in Scania, Sweden 1955-1970. 25 May 1973.
22. ANDERS SÖDERGREN. Transport, distribution, and degradation of organochlorine residues in limnic ecosystems (defended at the Dept of Limnology). 23 May 1973.
23. BERITH PERSSON. Effects of organochlorine residues on the whitethroat Sylvia communis Lath. 7 December 1973.
24. PLUTARCO CALA. The ecology of the ide Idus idus (L.) in the river Kävlingeån, South Sweden. 23 May 1975.
25. ÅKE GRANMO. Effects of surface active agents on marine mussels and fish. 26 May 1975.
26. BO W SVENSSON. Population ecology of adult Potamophylax cingulatus (Steph.) and other Trichoptera at a South Swedish stream. 15 October 1975.
27. STEN NORDSTRÖM. Associations, activity, and growth in lumbricids in southern Sweden. 6 April 1976.
28. STEN RUNDGREN. Environment and lumbricid populations in southern Sweden. 8 April 1976.
29. CHRISTIAN OTTO. Energetics, dynamics and habitat adaptation in a larval population of Potamophylax

cingulatus (Steph.) (Trichoptera). 9 April 1976.

30. JAN LÖFQVIST. The alarm-defence system in formicine ants. 21 May 1976.

31. LARS HAGERMAN. Respiration, activity and salt balance in the shrimp Crangon vulgaris (Fabr.). 22 October 1976.

32. THOMAS ALERSTAM. Bird migration in relation to wind and topography. 29 October 1976.

33. LARS M NILSSON. Energetics and population dynamics of Gammarus pulex L. Amphipoda. 20 December 1977.

34. ANDERS NILSSON. Ticks and their small mammal hosts. 24 May 1978.

35. SÖREN SVENSSON. Fågelinventeringar - metoder och tillämpningar. (Bird censuses - methods and applications.) 23 May 1979.

36. BO FRYLESTAM. Population ecology of the European hare in southern Sweden. 1 June 1979.

37. SVEN G NILSSON. Biologiska samhällen i heterogena miljöer: En studie på fastland och öar. (Biological communities in heterogeneous habitats: A study on the mainland and islands.) 12 October 1979.

38. BJÖRN SVENSSON. The association between Epoicocladius flavens (Chironomidae) and Ephemera danica (Ephemeroptera). 26 October 1979.

39. GÖRAN HÖGSTEDT. The effect of territory quality, amount of food and interspecific competition on reproductive output and adult survival in the magpie Pica pica; an experimental study. 29 February 1980.

40. JON LOMAN. Social organization and reproductive ecology in a population of the hooded crow Corvus cornix. 9 April 1980.

41. GÖRGEN GÖRANSSON. Dynamics, reproduction and social organization in pheasant Phasianus colchicus populations in South Scandinavia. 26 September 1980.

42. TORSTEN DAHLGREN. The effects of population density and food quality on reproductive output in the female guppy, Poecilia reticulata (Peters). 27 February 1981.

43. AUGUSTINE KORLI KORHEINA. Environments and co-existence of Idotea species in the southern Baltic. 15 May 1981.

44. INGVAR NILSSON. Ecological aspects on birds of prey, especially long-eared owl and tawny owl. 9 October 1981.

45. TORBJÖRN von SCHANTZ. Evolution of group living, and the importance of food and social organization in population regulation; a study on the red fox (Vulpes vulpes). 23 October 1981.

46. OLOF LIBERG. Predation and social behaviour in a population of domestic cat. An evolutionary perspective. 11 December 1981.

47. BJÖRN MALMQVIST. The feeding, breeding and population ecology of the brook lamprey (Lampetra planeri). 12 March 1982.

48. INGVAR WÄREBORN. Environments and molluscs in a non-calcareous forest area in southern Sweden. 19 March 1982.

49. MAGNUS SYLVÉN. Reproduction and survival in common buzzards (Buteo buteo) illustrated by the seasonal allocation of energy expenses. 26 March 1982.

