EXPERIMENTALLY TESTED RESPONSES
OF FLOWER-VISITING INSECTS TO
HABITAT ESTABLISHMENT ON
FARMLAND

Doctoral thesis
Eeva-Liisa Korpela

ACADEMIC DISSERTATION
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LIST OF PUBLICATIONS AND CONTRIBUTIONS

This thesis is based on the following publications:


III) **Korpela**, E-L., Hyvönen, T. & Kuussaari, M. Logging in boreal field-forest ecotones promotes flower-visiting insect diversity and modifies insect community composition. submitted manuscript.

IV) Kuussaari, M., Saarinen, M., **Korpela**, E-L., Pöyry, J. & Hyvönen, T. Higher mobility of butterflies than moths connected to habitat suitability and body size in a release experiment. submitted manuscript.

The publications are referred to in the text by their roman numerals.

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Contributions: **ELK** = Eeva-Liisa Korpela (née Alanen), **MK** = Mikko Kuussaari, **MS** = Matias Saarinen, **TH** = Terho Hyvönen, **SL** = Sami Lindgren, **OH** = Oskari Härmä, **JP** = Juha Pöyry
ABSTRACT

This thesis focuses on the responses of bumblebees and diurnal Lepidoptera (butterflies and diurnal moths) to habitat establishment on farmland. The studied measures were long-term set-asides, sown wildflower strips and logging in field-forest ecotones. As regards to the focal species groups, bumblebees play an important role as pollination service providers in boreal agricultural landscapes. In diurnal Lepidoptera, species vary according to many species traits that are relevant in the process of insect community assembly. Body size, for instance, plays a crucial role in the ability of species to colonize new habitat patches in the landscape and therefore to benefit from habitat creation within agri-environmental schemes.

In the first paper, I studied the responses of bumblebees and diurnal Lepidoptera to long-term set-aside establishment in a six-year field experiment (paper I). Focusing on another on-field measure, sown wildflower strips, I carried out a four-year experiment and studied the ability of sown strips to promote three different aspects of flower-visiting insect diversity: pollination service availability, species diversity and species of conservation concern (paper II). As an off-field measure, I studied the benefits of logging in field-forest ecotones in terms of the same three aspects as in the wildflower strip experiment (paper III). Finally, I experimentally studied differences in butterfly and moth mobility as well as the role of species traits in butterfly mobility (paper IV).

Based on my results, long-term set-asides and wildflower strips are very effective in enhancing pollination service availability, as long as they are sown with nectar and pollen plants favored by bumblebees (I-II). In logged field-forest ecotones, the emergence of nectar and pollen plants relies on the local seed bank (III). Species diversity also increased rather quickly in the wildflower strip and logging experiments (II, III). Furthermore, my results showed that habitat specialist butterflies of conservation concern are best promoted in relatively forested landscapes (II) and that logging in field-forest ecotones (III) promotes them more effectively than establishing wildflower strips on cultivated fields (II). As regards to diurnal Lepidoptera in general, set-aside field parcels should be left in place for several, preferably for at least for five years, as it takes time for less mobile species to disperse to the created habitat patches and to establish local populations (I). The set-aside experiment showed that the colonization speed in butterflies and diurnal moths was strongly connected with body size measured by wingspan, and that diurnal moths were on the average slower colonizers than butterflies (I). The results of the mobility experiment confirmed the important role of wingspan in butterflies, but also connected mobility with release habitat suitability: those species for which the experimental set-aside was most suitable habitat, namely grassland species, showed less tendency to disperse after the experimental releases (IV).

All three studied measures can be applied in conventional agriculture in Finland. Combining different measures at landscape and regional levels is likely to promote multiple aspects of flower-visiting insect diversity. The potential of habitat creation in field-forest ecotones in particular is substantial in the Finnish countryside, as many farmers are also forest owners. Furthermore, as habitat establishment adds different grassland patches into the landscape, also less mobile species and species with specific habitat requirements are likely to benefit.
SUMMARY

1. Introduction

1.1. Background of the study

Mitigating the negative effects of intensive agriculture on farmland biodiversity sets the practical context for this thesis. The focus is on habitat establishment for flower-visiting insects on cultivated fields and in field-forest ecotones, in conventional agriculture. The focal species groups are bumblebees and within diurnal Lepidoptera, butterflies and diurnal moths.

Flower-visiting insects and associated regulating ecosystem services, such as crop pollination (Liss et al. 2013, Mace et al. 2013), are under a lot of pressure in modern agriculture. The decline of semi-natural grassland habitats has been particularly disadvantageous for insect diversity (Potts et al. 2010, Kennedy et al. 2013,) as well as for their taxonomic breadth (Andersson et al. 2013) in intensively cultivated landscapes. In southern Finland, agriculture is currently dominated by monoculture cereal production on large field parcels (Kuussaari et al. 2011), with a varying share of field parcels cultivated with insect-pollinated crops (Breeze et al. 2014). Each year, significant funding is targeted both within the EU and in Finland at agri-environmental support schemes, which aim at counteracting the loss of farmland biodiversity. However, recent studies have shown that such support is often rather ineffective in terms of the actual biodiversity benefits (Kleijn et al. 2011, Concepción et al. 2012, but see Carvalheiro et al. 2013). This is partly because widely applied on-field measures have been mainly targeted at reducing nutrient leaching into water bodies, and have thus little relevance for biodiversity (Bommarco et al. 2013). Furthermore, the uptake of specific measures that would effectively promote flower-visiting insects is often questionable and rather little is known on the factors that contribute to their long-term effectiveness.

Off-field, increasing the quantity and quality of semi-natural habitats is of major importance for flower-visiting insects (Bommarco et al. 2013). However, a wider array of measures that could be applied in conventional agriculture is required, especially
in such areas and individuals farms, where only scattered and small fragments of semi-natural habitats remain. There is an urgent need to provide alternative habitats for flower-visiting insects (see e.g. Wade et al. 2008). As regards to direct benefits for farming, recent studies have shown that pollinator habitats and habitat creation in the landscape can improve crop pollination (Carvalheiro et al. 2012, Holzschuh et al. 2012) as well as the provision of other ecosystem services (Wratten et al. 2012).

