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EFFECTS OF MANAGEMENT AND LANDSCAPE STRUCTURE ON BIODIVERSITY IN BOREAL AGRICULTURAL FARMLAND

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Academic dissertation

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This thesis is based on the following articles, which are referred to in the text by their Roman numerals:

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III Ekroos, J., Kuussaari, M. Landscape context affects the relationship between local and landscape species richness of butterflies in semi-natural habitats. (Submitted manuscript)

IV   Ekroos, J., Heliölä, J., Kuussaari, M., 2010. Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. Journal of Applied Ecology (in press).

Table of contributions

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ABSTRACT

Intensified agricultural practises introduced after the Second World War are identified as a major cause of global biodiversity declines. In several European countries agri-environment support schemes have been introduced to counteract the ongoing biodiversity declines. Farmers participating in agri-environment schemes are financially compensated for decreasing the intensity of farming practises leading to smaller yields and lower income. The Finnish agri-environment support scheme is composed of a set of measures, such as widened field margins along main ditches (obligatory measure), management of features increasing landscape diversity, management of semi-natural grasslands, and organic farming (special agreement measures). The magnitude of the benefits for biodiversity depends on landscape context and the properties of individual schemes.

In this thesis I studied whether one agri-environment scheme, organic farming, is beneficial for species diversity and abundance of diurnal lepidopterans, bumblebees, carabid beetles and arable weeds. I found that organic farming did not enhance species richness of selected insect taxa, although bumblebee species richness tended to be higher in organic farms. Abundance of lepidopterans and bumblebees was not enhanced by organic farming, but carabid beetle abundance was higher in mixed farms with both cereal crop production and animal husbandry. Both species richness and abundance of arable weeds were higher in organic farms.

My second objective was to study how landscape structure shapes farmland butterfly communities. I found that the percentage of habitat specialists and species with poor dispersal abilities in butterfly assemblages decreased with increasing arable field cover, leading to a dramatic decrease in butterfly beta diversity. In field boundaries local species richness of butterflies was linearly related to landscape species richness in geographic regions with high arable field cover, indicating that butterfly species richness in field boundaries is more limited by landscape factors than local habitat factors. In study landscapes containing semi-natural grasslands the relationship decelerated at high landscape species richness, suggesting that local species richness of butterflies in field boundaries is limited by habitat factors (demanding habitat specialists that occurred in semi-natural grasslands were absent in field margins). My results suggest that management options in field margins will affect mainly generalists, and species with good dispersal abilities, in landscapes with high arable field cover. Habitat specialists and species with poor dispersal abilities may benefit of management options if these are applied in the vicinity of source populations.

SUMMARY

1. INTRODUCTION

1.1. AGRICULTURAL INTENSIFICATION AND THE BIODIVERSITY CRISIS

Anthropogenic activity has had an enormous impact in a wide range of ecosystems (Vitousek *et al.* 1997b) leading to an elevated level of extinctions at both local and global scales (Pimm *et al.* 1995; Pimm and Raven 2000). The main drivers in recent extinctions of populations and species include habitat destruction and fragmentation (Hanski, 1999, 2005), the impact of invasive species (Vitousek *et al.* 1997a; Wilcove *et al.* 1998; see also Strayer *et al.* 2006) and overharvesting of wild populations (Vincent and Hall 1996; Pauly *et al.* 1998; Jackson *et al.* 2001). Recent studies have also shown that climate change has affected wild species and moderated the structure of animal and plant communities (Parmesan *et al.* 1999; Warren *et al.* 2001; Parmesan and Yohe 2003; Ibáñez *et al.* 2006). Modern extinction rates have been estimated to be up to 100–1000 times higher than natural extinction levels (Pimm *et al.* 1995; Pimm and Raven 2000; cf. Pereira and Daily 2006).

Intensified agricultural practises adopted after the Second World War are commonly identified as one major cause of global biodiversity declines (Matson *et al.* 1997; Robinson and Sutherland 2002; Benton *et al.* 2003; Tscharntke *et al.* 2005). Declining populations of a variety of organisms associated with agroecosystems have been reported, including birds (Krebs *et al.* 1999; Chamberlain *et al.* 2000; Donald *et al.* 2001; Benton *et al.* 2002; Thomas *et al.* 2004; Donald *et al.* 2006), arthropods (Kromp 1999; Sotherton and Self 2000; Maes and van Dyck 2001; Warren *et al.* 2001; Benton *et al.* 2002; Thomas *et al.* 2004; Goulson *et al.* 2005; Conrad *et al.* 2006; Öckinger *et al.* 2006) and plants (Erviö and Salonen 1987; Andreasen *et al.* 1996; Sotherton and Self 2000; Hyvönen *et al.* 2003b; Luoto *et al.* 2003; Thomas *et al.* 2004). A substantial part of all endangered species occur in managed landscapes, which makes integrating conservation efforts and productive agricultural systems a question of major importance (Pimentel *et al.* 1992; Bengtsson *et al.* 2003; Tscharntke *et al.* 2007; Bennet *et al.* 2006). Maintaining the sustainability of agricultural ecosystems is dependent on the conservation of farmland biodiversity (Tscharntke *et al.* 2005).

A typical consequence of intensified agriculture is the decrease of landscape heterogeneity. Increasing homogeneity of agricultural landscapes in turn leads to loss of species diversity, which tends to decrease in an asymmetrical manner – species in higher trophic levels are usually more strongly affected than species occupying lower trophic levels (Tscharntke *et al.* 2007). This reduces the potential benefits brought by pollinators and biological pest control agents in agricultural landscapes (Östman *et al.* 2001; Ricketts *et al.* 2004; Olschewski *et al.* 2006). As a response to landscape simplification, the functional diversity may decrease even faster than species richness (Flynn *et al.* 2009). Species with poor dispersal abilities can be expected to be influenced more by increasing landscape homogeneity than species with high mobility (Schweiger *et al.* 2005; Dormann *et al.* 2007; Diekötter *et al.*2008).

Agricultural intensification is a complex process, which results in a decreasing structural complexity of the landscape mosaic and a simplification of many natural systems, such as biogeochemical cycles and trophic chains (Farina 1998). Agricultural productivity has increased rapidly since the 1940s, with cereal yields being 2–3 times larger today (Robinson and Sutherland 2002; Tiainen 2004). Simultaneously, the number of active farms has decreased and today farms tend to be large production units specialized in either cereal production or animal husbandry (Robinson and Sutherland 2002; Tiainen 2004). Increased agricultural productivity has been achieved by increasing the cover of productive arable land (Hietala-Koivu 1999, 2002; Robinson and Sutherland 2002) and by increasing inputs of agrochemicals (Robinson and Sutherland 2002; Valkama *et al.* 2009; Stoate *et al.* 2009). Mineral fertilizers are applied to fields to enhance the growth of the crops, whereas herbicides are applied to minimize the competition between crop plants and arable weeds. Modern crop varieties are also highly competitive due to crop improvement. Fungal diseases and insect pest populations are suppressed with fungicides and insecticides, respectively.

1.2. AGRICULTURAL INTENSIFICATION IN FINLAND

Until the 1950s, most farms in Finland relied on mixed farming, with both cereal production and animal husbandry (Tiainen 2004). During the period of rapid intensification (i.e. late 1950s onwards to early 1990s), farms were specialized in either cereal or dairy farms. The availability of artificial fertilizers was a prerequisite for farm specialisation to take place. The percentage of farms with animal husbandry decreased from around 80% in 1959 to 20% in 1995, with large regional differences (Tiainen 2004). In the southern parts of Finland, farms were largely specialised in cereal production by 1995. Starting from the 1950s, fields were increasingly converted into cereal fields at the expense of hay and ley fields as well as pastures (Tiainen 2004). Farm specialisation had two important ecological consequences.

First, the abandonment of cattle husbandry decreased the availability of manure for fertilizing fields, which demanded an increased use of mineral fertilizers. Both increasing use of mineral fertilizers and decreasing use of manure contributes to reduction of soil quality and lower species richness (Pimentel *et al.*1992). Secondly, farm specialisation has lead to a simplified crop rotation, with stands being more homogeneous both within farms and also at a larger scale, within landscapes.