50. LARS-ERIC PERSSON. Structures and changes in soft bottom communities in the southern Baltic. 23 April 1982.

51. GÖRAN BENGTSSON. Ecological significance of amino acids and metal ions, a microanalytical approach. 24 May 1982.

52. JAN HERRMANN. Food, reproduction and population ecology of Dendrocoelum lacteum (Turbellaria) in South Sweden. 10 December 1982.

53. BO EBENMAN. Competition and differences in niches and morphology between individuals, sexes and age classes in animal populations, with special reference to passerine birds. 8 April 1983.

54. HANS KÄLLANDER. Aspects of the breeding biology, migratory movements, winter survival, and population fluctuations in the great tit Parus major and the blue tit P. caeruleus. 29 April 1983.

55. JOHNNY KARLSSON. Breeding of the starling (Sturnus vulgaris). 6 May 1983.

56. CARITA BRINCK. Scent marking in mustelids and bank voles, analyses of chemical compounds and their behavioural significance. 17 May 1983.
57. PER SJÖSTRÖM. Hunting, spacing and antipredatory behaviour in nymphs of Dinocras cephalotes (Plecoptera). 1 June 1983.
58. INGE HOFFMEYER. Interspecific behavioural niche separation in wood mice (Apodemus flavicollis and A. sylvaticus) and scent marking relative to social dominance in bank voles (Clethrionomys glareolus). 9 December 1983.
59. CHRISTER LÖFSTEDT. Sex pheromone communication in the turnip moth Agrotis segetum. 30 November 1984.
60. HANS KRISTIANSSON. Ecology of a hedgehog Erinaceus europaeus population in southern Sweden. 7 December 1984.
61. CHRISTER BRÖNMARK. Freshwater molluscs: Distribution patterns, predation and interactions with macrophytes. 19 April 1985.
62. FREDRIK SCHLYTER. Aggregation pheromone system in the spruce bark beetle Ips typographus. 26 April 1985.
63. LARS LUNDQVIST. Life tactics and distribution of small ectoparasites (Anoplura, Siphonaptera and Acari) in northernmost Fennoscandia. 10 May 1985.
64. PEHR H ENCKELL. Island life: Agency of Man upon dispersal, distribution, and genetic variation in Faroese populations of terrestrial invertebrates. 3 June 1985.
65. SIGFRID LUNDBERG. Five theoretical excursions into evolutionary ecology: on coevolution, pheromone communication, clutch size and bird migration. 7 November 1985.
66. MIKAEL SANDELL. Ecology and behaviour of the stoat Mustela erminea and a theory on delayed implantation. 8 November 1985.
67. THOMAS JONASSON. Resistance to frit fly attack in oat seedlings, and ecological approach to a plant breeding problem. 13 November 1985.
68. ANDERS TUNLID. Chemical signatures in studies of bacterial communities. Highly sensitive and selective analyses by gas chromatography and mass spectrometry. 3 October 1986.
69. BOEL JEPPSSON. Behavioural ecology of the water vole, Arvicola terrestris, and its implication to theories of microtine ecology. 27 May 1987.
70. TORSTEN GUNNARSSON. Soil arthropods and their food: choice, use and consequences. 2 June 1987.
71. THOMAS MADSEN. Natural and sexual selection in grass snakes, Natrix natrix, and adders, Vipera berus. 4 September 1987.
72. JENS DAHLGREN. Partridge activity, growth rate and survival: Dependence on insect abundance. 4 December 1987.
73. SCOTT GILBERT. Factors limiting growth of sympatric Peromyscus and Clethrionomys populations in northern Canada. 11 December 1987.
74. OLLE ANDERBRANT. Reproduction and competition in the spruce bark beetle Ips typographus. 8 April 1988.
75. EINAR B OLAFSSON. Dynamics in deposit-feeding and suspension-feeding populations of the bivalve Macoma baltica; an experimental study. 29 April 1988.
76. JAN-ÅKE NILSSON. Causes and consequences of dispersal in marsh tits, time as a fitness factor in establishment. 11 May 1988.
77. PAUL ERIC JÖNSSON. Ecology of the southern Dunlin Calidris alpina schinzii. 13 May 1988.
78. HENRIK G SMITH. Reproductive costs and offspring quality: the evolution of clutch size in tits (Parus). 20 May 1988.
79. BILL HANSSON. (A) Reproductive isolation by sex pheromones in some moth species. An electrophysiological approach. 14 October 1988.
80. ANDERS THURÉN. (E) Phthalate esters in the environment: analytical methods, occurrence, distribution and biological effects. 4 November 1988.