1.2. Effectiveness of conservation initiatives on farmland

Evaluating the effectiveness of conservation efforts on farmland is by no means a simple task (Kleijn et al. 2011). Evaluations tend to concentrate on species richness and abundance, while ignoring other important aspects, such as community composition and species traits (Filippi-Codaccioni et al. 2010). Furthermore, recent studies have pointed out that the local enhancement of insect abundance cannot be used to directly infer population-level effects (Kleijn et al. 2011). It is also noteworthy that the populations of flower-visiting insects typically fluctuate strongly from year to year (Teräs 1983, Stange et al. 2011) and that species turnover in habitat patches is high (Summerville et al. 2007), highlighting the importance of long-term monitoring and comparison with control habitats (Haaland et al. 2011).

However, some general patterns in conservation initiative effectiveness are now emerging. In the conceptual model of Kleijn et al. (2011), effectiveness is defined as the difference in biodiversity between sites with conservation management and conventionally managed sites. In turn, three model components contribute to this effectiveness: the ecological contrast, land-use intensity and landscape structure. In the context of my thesis the ecological contrast, which varies from small to large, is most relevant and is defined in the model as the extent to which management improves habitat conditions for the targeted species group relative to conventionally managed habitats. Initiatives creating a large contrast are not only more beneficial for target organisms, but can also be effectively applied in a wider range of land-use intensities, from intensively farmed to extensively farmed field parcels.

Species responses to the ecological contrast are further modified by landscape structure. Landscape structure varies along a gradient from cleared (< 2% semi-
natural habitats) and simple (2-20%) to complex (>20%) landscapes. Finnish agricultural landscapes in general have a rather complex composition, although Finland has a high forest cover and the role of forests in the model, originally developed for Central European conditions, is somewhat unclear. The model assumes that effectiveness is highest in simple landscapes. This is because cleared landscapes lack potential colonizers, which could benefit from conservation efforts, whereas in complex landscapes, many individuals spill from the surrounding landscape to conventionally managed sites. The study areas of this thesis are situated in the intensively cultivated southwestern part of Finland and thus there is a high potential for effectiveness due to the simple landscape structure.

Agri-environmental measures to promote flower-visiting insects on conventional farmland include establishing set-asides and fallows (e.g. Kovács-Hostyánszki et al. 2011, Kuussaari et al. 2011, Kovács-Hostyánszki & Báldi 2012, Toivonen et al. 2013) as well as different kinds of biodiversity strips (e.g. Haaland et al. 2011, Fabian et al. 2013). Furthermore, adjacent forests could be managed in order to create semi-natural habitat in the field-forest ecotone, but this option has remained largely unexplored. The applied measures should ideally result in as large ecological contrast as possible (see the model presented above), and they should thus be designed according to the habitat requirements of target species. As the most effective measure is likely to vary between species groups, a combination of different measures is the preferable solution at landscape and regional levels. Applying multiple measures will also increase habitat heterogeneity in the wider farmland landscape, which is known to be beneficial for biodiversity (Benton et al. 2003, Shreeve & Dennis 2011, Fahrig et al. 2013, but see Batary et al. 2011) and soften the agricultural matrix (Donald & Evans 2006, Driscoll et al. 2013). Creating linear elements may also act as dispersal corridors in the landscape (Sutcliffe & Thomas 1996, Haddad & Tewksbury 2005, Öckinger & Smith, 2008, Delattre et al. 2013b).

1.3. Insect community assembly in novel habitat patches

As a novel habitat patch is established, the process of insect community assembly begins. This process typically follows different trajectories in different situations (see Prach & Walker 2011), making the prediction of resulting species composition
challenging (Ozinga et al. 2005). Community assembly as a framework has yet to be fully established (recently reviewed by Weiher et al. 2011), but in terms of restoration ecology, the term is usually defined as the combination of environmental filters, assembly rules and succession (Temperton et al. 2004). To my knowledge, insect responses to agri-environmental measures have not been discussed from this viewpoint before as community assembly theory has since its origin mainly evolved around plant ecology and the role of competition in plant communities (see Weiher & Keddy 1999). The controversial term ‘assembly rule’, closely related to the concept of ecological niches, has been used and discussed at least since the 1970’s (Cody & Diamond 1975) and challenged by the neutral theory (Hubbell 2001), but this debate is beyond the scope of this thesis. Recently, there have been attempts to reconcile the effects of niche-based and neutral processes in different situations (e.g. Gravel et al. 2006).

In any case, the arrival and possible establishment of targeted insect species representing different functional groups is central as regards to the effectiveness of conservation measures on farmland. Indeed, the result of community assembly will determine how large the ecological contrast (see above) created by each measure will be. The dynamic environmental filter model presented by Temperton et al. (2004) (see Fig. 2.) and developed based on long-term experiments in two degraded ecosystems (a grassland and a river) in Jena, Germany offers a useful framework to examine insect community assembly in my thesis. Environmental filtering is a central concept in restoration ecology and the action of filters by definition leads to restoration resistance.

The model includes two species pools (external and internal) from which species can become integrated into the pool of established species. The main components of the model are the two types of environmental filters presented in Fig. 1. The abiotic filter (such as climate and landscape structure) is usually more limiting, after which the biotic filter (such as trophic interactions and dispersal) further restricts species arrival and establishment. The distinction between the filter types is, however, not always clear and they can act simultaneously instead in a clearly ordered sequence. An example is the interaction of dispersal and landscape structure. Finally, environmental stress and disturbance (or in effect, habitat management) modify the
mesh size of the filters, the former usually having a stronger effect on the abiotic and the latter on the biotic filter. Disturbance may also be seen as a filter itself, which simultaneously shapes plant and animal communities for instance in burned forest areas (Moretti & Legg 2009).

Different filters are likely to be important at different stages of restoration and their complex and dynamic nature makes it difficult to predict the precise outcome of any restoration effort. Furthermore, the regional species pool is shaped by dispersal history (Weiher et al. 2011). However, some of the filters could be deliberately modified and desired insect species thus attracted to established habitat patches. A similar environmental filtering approach has been mainly applied to plants, recently by e.g. de Bello et al. (2013) and Lasky et al. (2013) and to stream invertebrates (recently by Grönroos et al. 2013). Among terrestrial insects environmental filtering has been studied e.g. in grasshoppers (Van der Plas et al., 2012) and ants (Wiescher et al. 2012, Frenette-Dussault et al. 2013), but only a few examples exist on flower-visiting insects and plant-pollinator networks (Albrecht et al. 2010, Hoiss et al. 2012, Pelissier et al. 2013).