The cover of arable land has increased through the removal of various non-crop habitats, such as field boundaries and semi-natural grasslands (Hietala-Koivu 1999, 2002; Comber *et al.* 2003) and these changes in landscape composition and configuration have had an enormous impact on species richness. The total area of species-rich habitats, most notably semi-natural grasslands, has decreased to less than 1% of its historical cover by the end of the 20th century (Pykälä 2000; Vainio *et al.* 2001). In Finland, 22% of all endangered species are associated with semi-natural grasslands and meadows (Rassi *et al.* 2001). A highly visible change in agricultural landscapes is the loss of arable field boundaries due to subsurface drainage. The mechanisation of farmland practises favoured large and regular-shaped field parcels, which encouraged farmers to replace open ditches with subsurface drainage pipes. Between 1959 and 1995, the percentage of subsurface drainage increased from 8.5% to 65% in southern and western Finland (Tiainen 2004).

1.3. CHARACTERISTICS OF FINNISH AGRICULTURAL LANDSCAPES

In Finland, agricultural landscapes consist of cultivated fields and various non-crop habitats; field boundaries, semi-natural grasslands, settlement and forests. Boreal agricultural landscapes consist of a mosaic of agricultural land and forests (Luoto 2000). Depending on organism group, the key habitats may occur patchily, such as field boundaries and particularly semi-natural grasslands for butterflies (Clausen *et al.* 1998), or more continuously, such as open arable fields for true farmland bird species (Piha *et al.* 2007b). Arable fields occur in patches of very different sizes and shapes, ranging from small individual fields surrounded by forests to larger, contiguous farmland. Furthermore, the agricultural practises in Finland tend to be less intensive than those in central Europe (Hyvönen *et al.* 2003a; Roschewitz *et al.* 2005a, b). In Finland the area under cultivation is approximately 7% of the total land area, but agriculture is concentrated to the southern and western parts of the country, where climatic and edaphic conditions are profitable (Anon. 2006). Arable land is unevenly distributed in the country, with the majority of fields falling within a 100 km broad zone around the coast. In southern and western parts of Finland, the proportion of arable land is roughly 30% (Anon. 2006). Roughly the half of all arable land (55%) is cultivated with cereals and in contrast to e.g. central and Western Europe, around 94% of the overall cereal production consists of spring-

sown cereals (Anon. 2006). Some 75% of the total land cover in Finland consists of different types of forests (Anon. 2005). Due to different farming practises and landscape structure, boreal agricultural landscapes offer a contrasting system for studies on the effect of landscape structure and farming practises. This allows for testing the generality of hypotheses suggesting that farmland biodiversity is affected by landscape composition and farming practises.

In general, the majority of all species associated with farmland habitats are found in different non-crop habitats, such as field boundaries and semi-natural grasslands (Clausen *et al.* 1998; Svensson *et al.* 2000; Kells and Goulson 2003; Clough *et al.* 2007a). Extensive surveys in Finland found 160 arable weed species in cereal fields in 1997–1999 (Salonen *et al.* 2001), whereas over 300 species were recorded in different non-crop habitats (mainly field boundaries or boundaries bordering forests or homesteads, but also some semi-natural grasslands) in 2001 and 2005 (Jauni and Helenius 2008). Butterflies and bumblebees, as an example, benefit from field boundaries with a rich supply of nectar sources (Clausen *et al.* 1998; Bäckman and Tiainen 2002; Kuussaari *et al.* 2007b). Spiders, carabid beetles and other beneficial arthropods find suitable over-wintering habitats in field boundaries and other semi-natural habitats, which act as population sources from which individuals find their way into arable fields (Desender 1982; Sotherton 1984; Coombes and Sotherton 1986; Lee *et al.* 2001). In a similar vein, species richness in field boundaries is also dependent on landscape context, i.e. whether the surrounding farmland contains species-rich semi-natural grasslands with potential source populations (Kleijn and van Langevelde 2006; Öckinger and Smith 2007a, b). In boreal landscapes, forest verges may contain species-rich assemblages as they offer shelter and often rich vegetation for flower-visiting insects (Kuussaari *et al.* 2007b). The intensity of cropping practises as well as crop type or field use determines in which extent species are able to use fields as foraging habitats (Corbet 1995; Westphal *et al.* 2003).

1.4. AGRI-ENVIRONMENT SUPPORT SCHEMES

In several European countries agri-environment schemes have been introduced to counteract the ongoing biodiversity declines (Kleijn *et al.* 2001; Kleijn and Sutherland 2003). Agri-environment support schemes typically consist of various options aiming at improving (local) habitat quality and/or reducing land-use intensity, among which farmers can choose one or several schemes and gain financial compensation (Kleijn and Sutherland 2003). Alternatively, society can contribute to the expenses by paying higher prices for products produced in an environmentally sound way. Agri-environment support schemes are funded with huge amounts of money. Between 1994 and 2003, 15 EU-countries allocated 2.4 billion € annually on agri-environment support schemes – in 2003, the sum was

3.7 billion € (Kleijn and Sutherland 2003; Kleijn *et al.* 2006). Agri-environment support schemes usually contain other objectives apart from providing benefits for farmland biodiversity, most notably to prevent nutrient leaching to waterways and the consequent eutrophication of various aquatic environments, but also to enhance landscape amenity. Schemes are typically applied at very small scales such as individual fields or grassy strips along the borders of fields, which set them apart from classical protected areas (Whittingham 2007).

In Finland, the agri-environment support scheme is organized in three hierarchical categories. The first category consists of six basic, compulsory measures which all farmers taking part in the support scheme need to fulfil. Most individual measures in the basic part are targeted at water protection. Among the basic measures, the most important for species richness is assumed to be the compulsory formation of at least one metre wide margins along main ditches and at least three metres wide border strips along larger water bodies (such as rivers, ponds and lakes). However, based on the evaluation of the Finnish agri-environment support scheme (2000–2006), the effect of newly established margins and border strips were rather insignificant for butterflies and plants (Heliölä and Kuussaari 2008; Jauni and Helenius 2008). The fact that biodiversity benefits did not appear was in part attributed to the mainly tall and highly competitive species forming the vegetation in field boundaries along ditches and main drains. Only a few farmers managed field boundary vegetation by mowing and removing the plant residues, which may improve the conditions for light-demanding and less competitive species (Jauni and Helenius 2008). The agri-environment support scheme for the years 2007–2013 expanded the border-strip measure to include the possibility to establish at least three metres wide border strips also along other field boundaries than those situated along ditches and main drains. This potentially beneficial modification warrants a further investigation on how the management of existing field boundaries and newly established margins and border strips could be more effective in enhancing species richness (Kuussaari *et al.* 2008).

The second category of the Finnish agri-environment support scheme contains five additional measures and 12 voluntary special measures. In the support scheme for the years 2007–2013, additional measures are focused completely on water protection, whereas special measures include two schemes potentially benefiting biodiversity: the formation and management of (ca 25 m wide) border zones along waterways (mainly rivers and lakes) and organic farming. The latter has been subjected to several recent studies (reviewed by Hole *et al.* 2005; Bengtsson *et al.* 2005). Organic farming operates without mineral fertilizers and pesticides, and employs a diverse crop rotation with grass-legume leys in order to keep soils fertile (Hole *et al.* 2005). The reduced use of agrochemicals lowers the impact of environmental stress on organisms living in the fields, whereas a diversified crop rotation enhances habitat heterogeneity both spatially and temporally (Benton *et al.* 2003). Hence, organic farms increase both within- and between-field heterogeneity

(Benton *et al.* 2003). Public concern has arisen about the negative impacts of intensive agriculture and there is an increasing market for products produced by using less intensive agricultural methods.

1.5. STUDY ORGANISMS AS BIODIVERSITY INDICATORS

As biodiversity declines have been reported across a wide range of species and higher taxonomical groups, it can be assumed that these declines are ubiquitous and concern more or less all major groups of animals and plants. However, to what extent different taxa have declined is largely unknown and restricted to well-known taxa (Pimentel *et al.* 1992). It has been suggested that some well-known taxa can be used as indicator species or groups, because changes in their populations are likely to correlate with changes in populations of less well-known species (Kremen 1992; Spector and Forsyth 1998). Arthropods make up the major fraction of all living organisms (Pimentel *et al.* 1992) and represent a good correlate for general species richness (Duelli and Obrist 1998). Among insects, the biology of several groups is thoroughly documented and their ecology is well understood.