81. KARIN LUNDBERG. (A) Social organization and survival of the pipistrelle bat (Pipistrellus pipistrellus), and a comparison of advertisement behaviour in three polygynous bat species. 10 February 1989.
82. HAKON PERSSON. (A) Food selection, movements and energy budgets of staging and wintering geese on South Swedish farmland. 6 December 1989.
83. PETER SUNDIN. (E) Plant root exudates in interactions between plants and soil micro-organisms. A gnotobiotic approach. 16 March 1990.
84. ROLAND SANDBERG. (A) Celestial and magnetic orientation of migrating birds: Field experiments with nocturnal passerine migrants at different sites and latitudes. 28 September 1990.
85. ÅKE LINDSTRÖM. (A) Stopover ecology of migrating birds. 12 October 1990.
86. JENS RYDELL. (A) Ecology of the northern bat Eptesicus nilssoni during pregnancy and lactation. 26 October 1990.
87. HÅKAN WITTZELL. (T) Natural and sexual selection in the pheasant Phasianus colchicus. 27 September 1991.
88. MATS GRAHN. (A) Intra- and intersexual selection in the pheasant Phasianus colchicus. 27 May 1992.
89. ANN ERLANDSSON. (A) Life on the water surface: behaviour and evolution in semiaquatic insects. 25 September 1992.
90. GUDMUNDUR A GUDMUNDSSON. (A) Flight and migration strategies of birds at polar latitudes. 2 October 1992.
91. IO SKOGSMYR. (T) Pollination biology, venereal diseases and allocation conflicts in plants. 9 October 1992.
92. ANDERS VALEUR. (E) Utilization of chromatography and mass spectrometry for the estimation of microbial dynamics. 16 October 1992.
93. LENA TRANVIK . (A) To sustain in a stressed environment: a study of soil Collembola. 27 November 1992.
94. KATARINA HEDLUND. (A) Animal-microbial interactions: The fungivorous Collembola.12 February 1993.
95. HANS EK. (E) Nitrogen acquisition, transport and metabolism in intact ectomycorrhizal associations studied by 15N stable isotope techniques.14 May 1993.
96. STAFFAN BENSCH. (A) Costs, benefits and strategies for females in a polygynous mating system: a study on the great reed warbler. 24 September 1993.
97. NOÉL HOLMGREN. (T) Patch selection, conflicting activities and patterns of migration in birds.15 October 1993.
98. ROLAND LINDQUIST. (E) Dispersal of bacteria in ground water - mechanisms, kinetics and consequences for facilitated transport. 3 December 1993.
99. JOHAN NELSON. (A) Determinants of spacing behaviour, reproductive success and mating system in male field voles, Microtus agrestis. 20 May 1994.
100. MARIA SJÖGREN. (A) Dispersal in and ecto-mycorrhizal grazing by soil invertebrates. 30 September 1994.
101. DENNIS HASSELQUIST. (A) Male attractiveness, mating tactics and realized fitness in the polygynous great reed warbler. 14 October 1994.
102. DORETE BLOCH. (A) Pilot whales in the North Atlantic. Age, growth and social structure in Faroese grinds of long-finned pilot whale, Globicephala melas. 16 December 1994.
103. MAGNUS AUGNER. (T) Plant-plant interactions and the evolution of defences against herbivores. 10 February 1995.
104. ALMUT GERHARDT. (E). Effects of metals on stream invertebrates. 17 February 1995.
105. MARIANO CUADRADO. (A) Site fidelity and territorial behaviour of some migratory passerine species overwintering in the Mediterranean area. 31 March 1995.
106. ANDERS HEDENSTRÖM. (T) Ecology of Avian Flight. 7 April 1995.
107. OLOF REGNELL. (E) Methyl mercury in lakes: factors affecting its production and partitioning between water and sediment. 21 April 1995.
108. JUNWEI ZHU. (A) Diversity and conservatism in moth sex pheromone systems. 4 May 1995.
109. PETER ANDERSON. (A) Behavioural and physiological aspects of oviposition deterrence in moths. 12 May 1995.