A major difference to plants has to be taken into account in when applying the framework to mobile insects. Plants are sedentary after propagule dispersal and establishment, and typically reach high population densities, which makes niche-based processes and competition important in plant community assembly (Weiher et al. 2011). In mobile animals, neutral processes tend to play a more important role and insect occurrence in a habitat patch is by no means equal to local population establishment. Indeed, behavioral vs. population-level effects are one of the current topics in agri-environmental scheme evaluation (Kleijn et al. 2011, Dicks et al. 2013). Relevant biotic filters in the case of flower-visiting insects include nectar and pollen plants for bumblebees and larval host plants for diurnal Lepidoptera. I will return to this theme in the discussion of this thesis, where I apply the model to my own results. Furthermore, it is noteworthy that the filters are likely to act on species traits rather than on species identity per se (see e.g. Déri et al. 2011, Weiher et al. 2011).
1. The dynamic environmental filter model presented originally by Temperton et al. (2004) (figure modified). Thick black arrows represent a strong effect, thin black arrows a weak effect and dashed black arrows an eventual effect in case of serious stress. The grey arrows show how a series of filters sift species out of the regional pool (either internal or external). The pool of established species then feeds back into the filters, although this effect is more likely in plant than insect communities.

2. Aims of the thesis

In my thesis I searched answers to three main study questions (see below). I discuss the results of the four papers in the context of insect community assembly in established habitat patches. In particular, I discuss the relevant filtering effects for each studied species group (bumblebees, butterflies and diurnal moths).

- What are the benefits of three different habitat creation measures in enhancing flower-visiting insects on boreal farmland? The studied measures were long-term set-asides (I), sown wildflower strips (II) and logging in field-forest ecotones (III).

- How do the responses of pollination service availability and intrinsic aspects of insect diversity to habitat establishment differ on-field (II) and in the field-forest ecotone (III)?

- Which species traits affect mobility in butterflies and diurnal moths and thus their ability to colonize established habitat patches (I and IV)?
3. Materials and methods

3.1. Four field experiments

Data for each paper (I-IV) were collected in four separate field experiments (A-D, respectively). The locations of the experiments within southwestern Finland are shown in Fig. 2. The long-term set-aside experiment (A) and the mobility experiment (D) were carried out in the same experimental set-aside field and in its surroundings in years 2003-2008 (A) and in year 2011 (D). The wildflower strip experiment (B) was carried out in six study field parcels in years 2007-2010 and the field-forest ecotone experiment (C) in 15 forest stands in years 2009-2011.

In the first three experiments (A-C), bumblebees, butterflies and diurnal moths were monitored by using the line-transect method (Pollard & Yates 1993) and in the mobility experiment (D), the mark-release-recapture (MRR) method (Settele et al. 2009) was applied. In experiment A, line-transects were 250 meter long and counts were made four times at 2-week intervals, from early June to late July, whereas in experiments B and C, the transects were 50 meters long and counts were made seven times at 2-week intervals, from late May to late August.
In the long-term set-aside experiment (A, results reported in paper I) (Fig. 3), insects were monitored in one large set-aside field, which was established in a relatively simple landscape (see also Tscharntke et al. 2011) as well as in surrounding, untreated field margins (n = 10). The set-aside plots (n = 24) were established with three different seed mixtures (8 plots each) and half of the plots were managed with annual, late-summer mowing. The field margin data provided valuable information on species richness and abundance patterns in a permanent habitat, to which the development of insect occurrence in the set-aside plots could be compared. The experiment did not include an actual conventionally managed site vs. site with conservation management comparison (see Kleijn et al. 2011), as no data in the surrounding (spring cereal) fields were collected. The seed mixtures were a commonly used, highly competitive mixture of grasses and clover and two alternative mixtures, which were expected to provide more resources for flower-visiting insects: a less competitive grass mixture and a diverse mixture including 12 flowering plant species.

In the wildflower strip experiment (B, results reported in paper II) (see upper photo in the cover of this thesis), insects were monitored in wildflower strips, in surrounding field margins and in reed canary grass and spring cereal fields. There were six different types of wildflower strips, which were experimentally varied according to their sown seed mixture, shape and placement within the study field parcel. Three of these strip types were compared to control habitats with an identical location within the field parcel. Wildflower strips located next to forest or at open field parcel edge were compared to adjacent field margins and similarly located reed canary grass controls. Wildflower strips located in the middle of the field parcel were compared to similarly located reed canary grass and spring cereal controls. Spring cereal represented the dominating production system in the area (conventional management), reed canary grass was a bioenergy crop with low value for biodiversity and field margins provided additional information of insect occurrence patterns, as in the long-term set-aside experiment.

In the field-forest ecotone experiment (C, results reported in paper III) (see lower photo in the cover of this thesis), insects were monitored in field-forest ecotones logged in winter 2009-2010 both before and after logging, as well as in unlogged
control ecotones. Control plots were situated in the same forest stands as the logged areas and represented conventional, commercial forest management in the area. The stands were managed after guidelines of good forestry practices in Finland. Experimental logging was carried out differently at the immediate forest edge, where a 5-meter wide strip was clear-cut and in the forest interior behind this strip, which was thinned to a basal area of 8 m²/ha. These two parts of the logged area were compared to similarly situated controls.

In the mobility experiment (D, results reported in paper IV) (Fig. 3), butterflies and diurnal moths were first collected both from the experimental set-aside field and from semi-natural habitats in the surrounding landscape and marked with an individual number (butterflies) or with a spot on the wing (diurnal moths). Marked individuals were then released within the 11 ha set-aside field, in the center of a release area (a 25 x 25 m plot). Recaptures were searched for in the set-aside as well as in nearby field margins, forest edges and grassland patches. The study was carried out in two periods, from late May to mid-June and late June to mid-July.