Butterflies (Lepidoptera, Papilionoidea and Hesperioidea) are considered to be a good indicator group as their biology, habitat requirements and taxonomy are well-studied issues (New 1991; Pollard and Yates 1993; Thomas 2005). Furthermore, species-specific habitat preferences and dispersal abilities of many butterflies are well-known (e.g. Komonen *et al.* 2004; Kuussaari *et al.* 2007a), which offer an ideal opportunity to study how landscape structure affects butterfly assemblages. Thomas *et al.* (2004) found that 70% of all butterflies inhabiting Britain have declined during the last 40 years. Butterflies with intermediate dispersal abilities have declined more than species with poor or good dispersal abilities, which may be a consequence of these species neither moving far enough to find suitable habitats nor close enough to stray back to the source habitat they left behind (Thomas 2000). In Finland, around 60% of the butterfly species which are associated with semi-natural grasslands have declined during the last 50 years (Kuussaari *et al.* 2007a). The ecological traits of (diurnal) moths, consisting mainly of Geometroidea and Noctuoidea, are not as well-known as concerning butterflies (but see e.g. Nieminen 1996; Nieminen *et al.* 1999). Neither are the changes in population trends of moths documented as comprehensively as for butterflies, but the scant evidence points at widespread declines (Conrad *et al.* 2006).

Bumblebees (Hymenoptera, *Bombus* spp.) are among the most important pollinating insects in northern Europe (Proctor *et al.* 1996). Bumblebees exhibit species-specific differences in proboscis length and landscape perception, contributing to different foraging strategies and distances (Ranta and Lundberg 1980; Ranta 1982; Darwill *et al.* 2004; Westphal *et al.* 2006). For instance, large

species have been found to forage over larger areas than small species (Westphal *et al.* 2006). As with other pollinating insects also bumblebees have declined markedly, although the reasons and magnitude of these declines are rather insufficiently documented (Thomas 2005; Benton 2006; Goulson *et al.* 2006).

Carabid beetles (Coleoptera, Carabidae) are taxonomically and ecologically well-known, forming diverse species assemblages in open habitats (Niemelä and Halme 1992; Niemelä *et al.* 2000). Carabid beetles are considered to be important in contributing to biological control of pest species (Edwards *et al.* 1979). Carabid beetles are morphologically diverse and species can be classified into e.g. short- and long-winged as well as wing-dimorphic species, or as herbivores, omnivores and predatory species (Thiele 1977). Classifications of observed species according to their ecological traits have been used in several studies, e.g. wing-length in distinguishing species with different dispersal abilities (Döring and Kromp 2003), and dietary preference for examining differences between trophic levels (Harvey *et al.* 2008). There are not many studies on changes in carabid population trends, but at least some carabid beetle populations have declined in Europe (Kromp 1999).

Arable weeds are viewed as an important component of farmland biodiversity in agricultural landscapes (Marshall *et al.* 2003; Norris and Kogan 2005; Hyvönen and Huusela-Veistola 2008). Decreasing weed species diversity has been shown to decrease the numbers of arthropods associated with weeds, which in turn have resulted in decreases of bird populations utilizing these insects (Green 1984; Pulliainen 1984; Rands 1985; Wilson *et al.* 1999; Holland *et al.* 2006). The species assemblages of arable weeds have changed in many parts of Europe (Andreasen *et al.* 1996; Sutcliffe and Kay 2000; Robinson and Sutherland 2002). Changes in arable weed populations have been dramatic and several species have been red-listed (see e.g. Albrecht and Mattheis 1998). In Finland and Denmark, a marked change in weed communities coincided with the intensification of agricultural practices from the 1960s to the 80s (Mukula *et al.* 1969; Erviö and Salonen 1987; Andreasen *et al.* 1996; Hyvönen and Huusela-Veistola 2008). Since the 1980s, a slight increase in weed abundance has been reported both from Finland (Salonen *et al.* 2001; Hyvönen *et al.* 2003b; Hyvönen and Huusela-Veistola 2008) and Denmark (Andreasen and Stryhn 2008). The initial declines were a result of increased applications of herbicides and nitrogen fertilizers as well as a general increase in monoculture cropping practices (Erviö and Salonen 1987; Andreasen *et al.* 1996), whereas the recent increase is mainly related to reduction in herbicide use and increase in the area of organic farming in Finland (Salonen *et al.* 2001) and to increased areas of winter crops and changes in weed control measures in Denmark (Andreasen and Stryhn 2008).

1.6. CHOOSING MEASURES OF BIODIVERSITY

Although measuring the number of species may not be an all-embracing measure of biodiversity, it provides a good indicator of the state of the environment in ecosystems dominated by human activities (Duelli and Obrist 1998). However, measuring only species richness may not bring ecological insights in which factors contribute to observed patterns in species diversity. As an example, local species assemblages may be composed by either habitat specialists or generalists and still contain an equal amount of species. If species richness is measured in several plots within a field or landscape the overall species richness, i.e. the sum of all species observed in the plots, can be partitioned into alpha and beta diversity (Allan 1975). The additive partitioning approach defines alpha diversity as the average number of species observed in individual plots, whereas beta diversity corresponds to the dissimilarity between communities in the different plots by giving the number of species not observed, on average, in a particular plot (Lande 1996; Wagner *et al.* 2000; Veech *et al.* 2002). Examining both alpha and beta diversity has been advocated in recent studies because, in theory, management effects may be opposite for alpha and beta diversity. Hence, examining only overall species richness may fail to detect any effects attributable to management (Clough *et al.* 2007a). The additive partitioning approach of overall species richness allows the partitioning of overall (gamma) diversity into alpha and beta diversity measured on the same scale, which makes a direct comparison of diversity partitions feasible (Wagner *et al.* 2000).

In addition to partitioning overall diversity into alpha and beta components, an examination of ecological traits may bring meaningful ecological interpretations to observed patterns in species richness and the distribution of species (Gabriel *et al.* 2006; Clough *et al.* 2007a, b). An ecological trait classification enables a closer examination of how e.g. landscape context or farming regime affects species assemblages by revealing which traits are most affected (Ribera *et al.* 1999, 2001). It is suggested that patterns in beta diversity (or community similarity, the inverse of beta diversity) are tightly linked to the interplay between dispersal ability and degree of habitat specificity and how these two traits are affected by human land-use (Dormann *et al.* 2007). According to this conceptual model increasing land-use intensity leads to decreasing beta diversity if increased land-use intensity affects habitat specialists stronger than poor dispersers. Such a scenario would lead to local assemblages consisting of species with good dispersal abilities, but the species composition between different parts of the landscape would be increasingly similar with increasing land-use intensity. However, increasing land-use intensity may also lead to increasing beta diversity, namely if increasing land-use intensity primarily disrupts the migration process and to a lesser extent reduces habitat availability (Dormann *et al.* 2007). In this case increasing land-use intensity produces distinct habitat patches separated from other such patches, and movement between these

are strongly suppressed. This may lead to decreased community similarity between sample plots within a given landscape.

2. AIMS OF THE THESIS

In this thesis I first evaluate whether one specific measure of the Finnish agri-environment support scheme, organic farming, is associated with higher local species richness compared with conventional farming practises. I compared species richness and abundance of butterflies, day-active moths, bumblebees, carabid beetles and arable weeds between the two farming regimes. Although the main objective of organic farming is not to bring benefits for biodiversity, it has been advocated as a tool for enhancing farmland species richness (van Elsen 2000). Most published studies on the efficacy of agri-environment schemes originate from Germany, the Netherlands and the United Kingdom (Kleijn *et al.* 2006). In Finland, recent studies on biodiversity benefits brought by organic farming have dealt only with arable weeds (Hyvönen *et al.* 2003a) and birds (Piha *et al.* 2007b). The effect of organic farming on arthropods in Finland has not previously been thoroughly studied.

Although I expected organic farming to be beneficial for farmland species richness based on published literature (e.g. Bengtsson *et al.* 2005; Hole *et al.* 2005), the question needed to be addressed by empirical studies, since the landscape structure and farming practises differ between Finland and continental Europe. Organic farming is hypothesized to benefit biodiversity as farming practises in organic farms are less intensive as compared with conventional farming (Hole *et al.* 2005). However, conventional farming practises tend to be less intensive in boreal regions than in continental Europe (Hyvönen *et al.* 2003a; Holzschuh *et al.* 2007), which may reduce the difference between organic and conventional farming. I analyzed the effect of organic farming on species richness of lepidopterans and bumblebees in field boundaries and arable weeds and carabid beetles within the cultivated fields in two separate studies (**I, II**).