110. JEP AGRELL. (A) Female social behaviour, reproduction and population dynamics in a non-cyclic population of the field vole (Microtus agrestis).19 May1995.
111. SUSANNE ÅKESSON. (A) Avian Migratory Orientation: Geographic, Temporal and Geomagnetic Effects. 22 September 1995.
112. ADRIAN L. R. THOMAS. (A) On the Tails of Birds. 29 September 1995.
113. WENQI WU.(A) Mechanisms of specificity in moth pheromone production and response. 8 December 1995.
114. PER WOIN.(E) Xenobiotics in Aquatic Ecosystems: Effects at different levels of organisation. 15 December 1995.
115. K. INGEMAR JÖNSSON. (T) Costs and tactics in the evolution of reproductive effort. 12 April 1996.
116. MATS G.E. SVENSSON. (A) Pheromone-mediated mating system in a moth species. 30 October 1996.
117. PATRIC NILSSON. (T) On the Ecology and Evolution of Seed and Bud Dormancy. 9 May 1997.
118. ULF OTTOSSON. (A) Parent-offspring relations in birds: conflicts and trade-offs. 16 May 1997.
119. ERIK SVENSSON. (A) Costs, benefits and constraints in the evolution of avian reproductive tactics: a study on the blue tit. 6 June 1997.
120. MARIA SANDELL. (A). Female reproductive strategies and sexual conflicts in a polygynous mating system. 6 March 1998.
121. ULF WIKTANDER. (A) Reproduction and survival in the lesser spotted woodpecker. Effects of life history, mating system and age. 3 April 1998.
122. OLA OLSSON. (A) Through the eyes of a woodpecker: understanding habitat selection, territory quality and reproductive decisions from individual behaviour. 17 April 1998.
123. PETER VALEUR. (A) Male moth behaviour and perception in the pheromone plums. 24 April 1998.
124. LARS PETTERSSON. (A) Phenotypic plasticity and the evolution of an inducible morphological defence in crucian carp. 19 March 1999.
125. JOHANNES JÄREMO. (T) Plant inducible responses to damage: evolution and ecological implications. 23 April 1999.
126. ÅSA LANGEFORS. (A) Genetic variation in Mhc class IIB in Atlantic Salmon: Evolutionary and Ecological Perspectives. 10 September 1999.
127. NILS KJELLÉN. (A) Differential migration in raptors. 12 November 1999.
128. ANDERS NILSSON. (A) Pikeivory: behavioural mechanisms in northern pike piscivory. 14 January2000.
129. JÖRGEN RIPA. (T) Population and community dynamics in variable environments. 21 January 2000.
130. BJÖRN LARDNER. (A) Phenotypic plasticity and local adaptation in tadpoles. 28 April 2000.
131. IRENE PERSSON. (A) Parental and embryonic behaviours in precocial birds. 19 May 2000.
132. ROGER HÄRDLING. (T) Evolutionary resolutions of conflicts with mates and offspring. 6 October 2000.
133. ÅSA LANKINEN. (T) Pollen competition as a target for sexual selection in plants. 17 November 2000.
134. THOMAS OHLSSON. (A) Development and maintenance of quality indicators in pheasants. 15 December 2000.
135. ANDERS KVIST. (A) Fuelling and flying: adaptations to endurance exercise in migrating birds. 20 April 2001.
136. ANNA-KARIN AUGUSTSSON. (A). On enchytraeids and naidids: Life-history traits and response to environmental stress. 23 May 2001.
137. MARIO PINEDA. (T). Evolution in Multicellular Mitotic Lineages. 31 August 2001.
138. LIV WENNERBERG. (A). Genetic variation and migration of waders. 9 November 2001
139. NICLAS JONZÉN. (T). Inference and management of populations in variable environments. 14 December 2001.
140. DAGMAR GORMSEN. (A). Colonization processes of soil fauna and mycorrhizal fungi. 21 December 2001.
141. PETER FRODIN. (T). Species interactions and community structure. 15 Mars 2002.
142. JOHAN BÄCKMAN (A). Bird Orientation: External Cues and Ecological Factors. 26 April 2002.
143. MÅNS BRUUN. (A). On starlings and farming: population decline, foraging strategies, cost of reproduction and breeding success. 7 June 2002.