Figure 3. In the long-term set-aside experiment, *Phacelia tanacetifolia* was flowering during the first year in the plots sown with the diverse seed mixture (a). Mobility in diurnal Lepidoptera was studied in the same area, in a release-experiment of 4300 marked individuals (b and c). Photos: Oskari Härmä (a) and Terho Hyvönen (b-c).
3.2. Response variables and studied species traits

The insect response variables formed for the purpose of statistical analyses varied between the four papers (I-IV), according to specific study questions. In papers II and III, the aim was to describe three different aspects of flower-visiting insect diversity: (i) pollination service availability, (ii) species diversity and (iii) occurrence of species of conservation concern, the latter two representing intrinsic aspects of insect diversity. The aspects were measured, respectively, by (i) bumblebee abundance, (ii) total species richness of bumblebees, butterflies and diurnal moths and (iii) the abundance of habitat specialist butterflies. As regards pollination services, although crop pollination success and yield cannot be directly inferred from pollinator abundance, the measure is both practical and widely used. Furthermore, using pollinator abundance to infer pollination service availability highlights the importance of maintaining pollinator habitats and may thus accelerate the uptake of sustainable, wildlife-friendly farming practices (Liss et al. 2013).

As regards to species of conservation concern, habitat specialist butterflies in this thesis included species which are still rather common, but have nevertheless suffered from agricultural intensification in Finland (Ekroos et al. 2010). Many of such species have declined more strongly in other parts of Europe and even farmland generalists are threatened in the most intensively cultivated areas (Van Dyck et al. 2008). In the UK and France, e.g. *Boloria euphrosyne* and *Argynnis adippe* have additionally suffered from the cessation of woodland management by coppicing (Dapporto & Dennis 2013, Fartmann et al. 2013) and such species tend to be limited in their nectar plant use (Tudor et al. 2004). Furthermore, Bergman et al. (2004) suggested that *B. euphrosyne* and other fritillaries could be used to indicate species-rich landscapes.

In paper I, the response variables were the species richness and abundance of bumblebees, butterflies and diurnal moths. In paper IV, they were the mean moved distance (m) and the emigration and recapture rate (%) in butterflies and moths. Moved distance was measured for each individual between the release point and the location of the recapture, whereas an individual was considered emigrated, if it was recaptured outside the set-aside field. In butterflies, records were collected in relation
to the last recapture, whereas in moths all recaptures were considered as independent observations.

I also studied the role of insect species traits, as they are known to play a major role in insect community assembly, the effectiveness of agri-environmental schemes and species responses to habitat fragmentation (e.g. Summerville et al. 2006, Öckinger et al. 2010, Börschig et al. 2013, Ekroos et al. 2013). One of the species traits was habitat specificity (see Clavel et al. 2011), which was used to form one of the response variables in papers II-III as described above and was studied in relation to butterfly mobility in paper IV. Other studied species traits were tongue length (bumblebees, paper I), body size measured by wingspan (butterflies and diurnal moths, papers I and IV), larval specificity (butterflies and diurnal moths, papers I and IV), larval host plant type (butterflies and diurnal moths, papers I and IV), habitat preference (butterflies, paper IV) and release habitat suitability (butterflies, paper IV).

### 3.3. Habitat quality and environmental data

In order to better understand insect responses to habitat establishment, habitat quality and environmental data (as recommended e.g. by Dennis 2004) were collected as summarized in Table 1.

Table 1. The measured variables in the field experiments and the management practices (if any) carried out in order to modify these variables. In the wildflower strip experiment (B), field parcels were not chosen according to forest cover. In the field-forest ecotone experiment (C), logging residue was left to the ground and its coverage (not controlled) varied between study areas. Shrub coverage was not controlled in the experimental set-up and regrowth of shrubs was not removed during the experiment.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Measured variables</th>
<th>Management practices</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Flower coverage and vegetation structure (plant coverage)</td>
<td>Alternative seed mixtures used in establishment</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Annual, late-summer mowing</td>
</tr>
<tr>
<td>B</td>
<td>Flower coverage</td>
<td>Wildflower seed mixture used in establishment</td>
</tr>
<tr>
<td></td>
<td>Forest cover in the landscape</td>
<td>-</td>
</tr>
<tr>
<td>C</td>
<td>Flower coverage</td>
<td>Logging</td>
</tr>
<tr>
<td></td>
<td>Temperature data (degree days)</td>
<td>Logging</td>
</tr>
<tr>
<td></td>
<td>Shrub coverage</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Logging residue coverage</td>
<td>-</td>
</tr>
</tbody>
</table>
3.4. Data analyses

Linear models

I first carried out the main analysis of each experimental set-up according to the models presented in Table 2. In papers I-III, the models were linear mixed models (LMMs). In paper IV, moved distances were studied by LMMs, whereas emigration and recapture rate were studied by generalized linear mixed models (GLMMs).

Table 2. Main analyses of the experimental set-up in each paper. Corresponding study questions are presented in the text below.

<table>
<thead>
<tr>
<th>Paper</th>
<th>Experiment</th>
<th>Model</th>
<th>Response variables</th>
<th>Fixed factors</th>
<th>Random factor</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Long-term set-aside experiment</td>
<td>Linear Mixed Model (LMM)</td>
<td>Species richness and abundance of bumblebees, butterflies and diurnal moths (6 variables)</td>
<td>Seed mixture, mowing, study year and the pairwise interactions of these factors</td>
<td>Replicate block within the experimental set-aside field (n = 4)</td>
</tr>
<tr>
<td>II</td>
<td>Wildflower strip experiment</td>
<td>LMM</td>
<td>Bumblebee abundance, total species richness of bumblebees, butterflies and diurnal moths (3 variables)</td>
<td>Treatment type (wildflower strip vs. corresponding controls; reed canary grass, spring cereal and/or field margin), study year and the interaction of these factors</td>
<td>Study field parcel (n = 6)</td>
</tr>
<tr>
<td>III</td>
<td>Field-forest ecotone experiment</td>
<td>LMM</td>
<td>as in paper II (3 variables)</td>
<td>Treatment type (logged in winter 2009-2010 vs. untreated control; separately for forest edge and interior), study year and the interaction of these factors</td>
<td>Study area (n = 15)</td>
</tr>
<tr>
<td>IV</td>
<td>Mobility experiment</td>
<td>1) LMM, 2) Generalized Linear Mixed Model (GLMM)</td>
<td>1) Moved distance (m), 2) Emigration and recapture probability (%) (3 variables)</td>
<td>Species group (butterfly, geometroid moth or noctuid moth)</td>
<td>Species (n = 18 in butterflies and n = 8 in moths)</td>
</tr>
</tbody>
</table>
In paper I, the main analysis examined the promotion of flower-visiting insects during the six-year set-aside experiment, in plots sown with three different seed mixtures and with or without the mowing treatment. In paper II, the main analysis examined the promotion of flower-visiting insects by wildflower strips in comparison with corresponding control habitats. In paper III, the main analysis examined the promotion of flower-visiting insects in logged field-forest ecotones, separately at the clear-cut edge and in the thinned forest interior, in comparison with unlogged controls. In paper IV, the main analysis examined mobility differences in butterflies, geometroid moths and noctuoid moths.