Species richness in agricultural landscapes is expected to increase with increasing landscape heterogeneity (Weibull *et al.* 2000) and availability of semi-natural grasslands (Öckinger and Smith 2007a, b). Hence, the second aim of my thesis was to explore how landscape structure affects (i) local species richness of butterflies in non-crop habitats, and (ii) two key ecological traits, habitat specificity and mobility, which in turn determine the species composition in butterfly communities. First, I related the local species richness observed in field boundaries to the species richness observed in the surrounding landscape (i.e. landscape species richness), in order to examine whether local or landscape factors are more likely to shape the species richness in

field boundaries (**III**). This question is important for conserving species richness, because it dictates which management options may be most effective (Cresswell *et al.* 1995). Field boundaries are by far the most frequent non-crop habitats in boreal agricultural landscapes. Hence field boundaries are potentially highly important in maintaining species richness in agricultural landscapes and identifying optimal management actions becomes a crucial question in maximising biodiversity benefits.

Secondly, I studied how landscape structure affects (i) alpha and beta diversity of butterfly communities and diurnal geometrid moths, and (ii) the distribution of habitat specialists and less mobile species in butterfly communities. Finally, I related the degree of habitat specificity and mobility of butterfly communities to changes in alpha and beta diversity (**IV**). If decreasing beta diversity is related to increasing mean mobility and percentage of generalists in butterfly communities, this relationship would provide evidence for biotic homogenization due to increasing land-use intensity, quantified as arable field cover (McKinney and Lockwood 1999; Olden *et al.* 2004; Olden and Rooney 2006; Dormann *et al.* 2007). Although biotic homogenization due to increasing cover of arable fields is theoretically expected, large-scale empirical evidence has still not been published (but see e.g. Schweiger *et al.* 2005; Dormann *et al.* 2007).

3. MATERIAL AND METHODS

3.1. STUDY AREAS

Data were collected in agricultural landscapes situated in the southern and central parts of Finland, in five geographic regions in the following six biogeographical provinces (see Kullberg *et al.* 2002): *Alandia, Aboensis, Nylandia* and *Tavastia australis* in the south, and *Karelia borealis* and *Ostrobothnia australis* in the north. *Alandia, Nylandia* and *Aboensis* are situated in the hemiboreal and southern boreal zones, *Tavastia australis* in the southern boreal zone and *Ostrobothnia australis* and *Karelia borealis* in the middle boreal zone (Ahti *et al.* 1968). Data addressing the effect of organic farming were collected in a study area in *Nylandia* (60°40' N, 25°38' E), dominated by arable fields (mean arable field cover in the study landscape was 70%; **I**) and in five neighbouring municipalities in *Tavastia australis* and *Nylandia* (60°40'– 61°05'N; 25°42'– 25°42'E; **II**). In chapter **III** and **IV**, I utilized data from the provinces *Alandia, Aboensis, Nylandia, Ostrobothnia australis* and *Karelia borealis* (59°57'–63°42'N; 19°41'–30°53'E).

The percentage of arable field cover in the studied landscapes differed markedly between the six biogeographical provinces (regional average ranging from ca 39% to 63%). Among southern provinces, the lowest field cover was found in *Alandia*, where landscapes consisted of highly heterogeneous mosaics with mainly forests and rocky outcrops, but also with relatively high percentages of open semi-natural habitats, meadows and pastures (Kivinen *et al.* 2006; Kuussaari *et al.* 2007b). Animal husbandry was common, and the percentage of cereal fields was only 31% of all productive agricultural land in the early 2000s (according to the Finnish Information Centre of the Ministry of Agriculture and Forestry). Climatic and edaphic factors in *Nylandia* and *Aboensis* were most suitable for agriculture and hence study sites in these provinces had the highest percentage of cultivated fields (around 63% each). The productive arable land was mainly used for cereal production (66% and 71%, respectively). In the north, *Ostrobothnia australis* and particularly *Karelia borealis* were mainly dominated by forests and to a lesser extent mires. In these provinces, the agricultural land concentrated to the most productive patches along rivers and close to lakes and the percentage of cereal production (54% in *Ostrobothnia australis* and 36% in *Karelia borealis*) were rather low as compared to *Nylandia* and *Aboensis*.

3.2. FIELD WORK AND VARIABLE CALCULATIONS

3.2.1. Effect of organic farming on lepidopterans and bumblebees (I)

The first chapter is based on data on butterflies, diurnal moths and bumblebees collected between late May/early June and late August 2001–2003 in three study landscapes measuring 1 km² each (Figure 1). All study regions contained both conventional and organic farms. The organic farms included in the study were
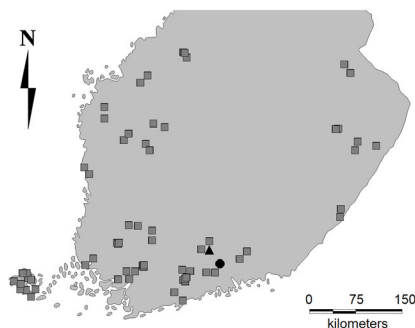

Figure 1. The location of the study areas. The study areas where the effect of organic farming on species richness was conducted are shown with black symbols (circle, chapter **I**; triangle, chapter **II**). The study landscapes used in the studies on the effect of landscape structure on lepidopterans are shown with grey squares (chapters **III** and **IV**).

certified as such during 1996 and 1997 and thus organic management had been applied in organic farms for at least four years before the first field season. The percentage of organic fields in the study landscapes varied between 5% and 40%. In each study landscape, 20 transects (50 m long) were established in field boundaries, which situated either between two fields, between a field and a forest or between a field and a road or dirt-track. The sampled field boundaries were usually narrow (median 1.2 m) and only three sampled field boundaries were over 5 m wide (max 10 m). The data thus consisted of 60 line transects (see Table 1). Each transect represented either an organic or a conventional farm and farm type was treated as a categorical variable.

Table 1. Methods used in chapters **I** and **II** for examining the effect of organic farming as compared to conventional farming practises. For details on the sampling protocol, see chapters **I** and **II**.

Study organisms	*Methods used*
Lepidopterans and bumblebees (**I**)	50 m long line transects were placed in field boundaries in organic and conventional farms. 20 transects were placed in three study landscapes (n = 60 transects, with 15 in organic farms and 45 in conventional farms).
Carabid beetles (**II**)	Two to three study fields were selected from six study areas (n = 48, with 15 fields in organic, 16 in conventional mixed and 17 in conventional cereal farms). Nine pit-traps were placed in each study field.
Arable weeds (**II**)	Ten sample quadrats were placed in each study field, which were selected from six study areas (see *above*).

Butterflies, diurnal moths and bumblebees were counted along transects according to the method originally described by Pollard (1977). During these counts, transects were walked through in a steady and slow pace. All encountered butterflies, diurnal moths and bumblebees were counted species-specifically. Identification was aided by the use of binoculars and a hand net. If an individual could not be identified to species level, it was assigned to a species-pair, genus, genus-pair or family as exactly as possible. The observation was then added to the species list for the particular transect if it added species-level information (i.e. no other species belonging to the same larger-level identification had been observed).

The sampled field boundaries were classified into dry, mesic or moist meadow habitat type based on the characteristics of the vegetation. Moist meadow habitat type was typical for broad field boundaries bordering main drains. Only five transects were situated in such field boundaries and since none of these was situated in organic

farms, I excluded them from the analyses. Floral abundance in field boundaries was measured on a categorical scale ranging from 0 to 4. The classes depicted floral abundance according to the following: 0 = no flowering plants, 1 = less than 15–20 flowering shoots observed, 2 = at least 5–10%, 3 = at least 25–30% and 4 = over 50% of transect area covered with flowering shoots. Because the width of the field boundaries varied very little after omitting transects in field boundaries with moist meadow habitat type, I measured field boundary area by multiplying field boundary width (measured in the field) with field boundary length. In order to roughly account for landscape structure I calculated the distance from the midpoint of each line transects to the nearest forest verge by using a geographical information system (MapInfo Corporation). As the study landscapes almost completely lacked semi-natural grasslands, forest verges were expected to be the main landscape characteristic influencing species richness and thus important to control for in the analyses (see e.g. Kuussaari *et al.* 2007b).