144. JAKOB LOHM. (A). MHC and genomic diversity in Atlantic salmon (Salmo salar L.) 11 October 2002.
145. LARS RÅBERG. (A). Costs in ecology and evolution of the vertebrate immune system. 18 October 2002.
146. HELENE BRACHT JÖRGENSEN. (A). Food selection and fitness optimisation in insects. 13 December 2002.
147. MARTIN GREEN. (A). Flight strategies in migrating birds: when and how to fly. 31 January 2003.
148. BENGT HANSSON (A). Dispersal, inbreeding and fitness in natural populations. 21 February 2003.
149. MIKAEL ROSÉN. (A). Birds in the flow: Flight mechanics, wake dynamics and flight performance. 11 April 2003.
150. JONAS HEDIN. (A). Metapopulation ecology of Osmoderma eremita - dispersal, habitat quality and habitat history. 23 May 2003.
151 HELENA WESTERDAHL. (A). Avian MHC: variation and selection in the wild. 10 October 2003.
152. KEN LUNDBORG. (T). Food hoarding: Memory and social conditions - an evolutionary approach. 16 January 2004.
153. RICHARD OTTVALL (A). Population ecology and management of waders breeding on coastal meadows. 19 February 2004.
154. RACHEL MUHEIM (A). Magnetic Orientation in Migratory Birds. 20 February 2004.
155. MARIA HANSSON (A). Evolution and ecology of AhR genes in Atlantic salmon (Salmo salar L.). 23 April 2004.
156. MARTIN STJERNMAN (A). Causes and consequences of blood parasite infections in birds. 29 October 2004.
157. MARTIN GRANBOM (A). Growth conditions and individual quality in starlings. 19 November 2004.
158. ANNA GÅRDMARK (T). Species interactions govern evolutionary and ecological effects of population harvesting. 27 May 2005.
159. JONAS WALDENSTRÖM (A). Epidemiology and population structure of Campylobacter jejuni and related organisms in wild birds. 2 December 2005.
160. HELEN IVARSSON (T). Strategy Games: on survival and reproduction. 9 December 2005.
161. SEBASTIAN TROËNG (A). Migration of sea turtles from Caribbean Costa Rica: Implications for management. 14 December 2005.
162. EMMA SERNLAND (T). Optimal strategies and information in foraging theory. 16 December 2005.
163. MIKAEL ÅKESSON (A). Quantitative genetics and genome structure in a wild population: the use of a great reed warbler pedigree. 29 September 2006.
164. LENA MÅNSSON (T). Understanding weather effects on, in and from large herbivore population dynamics. 13 October 2006.
165. ERIK ÖCKINGER (A). Butterfly diversity and dispersal in fragmented grasslands. 17 November 2006.
166. JESSICA K. ABBOTT (A). Ontogeny and population biology of a sex-limited colour polymorphism. 23 November 2006.
167. OLOF HELLGREN (A). Avian malaria and related blood parasites: molecular diversity, ecology and evolution. 15 December 2006.
168. ANNA NILSSON (A).The problem of partial migration - the case of the blue tit. 19 January 2007.
169. PATRIK KARLSSON NYED (T). Food webs, models and species extinctions in a stochastic environment. 16 February 2007.
170. MARKUS FRANZÉN (A). Insect Diversity in Changing Landscapes. 16 May 2007.
171. MAJ RUNDLÖF (A). Biodiversity in agricultural landscapes: landscape and scale-dependent effects of organic farming. 15 June 2007.
172. OSKAR BRATTSTRÖM (A). Ecology of red admiral migration. 21 September 2007.
173. MICHAEL TOBLER (A). Maternal programming: costs, benefits and constraints of maternal hormone transfer. 5 October 2007.
174. FREDRIK HAAS (T). Hybrid zones and speciation - insights from the European Crow hybrid zone. 25 January 2008.
175. JACOB JOHANSSON (T). Evolving ecological communities in changing environment. 1 February 2008.