I then proceeded into analyzing more details of the data sets. In paper I, I tested the occurrence of flower-visiting insects on experimental set-aside vs. untreated field margins by linear models (LMs), in which habitat type (set-aside or field margin), study year and their interaction were included as explanatory variables. In addition, I studied the role of species traits in set-aside colonization in bumblebees and diurnal Lepidoptera, using LMMs. Also using LMMs, I studied the role of Centaurea flower coverage and the proportion of forests in field parcel surroundings in insect responses to wildflower strips in paper II and the roles of microclimate and floral resources in varying insect responses to logging at clear-cut forest edge in paper III. Finally, in paper IV, I studied the roles of species traits in moved distances (LMMs) as well as emigration and recapture rate (GLMMs) in butterflies. In these analyses the roles of sex and phylogenetic relatedness were also taken into account, as explained in the original paper in more detail.

Ordination methods

Along with fitting linear models, I performed a set of other analyses to further interpret the results of the experiments (see the original papers for full details). Most importantly, I applied ordination methods in order to study changes in insect community composition. These analyses also helped to connect the main results of the set-aside (I) and field-forest ecotone (III) experiments to environmental variables. Furthermore, ordination analyses indicated some interesting details on the occurrence patterns of individual species, not revealed by the responses of the formed aggregate variables.
DCA (Detrended Correspondence Analysis) was employed to study changes in insect community composition. In paper I, I describe the development of insect communities during the set-aside experiment in comparison with surrounding field margins as well as the development of communities in set-aside plots sown with different seed mixtures. In paper III, I describe how community composition changed in the field-forest ecotones in response to logging, both at the clear-cut edge and in the forest interior. In both papers, I also carried out an Indicator Species Analysis (ISA) in order to indicate the typical species of set-asides or field margins (paper I) and open habitats or forest (paper III). The results of ISA provided additional information as to which species in particular benefited from the studied measures.

CCA (Canonical Correspondence Analysis) was utilized to study the relationships between insect community composition and environmental variables. In paper I, I studied the roles of various vegetation characteristics (e.g. coverage of Poaceae) and set-aside age (study year) and in paper III, I studied the roles of a set of vegetation (e.g. flower coverage) and environmental (temperature) variables (see also Table 2).

4. Results and Discussion

4.1. Results of the field experiments

The four field experiments (A-D, results reported in papers I-IV, respectively) produced novel information on the responses of flower-visiting insects to habitat establishment on farmland. In addition, the value of experiments A-C was in long-term monitoring, as many similar studies have covered only one field season. The long-term set-aside experiment (A), in particular, was unique in producing a six-year data set. The mobility experiment (D), experimentally compared the mobility in a large set of lepidopteran species in field conditions, which has not been achieved before. The main results are summarized in Table 3.
Table 3. Main results of papers I-IV.

<table>
<thead>
<tr>
<th>Paper</th>
<th>Main results</th>
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| I     | - Bumblebee abundance was rapidly promoted by floral resources in the diverse seed mixture  
       - Differences between seed mixtures diminished as vegetation succession proceeded  
       - Butterflies and in particular diurnal moths showed a slower response than bumblebees  
       - Colonization speed was strongly correlated with wingspan in diurnal Lepidoptera |
| II    | - Species diversity and pollination service availability were simultaneously enhanced  
       - *Centaura* flower coverage in wildflower strips had a strong positive effect on pollination service availability  
       - The promotion of species of conservation concern was slow and associated with forest cover in field parcel surroundings  
       - The benefits of wildflower strips were largely independent of experimentally varied strip properties |
| III   | - Logging effectively promoted species of conservation concern  
       - The promotion of open habitat species was associated with beneficial changes in microclimate and floral resources  
       - Microclimate was associated with forest edge orientation  
       - Logging residue left to the ground suppressed the emergence of nectar and pollen plants |
| IV    | - The mobility of butterflies was much higher than that of geometrid moths  
       - Noctuoid moths showed intermediate mobility  
       - Mobility in butterflies was strongly associated with release habitat suitability and wingspan  
       - Small species and species which naturally occurred on the experimental set-aside were least mobile |

*Long-term set-aside experiment (paper I)*

In this study, bumblebees and diurnal Lepidoptera showed distinctly different responses to set-aside establishment. Bumblebee abundance peaked already during the first year, whereas it took several years for diurnal Lepidoptera to colonize the experimental set-aside. As regards to community composition, set-aside age explained a large proportion of variation in lepidopteran communities. Sown seed mixture had important implications for flower-visiting insects, whereas the mowing treatment did not affect their species richness or abundance.
The diverse mixture was most beneficial for flower-visiting insects in the beginning of the experiment, but differences between seed mixtures diminished over time. Sown plant species (*Phacelia tanacetifolia*, *Vicia villosa* and *Centaurea jacea*) attracted most flower visits in the first four study years, whereas during the last two years, insects visited mainly naturally established species (*Vicia cracca* and *Lathyrus pratensis*). In butterflies, species feeding on grasses (Poaceae) as larvae were the most successful colonizers, but their abundance did not peak until the fifth year of the experiment. In diurnal moths, the most successful colonizers were species feeding on leguminous plants (Fabaceae) (see also Summerville et al. 2007). Within this group, *Scototeryx chenopodiata*, *Chiasmia clathrata* and *Euclidia glyphica* were identified as set-aside indicators. Body size as a species trait showed an interesting pattern, as the relative abundances of small and large species did not change significantly during set-aside succession. However, there was a significant correlation between the colonization speed and the actual wingspan in diurnal Lepidoptera (see also Woodcock et al. 2012). Furthermore, colonization speed was significantly higher in butterflies than moths. These observations gave rise to the study idea in paper IV.