3.2.2. Effect of organic farming on carabid beetles and arable weeds (II)

Data on arable weeds and carabid beetles were collected in June-August 1998 in six patches of farmland which were situated 10–30 km apart from each other, in neighbouring municipalities. In each study site (i.e. patch of farmland), 2–3 fields in either conventional cereal, conventional mixed or organic farms were selected as study fields (see Table 1). The organic farms had been certified four years before the sampling year (i.e. 1994, except one farm, which had been certified one year before the field season). The selected fields under organic management were in either cereal (four study sites) or mixed farms (two study sites). These were collectively treated as organic farms since both cereal and mixed organic farms were not available for comparison in these study sites. Study fields were cropped with spring-sown cereals with the exception of three fields under organic management, which were cropped with autumn-sown rye. Organically managed fields were fertilized either with manure and legumes (n = 5) or only legumes (n = 10). Crop rotation in organically managed fields included winter and spring cereals and leys in a sequence of 1–3 years. The fertilizing practises in conventional mixed farms varied, with either manure and mineral fertilizers or only mineral fertilizers or manure. Crop rotation included spring cereals and perennial leys. All conventional cereal farms applied mineral fertilizers and operated with only cereal cropping. Conventional farms (both cereal and mixed ones) used herbicides, whereas none of the farms had applied mechanical weed control.

Arable weed samples were taken in July-August 1998 during a two-week period, timed roughly a month after herbicide treatments of conventional fields. The study fields were divided into 100 candidate sampling plots. Ten cells were

selected randomly from the set of 100 candidate plots and in these a sample quadrat, measuring 25 × 40 cm, were placed. All shoots of arable weeds found within the sample quadrat were identified and counted individually. The ten sample plots in each field were pooled before the analyses. The observed arable weed species were classified into insect-pollinated and non-insect-pollinated species, including wind- and self pollination, according to traits supplied by Klotz *et al.* (2002).

Carabid beetles were collected using pitfall traps with a mouth diameter of 70 mm and a volume of 170 ml, half-filled with 70% ethylene glycol to which a small amount of detergent was added. Nine pitfall traps were used in each study field, and pitfalls were placed five metres apart from each other. The first pitfall trap was situated one metre from the field boundary and pitfall transects headed towards the centre of each study field. Pitfall sampling occurred in three two-week sampling periods during the first half of June, July and August. Carabid data from the three sampling periods were pooled prior to the analyses. To characterize the observed assemblages of carabid beetles three traits were chosen, each grouped into two classes. These classifications were based on body size (small species [<0.55 cm] vs. intermediate and large species [≥0.55 cm]), feeding guild (herbivores and omnivores vs. predators) and wing development (short-winged and dimorphic species vs. long-winged species) according to Thiele (1977).

For local-scale analysis, I used the number of species observed in all sampling units within each field (n = 48). Overall species richness of both arable weeds and carabid beetles, as well as species richness within ecological trait groups, were partitioned into alpha and beta diversity separately for the three different farm types at the scale of study landscapes (n = 18). As the six study areas varied in landscape composition I expected this variation to have an influence on species richness. I calculated two landscape metrics, quantifying landscape structure at two different spatial scales, in order to account for landscape structure in the analyses. The landscape metrics were field cover (including cultivated land, set-asides and fallows, but excluding meadows and pastures) within a 300-m radius around the central point of each study field, and Shannon-Wiener diversity index for 37 CORINE land-use categories within a 1-km radius around the central point of each study field (Härmä *et al.* 2004). I used the GRASS GIS software (GRASS Development Team 2006) to calculate landscape variables.

3.2.3. Effect of landscape structure on lepidopterans (III, IV)

I used data gathered in five geographical regions in southern and central Finland during 2001 and 2002 (Figure 1). In these regions, a total of 134 study landscapes (132 in chapter **III**), measuring 0.25 km², were placed in a pair-wise fashion in agricultural landscapes. Study landscapes were selected pair-wise within a 1 km²
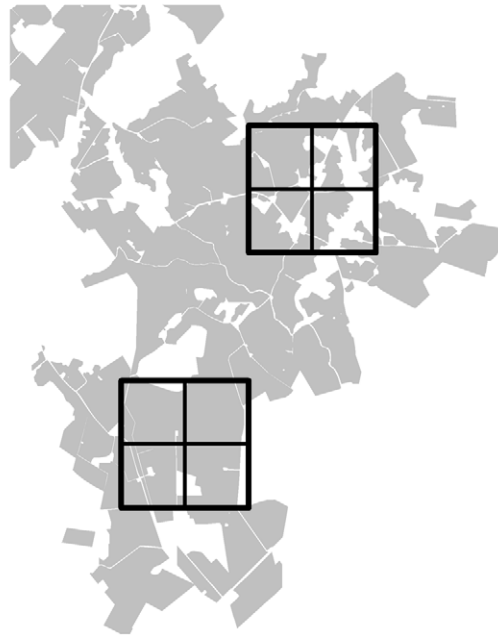
Figure 2. An example of two study squares (1 km²) divided into four candidate landscapes (chapters **III** and **IV**). Out of these candidate landscapes, the ones with highest and lowest landscape heterogeneity were chosen as study landscapes. In each study landscape, ten transects (50 m each) were established for sampling lepidopterans. Fields are shown in grey. For details on the sampling protocol, see chapters **III** and **IV**.

square, comprising of four candidate landscapes (Figure 2). Among these four candidate landscapes, the ones with highest and lowest landscape diversity were chosen as study landscapes. In each study landscape, ten transects, measuring 50 m each, were placed in field boundaries, forest verges and semi-natural grasslands. Transects were placed in these habitat types approximately according to their proportions within each study landscape.

In chapter **III,** I investigated the relationship between local species richness in field boundaries and semi-natural grasslands and landscape species richness, i.e. the species observed within each study landscape. Landscape species richness was quantified following Cresswell *et al.* (1995): for each local plot, the corresponding landscape species richness equals to the sum of species observed in all other plots within the landscape but excluding the local plot in question. This procedure circumvents the inherent correlation between local and landscape species richness, which may otherwise influence the results (Cresswell *et al.* 1995). I also related landscape-scale mean mobility and generalist percentage of butterfly communities to local species richness. I derived average mobility of butterfly assemblages by calculating the mean species-specific mobility rank provided by Komonen *et al.* (2004) of the species observed in a given community. The mobility rank is based on an expert opinion, where the least mobile species were given the lowest number and the most mobile species the highest number. Komonen *et al.* (2004) also quantified the habitat breadth of each species based on a literature survey. The variable on habitat breadth varied from 1 (the species is associated to only one major habitat

category) to 4 (the species can utilize all major habitat classes considered). I used the habitat breadth variable to calculate the percentage of generalist species occurring in a given butterfly community by dividing the number of species belonging to habitat breadth class 3 or 4 with all species observed in the assemblage.

Chapter **IV** deals with land-use driven biotic homogenization: how increasing arable field cover affects landscape-scale alpha and beta diversity mediated by the loss of habitat specialists and poor dispersers from landscapes. I calculated alpha and beta diversity by using the additive partitioning approach of overall diversity $\gamma = \alpha + \beta$. I calculated average mobility and generalist percentage using the same procedure as in chapter **III** presented above. Information on land-use variables were derived from aerial photographs (see Kivinen *et al.* 2006).

3.3. STATISTICAL METHODS

In landscape ecology, typical statistical issues relates to (i) spatial autocorrelation, which leads to correlated observations between plots situated close to each other (positive autocorrelation, see Legendre 1993), and (ii) collinearity between variables, particularly those which quantifies landscape structure (see Graham 2003). I used mixed models to overcome problems with correlated error variance between plots situated within a landscape (**I**) or a study site (**II**), as well as study landscapes situated pair-wise (**III, IV**). Random variables reduce the error degrees of freedom and correct statistical inference when study plots may be dependent on each other (Littell *et al.* 2006; Bolker *et al.* 2009). Other explanatory variables, such as farm type in chapters **I** and **II** and arable field cover in chapters **II–IV**, were treated as fixed factors.

To overcome collinearity problems in multiple regression models, Graham (2003) suggested three alternative statistical approaches: (i) principal components analysis, (ii) using residual values instead of raw values for the less important variable, and (iii) path analysis. All methods have their pros' and cons' and I used residual variation of the less important landscape metric after removing the influence of the more important variable (**II**). The variable which can be assumed to be affected is regressed against the variable that drives the relationship, and residuals of the response variable, the 'less important' of the two, is used instead of raw values. This approach is valid as long as the 'importance' of the variables can be assessed. In chapters **III** and **IV**, I chose to use only one landscape metric to describe landscape composition: arable field cover. In farmland, arable fields can be viewed as the most important component contributing to landscape composition.