176. THOMAS GOSDEN (A). The Preservation of Favoured Morphs in the Struggle Between Sexes. 29 May 2008.
177. ROINE STRANDBERG (A). Migration strategies of raptors – spatio-temporal adaptions and constraints in travelling and foraging. 24 September 2008.
178. SARA S. HENNINGSSON (A). On the role of migration for the distribution of arctic birds – a circumpolar perspective. 25 September 2008.
179. JONAS KNAPE (T). Population dynamics and demography – inference from stochastic models. 6 February 2009.
180. NICLAS NORRSTRÖM (T). Artificial neural networks in models of specialization and sympatic speciation. 20 February 2009.
181. JOHAN NILSSON (A). Causes and consequences of individual variation in energy turnover rates. 17 April 2009.
182. MARTA WOLF (T). Catching the Invisible: Aerodynamic Track and Kinematics of Bat and Bird Flight. 14 May 2009.
183. JULIANA DÄNHARDT (A). On the importance of farmland as stopover habitat for migrating birds. 15 May 2009.
184. SARA NAURIN (A). Avian GEnome Evolution – Gene Expression, Gene Divergence and Sexual Dimorphism. 23 October 2009.
185. JENNIE NILSSON (T). On the origin of polymorphism – consequences of competition and predation in heterogeneous environments. 13 November 2009.
186. FABRICE EROUKHMANOFF (A). The interplay between selection and constraints on phenotypic evolution and adaptive divergence. 20 November 2009.
187. SANNA HARRIS (A). Behaviour under predation risk – antipredator strategies, behavioural syndromes and sex-specific responses in aquatic prey. 15 January 2010.
188. PER HENNINGSSON (T). Always on the wing – Fluid dynamics, flight performance and flight behavior of common swifts. 29 Januari 2010.
189. HÅKAN KARLSSON (A). There and Back Again - Nocturnal migratory behaviour of birds during spring and autumn. 8 October 2010.
190. MARY NGOZI MOLOKWU (A). Costs of foraging in a dry tropical environment. 29 October 2010.
191. MARCUS LJUNGQVIST (A). Have a fling with your neighbour, you might be less related - The use of molecular markers to estimate genetic diversity and population structure in conversation biology. 5 November 2010.
192. KRISTINA KARLSSON GREEN (A). Maiting strategies and conflicts in aquatic invertebrates: consequences for evolutionary differentiation. 26 November 2010.
193. FLORIAN T. MUIJRES (T). Feathers by day, membranes by night – Aerodynamic performance in bird and bat flight. 28 April 2011.
194. MARTIN HARTVIG (T). Food Web Ecology – individual life-histories and ecological processes shape complex communities. 29 April 2011.
195. ANNA SOFIE PERSSON (A). Effects of landscape context on populations of bumblebees. 13 May 2011.

I Persson, A. S., Olsson, O., Rundlöf, M. and Smith, H. G. (2010). Land use intensity and landscape complexity - Analysis of landscape characteristics in an agricultural region in Southern Sweden. Agriculture Ecosystems & Environment, 136, 169-176.

II Persson, A.S. and Smith, H.G. Seasonal persistence of bumblebee populations is affected by landscape context. Manuscript.

III Persson, A.S, Rundlöf, M. and Smith, H.G. Bumblebees show trait-dependent tolerance to structural simplification of agricultural landscapes. Manuscript.

IV Persson, A.S. and Smith, H.G. Bumblebee colonies produce larger workers in complex landscapes. Submitted.

V Samnegård, U., Persson, A.S and Smith, H.G. Gardens as sources of pollinators in intensively managed farmland. Submitted.

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