**Wildflower strip experiment** (paper II)

In this study, pollination service availability and species diversity increased rapidly after strip establishment, whereas the response of species of conservation concern was much slower. All three studied aspects of insect diversity developed very similarly in the wildflower strips, whether the comparison to control habitats was made at open field parcel edge, next to forest or in the middle of the field parcel. Spring cereal, the conventionally managed habitat, supported very few individuals.

The visual inspection of experimental results indicated high levels of total species richness as well as habitat specialist abundance at forest edge and low levels in the middle of the field parcel. However, the preselected pair-wise comparisons of strip properties pointed out that the exact strip properties had minor relevance for flower-visiting insects. Only bumblebees tended to be more abundant in strips established in the field parcel center, which could be explained by higher flower availability and concentration effects. Furthermore, the analysis focusing on the roles of landscape structure (forest cover in field parcel surroundings) and local habitat patch quality
(sown *Centaurea* flower coverage) showed that the former positively affected species of conservation concern and the latter pollination service availability. For species diversity, no effects were detected.

*Field-forest ecotone experiment* (paper III)

In this study, logging promoted all three studied aspects of flower-visiting insect diversity, with the exception of pollination services in the thinned forest interior. In general, clear-cut edges supported higher levels of insect diversity than the thinned interior. Even the species of conservation concern were promoted relatively fast, which is in contrast to what was observed in the wildflower strip experiment (see also Haaland et al. 2011).

The inspection of insect community composition revealed that logging benefited butterflies in particular and that this change was closely associated with a warm microclimate in logged ecotones. Microclimate in turn was associated with forest edge orientation, so that edges opening towards the South/South-West were most beneficial and edges opening to North/North-East least beneficial. In addition, several species of bumblebees and butterflies showed an indicator value for open habitat. Open habitat indicator butterflies included generalists, but also two species of specialists (*Callophrys rubi* and *Boloria euphrosyne*). Furthermore all three aspects of insect diversity responded positively to flower coverage, which in turn was negatively correlated with the amount of logging residue left to the ground.

*Mobility experiment* (paper IV)

In this study, butterflies were much more mobile than geometroid moths, in terms of moved distances and emigration rate, which is in line with the observations made on lepidopteran colonization speeds in the set-aside experiment (paper I). Although sample size in noctuoid moths was small, their mobility seemed to be between the other two groups. In the closer inspection of butterfly mobility only two species traits got selected into the final model: body size and release habitat suitability. Here, body size explained additional variation in moved distance and emigration rate after habitat suitability had been taken into account. Furthermore, the latter was strongly
connected with another species trait, the habitat preference. This was because the set-aside provided a suitable habitat for grassland butterflies, but not for forest edge species. The latter tended to disperse from the set-aside after release.

4.2. Environmental filters acting on flower-visiting insects

In order to understand insect responses to habitat establishment, it is crucial to identify the most important filtering effects for each target species group (Temperton et al. 2004). Defining habitat quality and suitability is a closely related theme, which remains central in ecological research (see e.g. Hein et al. 2007). Relevant variables for Lepidoptera are widely discussed in literature (see for instance Shreeve et al. 2001, Binzenhöfer et al. 2005, Butler et al. 2009, Dennis et al. 2013) and those for bumblebees in Butler et al. (2009) and Goulson (2003). For diurnal Lepidoptera, the resource-based approach to habitat definition (Vanreusel & Vand Dyck 2007, Vanreusel et al. 2007, Dennis et al. 2013) is especially relevant here. In paper IV, an experimentally compiled measure of habitat suitability was developed for butterflies, to my knowledge for the first time. In previous studies actual habitat suitability (as experienced by the butterflies in field conditions) has often been inferred by egg-laying behavior of females (Fownes & Roland 2002, Dickins et al., 2013, Eilers et al., 2013), while males may have differing habitat preferences and tend to be more mobile (Schultz et al. 2012, Slamova et al. 2013).

An important aspect of my experiments in terms of environmental filtering was long-term monitoring, as environmental filters change continuously during succession. For instance, the structural complexity of vegetation develops over time (Martinko et al. 2006), as opposed to the rapid emergence of nectar and pollen plants (I). Furthermore, different environmental variables interact with each other during succession, some of them having direct and others indirect effects on flower-visiting insects. The former are the actual abiotic and biotic filters, while the latter act via modifying these. For instance, logging residue prevented flowering plant emergence in the field-forest ecotone experiment of this thesis, which in turn was harmful for flower-visiting insects (III). Likewise, forest edge orientation modified microclimate in the same experiment, which was important for butterflies in particular.
The abiotic and biotic filters identified in thesis are summarized in Fig. 4 and further discussed below. Identification of species pools (see Fig. 2 in Introduction) and thus the source habitats in each experiment remained partly unclear. The internal species pool was practically only present in the field-forest experiment (III). In the set-aside experiment, community composition on the set-aside plots approached that of the surrounding field margins, the most likely external species pool, during the experiment. Nevertheless, for instance the geometroid moth *Perizoma flavofasciatum* did not occur on the field margins, but had clearly established a local population on the set-aside by the end of the six-year experiment (I). This was rather surprising, as the species is known as a grassland specialist. The mobility experiment (IV) cast some further light on this issue, as many released butterflies, but also moths were recaptured in grassland patches even quite far away from the focal set-aside (see also Hovestadt et al. 2011). Long-distance movements may require passing inhospitable matrix habitats (Severns et al. 2013, Nowicki et al. 2014), such as spring cereal fields with few resources for flower-visiting insects (Pywell et al. 2011).