4. RESULTS AND DISCUSSION

4.1. EFFECTS OF FARM MANAGEMENT AND PRODUCTION SYSTEM ON SPECIES RICHNESS

I found no effect of organic farming on species richness of butterflies or carabid beetles, and only a weak suggestion for higher species richness of bumblebees (**I, II,** see Table 2). Compared to butterflies, bumblebees seem to benefit more from organic farming, probably because bumblebees are able to utilize a wider range of resources found in the fields. This result is consistent with results from southern Sweden (Rundlöf and Smith 2006; Rundlöf *et al.* 2008a). In particular, some nitrogen-fixating crops used in organic farms (Hole *et al.* 2005) may provide bumblebees with important food resources (see Bäckman and Tiainen 2002).

Table 2. Effects of organic or conventional farming practices in boreal farmland. The results are based on chapters **I** and **II** in this thesis, whereas the main conclusions relates these results to findings presented in a selection of key references.

Species group	Results (**I, II**)	Main conclusions
Butterflies	0	Landscape context[1] and the extent of organic farming[2] affects the relationship and may explain why farm type was not significant (**I**).
Bumblebees	(+)	The extent of organic management is likely to explain why the difference between farm type was small[3] (**I**). Also landscape structure may affect results[4].
Carabid beetles	0	Mixed farming may be more important than organic farming, but this needs further investigations (**II**). Earlier studies show mixed results but generally organic farming enhances carabid diversity[4].
Arable weeds	+	Organic farming affects (alpha) diversity. Insect-pollinated species does not benefit more than non-insect-pollinated species[5].

[1] Rundlöf and Smith 2006   [3] Rundlöf *et al.* 2008a   [5] Gabriel and Tscharntke 2007
[2] Rundlöf *et al.* 2008b   [4] Bengtsson *et al.* 2005

Some studies have suggested that the effect of landscape structure may be more important than the effect of farming regime (Weibull *et al.* 2000; Purtauf *et al.* 2005), and furthermore, there may be an interaction between the effects of farming regime and landscape structure so that effect of farming regime is evident only in homogeneous landscapes and not in heterogeneous ones (Roschewitz *et al.* 2005b; Rundlöf and Smith 2006; Rundlöf *et al.* 2008a). However, as the percentage of

arable fields around organic plots was roughly 60–70%, the difference in bumblebee species richness between organic and conventional plots was surprisingly small (**I**). Recently it has been shown that agricultural landscapes with a high percentage of fields under organic production (57% on average) benefits butterfly species richness (Rundlöf *et al.* 2008b). In the light of these results, it is possible that the small proportion of fields under organic farming in the study area (roughly 7% of all arable land) contributed to an insignificant difference in species richness between organic and conventional farms (**I**).

Concerning carabid beetles, earlier studies have shown rather mixed results (see e.g. Mäder *et al.* 2002; Purtauf *et al.* 2005), but Bengtsson *et al.* (2005) concluded in a meta-analysis that carabids are generally enhanced by organic farming. Some different results may be explained by differences in habitat type. As an example, carabid species richness has been found to be higher in organic pastoral habitats as compared to conventional ones, but within the same farms, no differences were found between organic and conventional arable systems (Wickramasinghe *et al.* 2004). My results suggest that a greater use of biological resources, such as manure, may benefit species richness of carabid beetles (**II**), which is consistent with earlier results (Purvis and Curry 1984). Given that herbicides are not applied to the fields, as in conventional farming regimes, the use of manure may also benefit arable weed diversity (see also Pimentel *et al.* 1992). Apart from the interaction between landscape structure and farming regime (Roschewitz *et al.*, 2005b; Rundlöf and Smith 2006; Rundlöf *et al.* 2008a) which may explain some inconsistent results (see above), one possible factor contributing to inconsistencies between studies on the benefits of organic farming may be whether manure is used or not (Pimentel *et al.* 1992; **II**).

I found that both species richness and abundance of arable weeds was higher in organic farms than in conventional ones (**II**). At a regional scale, organic farming benefited alpha diversity of arable weeds, but not beta diversity (cf. Gabriel *et al.* 2006). The proportion of insect-pollinated arable weeds did not differ between organic and conventional farms, as it has been shown to do in Germany (Gabriel and Tscharntke 2007). In Finland, insecticides are not used annually on conventional farms and several years can elapse between sprayings, which may reduce differences between organic and conventional farms (cf. e.g. Roschewitz *et al.* 2005a). Differences in the timing and quantity of herbicide applications may also explain different results (Hyvönen *et al.* 2003a; Roschewitz *et al.* 2005a, b; Rundlöf and Smith 2006; Rundlöf *et al.* 2008a). Herbicides are typically applied annually in conventionally managed fields, removing food resources for flower-visiting insects (Dover 1997; de Snoo 1999). My result suggests that organic and conventional farms in boreal landscapes may not differ from each other as much in terms of habitat quality for flower-visiting insects as in central Europe, although arable weeds (and insect-pollinated species among them) are benefited by the exclusion of herbicide

use (Hald 1999; Gabriel and Tscharntke 2007). Hyvönen (2007) demonstrated that organic farming does not restore arable weed communities in a short time-scale, but perennial and non-nitrophilous species may need several years of relaxed inputs of herbicides and mineral fertilizers to recover.

4.2. SEMI-NATURAL HABITATS AND SPECIES RICHNESS: THE ROLE OF LOCAL CHARACTERISTICS AND LANDSCAPE CONTEXT

I found that increasing abundance of floral resources (measured as the cover of flowering nectar-rich species) in field boundaries increased species richness and abundance of butterflies and bumblebees (**I**), corroborating findings in several earlier studies (Thomas and Marshall 1999; Meek *et al.* 2002; Carvell *et al.* 2007; Kuussaari *et al.* 2007b). I also found that increasing field boundary area was related to increasing numbers of butterflies, but bumblebee abundance was not affected by field boundary area (**I**). Butterflies as well as many moths are dependent on nectar sources for feeding (Clausen *et al.* 2001; Pöyry *et al.* 2004), whereas bumblebees both feed and collect pollen for feeding the larvae in the nests (Benton 2006). My results suggest that butterflies may be more restricted to non-crop habitats than bumblebees, a finding which may explain why bumblebees benefit more than butterflies from organic farming (Rundlöf and Smith 2006; Rundlöf *et al.* 2008a; **I**).

In regions with high arable field cover (63% on average) the relationship between local species richness of butterflies in field boundaries and landscape species richness was linear, suggesting that some landscape determinant limits the local species richness of butterflies in field boundaries (Figure 3). In these regions, local species richness increased with decreasing generalist percentage in the butterfly assemblage found in the study landscapes. As arable field cover increases, the area of forests decreases and also habitat specialists of forest verges is expected to decrease. My results suggest that improving the habitat quality in field boundaries in regions with high arable field cover may not be an effective way to enhance butterfly species richness, although management is likely to enhance populations of those generalist species which still occur in such homogeneous landscapes (Kleijn *et al.* 2006).

In regions with low–moderate arable field cover (43% on average), the relationship between local and landscape species richness was non-linear, with a decelerating gain of local species richness at high levels of landscape species richness (Figure 3). Because increasing landscape heterogeneity is associated with increasing species richness (Weibull *et al.* 2000), landscape species richness may be high when arable field cover is low and when the landscape level habitat heterogeneity supplies a species-rich assemblage with potential colonizing species. Therefore, local species richness may be enhanced by improving local habitat quality in such landscapes. However, the non-linear response suggesting that some local factor limits local

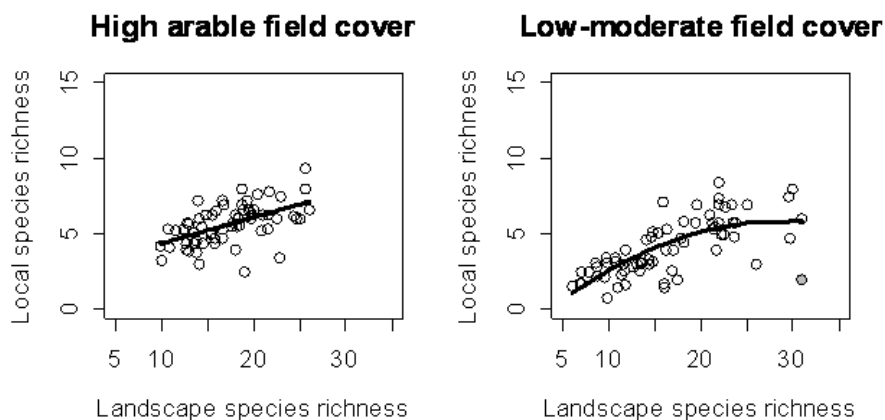## High arable field cover   Low-moderate field cover

Figure 3. The relationship between local and landscape species richness of butterflies in regions with high and low-moderate arable field cover. In regions with high arable field cover (left-hand panel), the relationship between local and landscape species richness was linear, which suggests that local species richness of butterflies in field boundaries may be primarily limited by some landscape factor, such as dispersal limitation. In landscapes with low-moderate arable field cover (right-hand panel), this relationship was non-linear, where local species richness did not increase at high levels of landscape species richness. Such a relationship may provide evidence for some local rather than regional limiting factor on local species richness, most likely relating to habitat quality of field boundaries. However, the non-linear relationship was conditional on one influential data point (denoted by grey colour in right-hand panel of the figure).

species richness was conditional on one data point and hence the robustness of the result is questionable. Moreover, the local species richness was related to decreasing generalist percentage in the landscape, suggesting that landscape structure may actually be the primary factor limiting local species richness also in these landscapes. Some species associated to forest verges tend to be rather mobile. Particularly *Gonepteryx rhamni*, but also *Ochlodes sylvanus* and *Nymphalis c-album*, are commonly encountered in field boundaries. However, many species associated to forest verges are reluctant to leave the verge and these may not be observed in field boundaries unless the landscape contains a high proportion of forests.

In landscapes with semi-natural grasslands, I found that the relationship between local butterfly species richness in field boundaries and the landscape species richness was non-linear, with a decelerating gain of local species richness at high levels of landscape species richness (Figure 4). This result indicated that local species richness in field boundaries is limited by local habitat quality rather than by some landscape factor, such as limited amount of immigrants, in landscapes with semi-natural grasslands (**III**). My results suggest that increasing the habitat quality in field boundaries may be more efficient in landscapes where semi-natural grasslands are found, because these habitats contribute most to the species pool of potential source populations (Öckinger and Smith 2007a, b). Furthermore, local species richness in field boundaries in landscapes with semi-natural grasslands was not related to either generalist percentage or mean mobility of the landscape level species assemblage
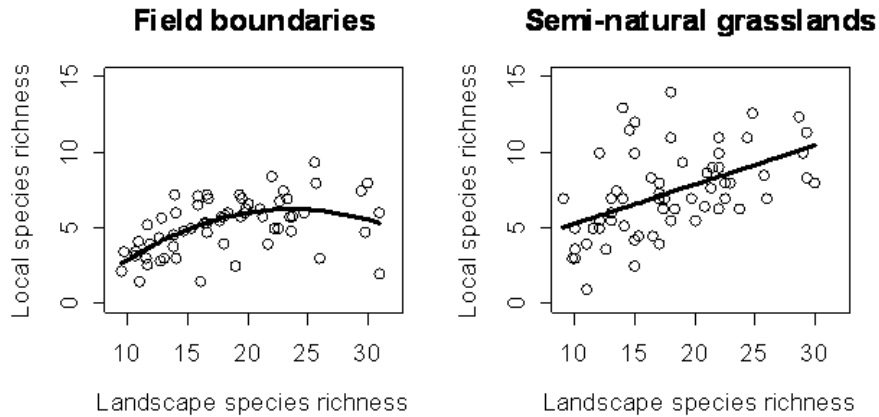
Figure 4. The relationship between local butterfly species richness in field boundaries (left panel) and semi-natural grasslands (right panel) and landscape species richness in landscapes where semi-natural grasslands are present. Local species richness in field boundaries was non-linearly related to landscape species richness, suggesting that some local habitat factors limit species richness in field boundaries in landscapes with semi-natural grasslands present. Furthermore, local species richness in field boundaries was not related to generalist percentage or average mobility of the species assemblage observed in the landscapes, giving further evidence for habitat factors limiting local species richness in field boundaries. In semi-natural grasslands, local species richness was linearly related to landscape species richness, which suggests that local richness is limited by landscape-scale factors. Average mobility was negatively related to local species richness in semi-natural grasslands, suggesting that local species richness may be dispersal-limited.

(**III**). The observed relationships give further support for the hypothesis that semi-natural grasslands contain source populations which may colonize nearby field boundaries, given that these are suitable in terms of habitat quality. In semi-natural grassland, local species richness increased linearly with landscape species richness (Figure 4), and furthermore, high local species richness was associated with low average mobility of the landscape butterfly assemblage (**III**).

I also found the relative species richness in field boundaries (i.e. the percentage of species observed locally of all species recorded in the study landscape) to increase with increasing arable field cover in regions with high arable field cover, but not in the regions with low-moderate arable field cover (**III**). Although species richness in absolute terms decrease with increasing arable field cover, the remaining species in intensively cultivated landscapes are increasingly concentrated to the field boundaries, which are the only semi-natural habitats available. My results suggest that field boundaries situated in homogeneous landscapes dominated by arable fields contain a high proportion of all butterfly species found in the landscape, as could be expected based on earlier work demonstrating that non-cropped habitats are important for butterflies (see e.g. Clausen *et al.* 1998). Therefore, maintaining field boundaries in such homogeneous landscapes is important to ensure available habitats for the remaining species, although they are likely to be habitat generalists (Tscharntke *et al.* 2005, 2007; **IV**).

4.3. EFFECT OF LANDSCAPE STRUCTURE ON SPECIES RICHNESS

In chapter **I**, landscape structure was measured as the distance of forest verges to each line transect, but this variable did not explain any variation in species richness of lepidopterans or bumblebees (**I**). In chapter **II**, I found that increasing landscape diversity was associated with increasing beta diversity of carabid beetles, whereas arable weeds were not affected by landscape variables (**II**). In chapter **IV,** I found that increasing arable field cover in the study landscapes was related to decreasing beta diversity of butterflies and geometrid moths, whereas alpha diversity was either unaffected or exhibited only marginally significant decreases. Neither was increasing landscape diversity related to alpha diversity of carabid beetles, except for alpha diversity of large and intermediate species, which decreased with increasing field cover (**II**). Landscape heterogeneity is identified as a key determinant for farmland species richness (Weibull *et al.* 2003; Weibull and Östman 2003; Purtauf *et al.* 2005; Schmidt *et al.* 2005; Schweiger *et al.* 2005). Landscape heterogeneity may also ensure that spatially segregated resources occurring in different habitats, which are needed under different phases in the life of an organism, are found in a landscape (Ouin *et al.* 2004). Furthermore, landscape heterogeneity provides a buffering effect against extreme environmental conditions (Piha *et al.* 2007a).

In chapter **IV**, I found that increasing arable field cover had a strong negative effect on beta diversity of butterflies (Figure 5). Decreasing beta diversity was strongly
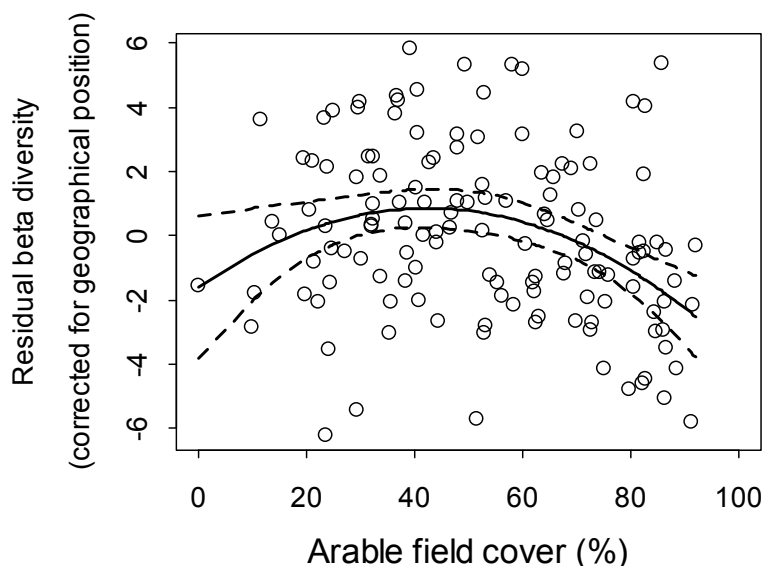