Figure 4. The dynamic environmental filter model (see also Fig. 2) applied to the results of this thesis. Listed species traits were shown to play a role in insect community assembly. In paper I, results are from CCA, in which butterflies and moths were analyzed as one group. In papers II-III, diurnal moths contributed to the measure of species diversity, but were not studied separately. In paper II, flower coverage results are for the analysis of *Centaurea* coverage.
Abiotic filters

In wildflower strips, low forest cover in the landscape filtered habitat specialist butterflies (II). Similar results are discussed by e.g. Bergerot et al. (2001), Saarinen et al. (2005), Berg et al. (2011) and Krämer et al. (2012) who showed that forest cover and distance to woodland modify butterfly community composition. Forest cover acting on pollinators may also influence the pollination success of wild plants, as shown in the study of Valdes & Garcia (2011) on *Primula vulgaris* pollination.

Furthermore, habitat microclimate and light availability modified by forest edge orientation acted as strong abiotic filters in the field-forest ecotone especially for butterflies (III). South/South-West facing edges become warmest during the day and were thus the most beneficial. Meyer & Sisk (2001) presented opposite results, but this is understandable, as their study concentrated on the onset of flight in butterflies during the morning hours. Based on previous studies as well, temperature is known to promote the occurrence of adult butterflies (Menendez et al. 2007, Vande Velde et al. 2011) and the speed of larval development (Bryant et al. 2002). Bumblebees, on the other hand, are able to control their body temperature using their flight muscles (Heinrich 1979), and microclimate thus plays a smaller role in their occurrence. In butterflies, temperature is also known to facilitate dispersal, which is important in terms of habitat patch colonization (Cormont et al. 2011, Delattre et al. 2013a).

When thinking about the spatial arrangement of established habitat patches and potential source habitats, the interplay between dispersal (a biotic filter) and landscape structure (an abiotic filter) becomes evident. Butterflies and diurnal moths, particularly those species feeding on forest plants as larvae, may fail to colonize established habitat patches located far away from the nearest forest edge (I). On the other hand, the observed pattern is complicated with the interplay between habitat suitability and habitat preference (IV) and it can be asked, whether forest edge species should even be targeted by on-field measures. Although not studied here, foraging ranges are known to vary between bumblebee species and even between individual colonies (Knight et al. 2009, Carvell et al. 2012), which may lead to dispersal limitation in this species group as well (but see Albrecht et al. 2010).
Biotic filters

Focusing on dispersal as a biotic filter, body size (I, IV) and habitat suitability, which was strongly connected with habitat preference (IV), were identified as important species traits in passing this filter (see also Slade et al. 2013) in butterflies and diurnal moths. Small geometroid moths with fragile wings are poor dispersers (IV), although their populations can reach high densities once they have colonized the established habitat patch (I) (but see Merckx et al. 2012).

Other biotic filters identified were vegetation characteristics. The focal species groups in this study, the bumblebees and diurnal Lepidoptera, are ecologically fundamentally different in that bumblebees are central place foragers. In my study, the dependence of flowers and thus the importance of flower availability differed both between these groups and within Lepidoptera (I-III), bumblebees being most and diurnal moths least dependent. Bumblebee abundance was thus very strongly associated with the flower coverage of their preferred forage plants (I-III) (see also Lazaro & Totland 2010, Garibaldi et al. 2011, Proctor et al. 2012), but flowers played a major role in the occurrence of butterflies as well (see also Saarinen et al. 2005, Bergman et al. 2008, Krämer et al. 2012). As a conclusion, nectar and pollen plants are a strong biotic filter for flower-visiting insects and this filter can be modified by sowing attractive plants, which should preferably be native species of regional seed origin (Isaacs et al. 2009, Tscharntke et al. 2011). Offering nectar and pollen sources is especially important in simple landscapes, where late-season bumblebee abundance can become resource-limited (Persson & Smith 2013). Furthermore, the array of available nectar and pollen plants filters bumblebees according to their tongue length (I), which can be taken into account in choosing the plant species.

In terms of other vegetation characteristics, the occurrence of flower-visiting insects often mirrors plant diversity and plant community composition (Schaffers et al. 2008, Hudewenz et al. 2012, Koch et al. 2013, Nicholls & Altieri 2013). The availability of larval host plants plays an important role in lepidopteran community assembly (I) (Wallis de Vries & Ens 2010, Krämer et al. 2012), which could also be taken into account in the establishment method of set-asides and wildflower strips. In addition, the structural complexity of vegetation typically increases during succession, which is
beneficial for diurnal Lepidoptera (I) and other phytophagous insects (Woodcock et al. 2009). However, the downside of ongoing succession is the increasing shrub coverage after logging in field-forest ecotones (III) (see also Komonen et al. 2013) and it is costly to maintain habitat openness. On field, maintenance of sown plant coverage (II) may require weeding (Roscher et al. 2013) or other management practices (Lawson et al. 2004) to prevent encroachment by surrounding vegetation.

4.3. Implications for agri-environmental scheme targeting

Different agri-environmental measures are typically needed to enhance intrinsic aspects of biodiversity and ecosystem services (Macfadyen et al. 2012 and Table 4). Short-term, behavioral responses are in many cases sufficient to maintain ecosystem services, whereas long-term, population-level responses are needed in conservation (Kleijn et al. 2011, Williams et al. 2012). In line with what is presented in Table 4, habitat specialist butterflies were best promoted in complex landscapes with a high forest cover in my study (II) and such landscapes should thus be chosen when the aim is to target species of conservation concern. In some other aspects, however, the measures studied in my thesis and their benefits for flower-visiting insects seem not to fit very well in Table 4. For instance, wildflower strips were able to promote both pollination service availability and species diversity simultaneously and regardless of their exact properties, although they were established in relatively simple landscapes (II) (see also Schepers et al. 2013). Wildflower strips sown with suitable plants (such as Centaurea) are therefore useful to attract pollinators in intensively cultivated areas and on boreal farmland they can help in sustaining intrinsic aspects of insect diversity. Such strips are relatively easy to establish (requiring little change in farming activities) and are already being widely applied in Europe. The wildflower strip measure is currently not included as such in the Finnish agri-environmental support system, but is incorporated in the draft plan of the forthcoming system.