Figure 5. The relationship between arable field cover and beta diversity of butterflies, corrected for geographical postion. Beta diversity peaks in landscapes with arable field cover ranging between 40–50% and the declining trend accelerates when arablwe field cover exceeds 60%. Beta diversity is also lower in landscapes with low arable field cover, although the uncertainty, in terms of the standard deviation of the regression line, also increases at low numbers of arable field cover.

related to an increasing percentage of generalist species and mean mobility of species assemblages in regions with high arable field cover (Figure 6). I did not find a similar relationship in regions with low-moderate arable field cover (Figure 6). My results provide empirical evidence of land-use driven biotic homogenization. Some early papers which suggested patterns of biotic homogenization related e.g. community similarity to land-use gradients, but these did not measure responses in mobility or proportions of habitat specialists (see Table 1 in Olden and Rooney 2006). In fact, it has been advocated that in order to demonstrate biotic homogenization, one has to compare documented changes in landscape structure with survey data between different time-periods (Olden and Rooney 2006). As a rare example of such a study, Rooney *et al.* (2004) compared the rate of change in native and exotic plant species richness between two points in time. Chapter **IV** presents how species-specific information on mobility and habitat specificity can be used in studies considering the homogenizing effect of land-use intensity. The correlative approach used in this study is consistent with theory predicting land-use driven biotic homogenization (Dormann *et al.* 2007). My results suggest that the percentage of habitat specialists and mean mobility of the butterfly assemblages decrease in boreal agricultural landscapes where arable field cover exceeds 60%. This decrease leads to lower beta diversity, i.e. increased similarity between local communities.
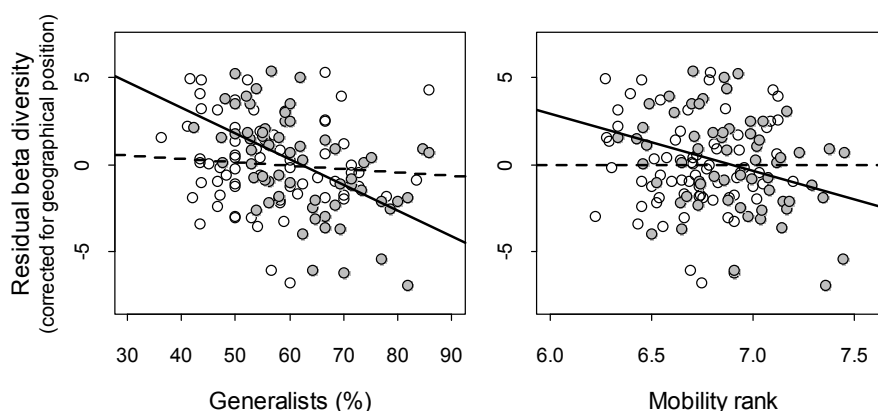

Figure 6. The relationship between beta diversity of butterflies and the percentage of observed species which are habitat generalists (left panel) and average mobility of the species forming the butterfly communities (mobility rank; right panel). The relationships are shown separately for regions with high arable field cover (grey, filled circles and solid regression line) and regions with low-moderate arable field cover (open circles and dashed regression line). In regions with high arable field cover, beta diversity of butterflies is strongly and negatively associated with both generalist percentage and average mobility, but in regions with low-moderate arable field cover these is no such relationship between beta diversity and ecological traits.

5. CONCLUSIONS AND IMPLICATIONS FOR CONSERVATION

During 2000–2006 the Finnish agri-environment support scheme addressed mainly environmental aspects not related to biodiversity. Of the mandatory and additional measures, only two addressed biodiversity enhancement and landscape amenity. The third part of the support scheme was optional and consisted of 12 measures (e.g. organic farming). Out of these 12 measures, two were directly aimed at protecting species richness and one at landscape amenity. In the current agri-environment support scheme, running during 2007–2013, one of the additional measures aimed at protecting biodiversity in the previous support scheme (2000–2006) was abolished, and thus the targets in the present support scheme is even less about promoting biodiversity than it was before. The main goal in the current support scheme is to cut down nutrient runoffs and hence protect water quality.

National statistics suggest that organic farming may be more common in regions with a low cover of arable field, which is shown to be the case in Sweden (Rundlöf and Smith 2006). In 2002, the percentage of all farms being under organic management was 4.7% in *Aboensis* and 9.6% in *Karelia borealis*, a region with low arable field cover (Puurunen 2004). As organic farming is most beneficial for species richness in homogeneous landscapes, this regional pattern ought to be the reverse, and promoting organic farming in regions with high arable field cover, particularly *Aboensis,* could be a part of the Finnish agri-environment support scheme. In addition, the support schemes should favour larger areas, such as several field parcels or whole farms, to be converted into organic production (Rundlöf *et al.* 2008b). Rundlöf and Smith (2006) suggested that the management of non-crop habitats, such as field boundaries or semi-natural grasslands, could be included in the regulations for organic farming (see also Kells *et al.* 2001). In addition, promoting organic mixed farming seems particularly appropriate as several taxa may benefit from the combined effects of reduced pesticide inputs and animal husbandry (Møller 2001; Ambrosini *et al.* 2002; Piha *et al.* 2007b; **II**).

Hansen *et al.* (2001) suggested that nitrogen runoffs from the fields are suppressed by organic farming, which in turn may enhance water quality. Species richness in aquatic habitats situated in organic farms has been found to be higher as compared to similar habitats in conventional farms, which is attributed to the higher capacity of nutrient retention in organic farms (Wickramasinghe *et al.* 2004). Even these findings corroborate that organic farming should be concentrated to regions with high arable field cover, but whether organic farming really does suppress nutrient leaching is still a controversial issue. Another open question is whether the effect of organic farming delivers higher benefits for species richness with increasing time elapsed after the certification.

In landscapes with high arable field cover, field boundaries are important habitat elements although they cannot maintain a high regional species pool by themselves (**III**). Nevertheless, they often are the only non-crop habitats available in these landscapes. According to Hietala-Koivu *et al.* (2004a), on average 69% of the area of field boundaries (ditch margins) disappeared between 1954 and 1997. This trend was particularly evident in southern Finland, where landscapes tend to be dominated by agricultural land use (Hietala-Koivu *et al.* 2004b). Even during the period of the second agri-environment scheme in Finland (2000–2006), the simplification of landscape structure continued in many regions due to loss of field boundaries (Kivinen *et al.* 2008). Based on my results on butterfly communities in semi-natural habitats, I suggest the following modifications in the Finnish agri-environment scheme:

o Field boundary loss e.g. due to increased subsurface drainage should be avoided in landscapes with high (at least 60–70%) arable field cover. The Finnish agri-environment support schemes do not include any directives on retaining field boundaries. Butterfly species tend to concentrate in these remaining semi-natural habitats (**III**). Retaining field boundaries in open farmland will also positively affect bird populations (Piha *et al.* 2007b). The management of habitat quality, i.e. manipulating the composition and structure of the vegetation and/or field boundary width, in landscapes that lack semi-natural grasslands is likely to affect mainly generalist species with good dispersal abilities (**III, IV**; Öckinger and Smith 2007a, b).

o Management of field boundaries should be focused in landscapes where semi-natural grasslands are present. In such landscapes, local butterfly species richness in field boundaries may be limited by local factors, such as vegetation structure (Tarmi *et al.* 2002) or too narrow habitats. Current agri-environment schemes are applied without any reference to regional factors (**III**).

o Encourage the management of semi-natural grasslands to prevent habitat loss of grassland specialists. Semi-natural grasslands harbour high species richness and provide the necessary pool of species and source populations for other semi-natural habitats, such as field boundaries, given that the habitat quality is sufficient (Steffan-Dewenter and Tscharntke 1999; Kleijn and van Langevelde 2006; Öckinger and Smith 2007a, b). Species richness in semi-natural habitats may be limited by dispersal limitation, highlighting the importance of landscape-scale conservation strategies (**III**).

Increasing arable field cover leads to more homogeneous butterfly communities when arable field cover exceeds 60% and thus agri-environment schemes applied in such landscapes may benefit only species with good mobility and habitat

generalists (**IV**). In order to maximize the outcome of agri-environment schemes, different measures need to be promoted depending on the landscape context. In heterogeneous landscapes, where species richness can be expected to be highest, measures aimed at improving the quality of key habitats should be preferred. In homogeneous landscapes the promotion of organic farming and retaining field boundaries is likely to maintain general species richness, whereas in heterogeneous landscapes, measures improving the connectivity and habitat quality in semi-natural grasslands have the greatest potential to benefit habitat specialists and species with poor dispersal abilities.

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