As regards to set-asides, my results showed that long set-aside duration seems to partially compensate for the negative effects of intensive land use in the surrounding landscape (I) and that lepidopteran colonization speed is strongly associated with mobility (I, IV). However, including long-term measures within the agri-environmental support system still remains a challenge. Along with duration, the
benefits of set-aside were strongly modified by the sown seed mixture, especially in
the beginning of the experiment. The results obtained on suitable plant species have
already been applied in the set-aside measure of the current support system, namely
environmental fallows. A major part of environmental fallows in Finland are currently
sown with cheap grass mixtures (Toivonen et al. 2013), which can reach rather high
levels of biodiversity in the long term. Set-aside established with meadow plants is
even more beneficial for flower-visiting insects, and for pollination service providers
in particular, but also much more expensive to implement (Pywell et al. 2011, Török et
al. 2011, Miettinen et al. 2012). At least in Finland, there have also been problems with
seed availability.

As regards to measures applied in the field-forest ecotone, there is a very high
potential for this approach in the Finnish countryside. Many farmers are also forest
owners. When planned carefully according to forest edge orientation and forest type,
logging can be highly beneficial for flower-visiting insects and benefit species of
conservation concern (III). The latter is an encouraging and a novel finding, as most
agri-environmental tools tend to promote only common species (Haaland et al. 2011).
Commercial forests typically have little value for biodiversity (Nordberg et al. 2013)
and creating open habitat in their ecotones will add to the amount semi-natural
habitats at the landscape level. From land owners’ point of view, the measure is best
applied in such forest stands in which final felling is not imminent, but which already
contain a considerable amount of tree volume (Miettinen et al. 2012). It is also
noteworthy that the history of forest management plays an important role in
effectiveness. As shown by Ibbe et al. (2011), clear-cuts historically managed as
meadows tend to support more insect species and individuals and a higher
proportion of grassland specialists than clear-cuts with a history merely as forest. In
the Finnish support system, field-forest ecotone management is possible within the
measure ‘Promotion of biodiversity and landscape diversity’, but the option has not
been widely utilized. Stakeholders have identified the rapid reforestation of logged
ecotones as a considerable problem and the measure should be thus combined with
management, preferably with grazing.

Finally, I argue that there is an intrinsic value in maintaining diverse bumblebee
communities, although pollination service provision is stated to be independent of
species identity (see Table 4). Bumblebee species vary according to their tongue length and different species may thus functionally complement each other (Fründ et al. 2013). The question is also relevant in terms of conservation as many long-tongued species have declined in Northern Europe (Bommarco et al. 2011).

Table 4. Implementation criteria and management recommendations when aiming to promote intrinsic values of biodiversity and ecosystem services in agricultural landscapes, as modified from Kleijn et al. (2011).

<table>
<thead>
<tr>
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<th>Intrinsic biodiversity</th>
<th>Ecosystem services</th>
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<tbody>
<tr>
<td><strong>Implementation criteria: Where?</strong></td>
<td></td>
<td></td>
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<tr>
<td>Suitable areas?</td>
<td>Agriculturally marginal</td>
<td>Agriculturally profitable</td>
</tr>
<tr>
<td>Landscape complexity?</td>
<td>Structurally complex</td>
<td>Structurally simple</td>
</tr>
<tr>
<td>Initial level of biodiversity?</td>
<td>Areas with a high levels of biodiversity</td>
<td>All areas, except the most species-rich/-poor</td>
</tr>
<tr>
<td>Target species?</td>
<td>Areas with rare or endangered species</td>
<td>Independent of species identity (e.g. any bumblebee species)</td>
</tr>
<tr>
<td>Source populations?</td>
<td>Near source populations</td>
<td>All areas</td>
</tr>
<tr>
<td><strong>Management recommendations: How?</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Management practices?</td>
<td>Maintaining traditional management on agriculturally marginal land</td>
<td>Reducing management intensity on intensively farmed land</td>
</tr>
<tr>
<td>Measure specificity?</td>
<td>Targeted measures (often requiring significant changes in farming practices)</td>
<td>General measures (requiring little changes in farming practices)</td>
</tr>
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</table>
5. Conclusions and future perspectives

As discussed in the previous section in more detail, answers to my main study questions (see aims of the thesis on page 11) were as follows:

- All three studied measures benefited flower-visiting insects and can be applied in conventional agriculture. The ecological contrast created by each measure varied between target species groups, on-field measures being most effective for bumblebees and logging in the field-forest ecotone for habitat specialist butterflies.

- Pollination service availability generally responded to habitat establishment more rapidly than intrinsic aspects of insect diversity. However, the rather fast response of species diversity was somewhat surprising. Furthermore, intrinsic aspects are likely to benefit from long-term measures, as noted in the set-aside experiment.

- Body size, measured by wingspan, and habitat suitability were the species traits best explaining mobility differences in butterflies and diurnal moths. Habitat suitability was strongly connected with habitat preference.

My thesis has contributed to various knowledge needs on wild pollinators identified by Dicks et al. (2013). For instance, I have shown that long-term set-aside can support viable populations of grassland butterflies and moths, instead of just changing pollinator behavior. In addition, I have produced new information on pollinator movements in the agricultural landscape.

I have identified the most important environmental filtering effects for my focal species groups and addressed the important issue of agri-environmental scheme targeting. Based on my results, I argue that the land-sharing approach to conservation (Bommarco et al. 2013, Fischer et al. 2014) can work rather well in Finnish agriculture. Furthermore, my results highlight the importance of applying multiple measures at landscape and regional levels (Wade et al. 2008, Helin et al. 2013, McKenzie et al. 2013) as well as maintaining landscape-level habitat mosaics in agricultural areas (Debinski et al. 2001, Berg et al., 2011, Mandelik et al. 2012, Diekötter & Crist 2013). Multiple targets of flower-visiting insect diversity are likely to be best promoted in agricultural landscapes, where both on-field and off-field measures (Bommarco et al. 2013) are applied. In addition, there are amenity values associated with different kinds of flowering areas in particular (Odgaard et al. 2013). Finally, in
order to promote the uptake of effective measures by farmers and encourage long-term participation in agri-environmental schemes (see also Herzon & Mikk 2007, de Snoo et al. 2013), adequate funding needs to be targeted not only to the support system itself, but to rural and farmers’ advisory organizations.

Future studies should further address the factors affecting insect community assembly in differently structured agricultural landscapes. The combined effects of multiple agri-environmental measures at landscape and regional levels on flower-visiting insects remain largely unexplored. In addition, the comparison of short-term, behavioral responses with long-term, population-level responses deserves further attention and new methods for assessing these may need to be developed.

KIITOKSET

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