The Influence of Landscape Structure on Butterfly Diversity and Movement in Grasslands

A comparison of two agricultural areas in Southern Sweden

Christine Schneider
Department of Landscape Planning
Alnarp

Doctoral thesis
Swedish University of Agricultural Sciences
Alnarp 2003

Acta Universitatis Agriculturae Sueciae
Agraria 386

ISSN 1401-6249
ISBN 91-576-6432-3
© 2003 Christine Schneider, Alnarp
Tryck: Reproenheten, SLU Alnarp

Abstract

Schneider, C. 2003. *The influence of landscape structure on butterfly diversity and movement in grasslands - A comparison of two agricultural areas in Southern Sweden*. Doctoral dissertation.
ISSN 1401-6249, ISBN 91-576-6432-3.

The objective of this thesis was to investigate the influence of habitat and landscape factors on butterfly diversity and movement in grasslands. The studies were carried out in two agricultural areas in Southern Sweden that differed in landscape structure, including habitat amount and field size. The results show that both habitat characteristics and landscape structure influenced species numbers and abundance of butterflies in grasslands. The amount of adjacent forest, flower abundance, field size and estimated nutrient levels were factors identified as influencing butterfly species composition.

Mark-release-recapture experiments with two grassland butterflies (meadow brown, *Maniola jurtina* L. and scarce copper, *Lycaena virgaureae* L.) indicated that these species regularly move over distances of several hundred metres in a landscape with a high amount of habitat. The differences in movement pattern between the two species were greater in terms of movement frequency than total distances. A comparison with results of published mark-release-recapture data for the two studied species and other butterflies, made evident the dominant impact of the size of the study area on mean movement distances. A comparison of the movement patterns of the same species (*Maniola jurtina*) in the two different study areas showed that dispersal differed between the two areas. Dispersal rates were much lower in the study area with a low amount of habitat. The factors influencing patch immigration differed between the two study areas. The dispersal functions fitting proportions of individuals that moved were also different, which can be important in the context of modelling movement.

In marginal agricultural areas, abandonment is the greatest threat to semi-natural grasslands. Different degrees and patterns of abandonment were estimated to affect butterfly diversity and movement quite differently. This emphasises the importance of spatial planning for landscape change in agricultural areas in order to minimize negative impacts on species diversity.

Keywords: butterflies, dispersal, landscape planning, land-use change, *Lycaena virgaureae*, *Maniola jurtina*, mark-release-recapture, spatial scale.

Author's address: Christine Schneider, Swedish University of Agricultural Sciences, Department of Landscape Planning, Alnarp, P.O. Box 58, SE-230 53 Alnarp, Sweden. christine.schneider@lpal.slu.se

Contents

Appendix

Papers I-V

The present thesis is based on the following papers, which will be referred to by their Roman numeral:

I. Schneider, C. & Fry, G.L.A. 2001. The influence of landscape grain size on butterfly diversity in grasslands. *Journal of Insect Conservation 5*, 163-171.

II. Schneider, C., Dover, J. & Fry, G.L.A. 2003. Movement of two grassland butterflies in the same habitat network: the role of adult resources and size of the study area. *Ecological Entomology 28*, 219-227.

III. Schneider, C. 2003. The influence of spatial scale on quantifying insect dispersal: an analysis of butterfly data. *Ecological Entomology 28*, 252-256.

IV. Schneider, C. & Fry, G.L.A. Dispersal of the Meadow Brown butterfly *Maniola jurtina* in two different habitat networks. (Submitted manuscript).

V. Schneider, C. & Fry, G.L.A. Estimating the consequences of land-use changes on butterfly diversity in a marginal agricultural landscape. (Manuscript).

Paper I is reproduced with kind permission of Kluwer Academic Publishers. Papers II and III are reproduced with kind permission of The Royal Entomological Society, who is the copyright holder of *Ecological Entomology*.

Introduction

Background

Agricultural practices in Europe have undergone profound changes in the last century and especially during the last 50 years. Intensification of land use on productive land on one hand and abandonment or afforestation of marginal agricultural areas on the other have led to far-reaching landscape changes (Jongman, 2002). In areas with profitable agriculture production, farm units and field size have increased with the removal of field boundaries, such as species-rich field margins, hedges, tree lines, ditches, wooden fences and stone walls. Small remnant biotopes such as ponds and *åkerholmar* (=rock outcrops within arable) have been removed. Extensive land uses have been converted to intensive land uses, as for example the change from traditional hay making to intensive fodder production on non-permanent grasslands or from pasture to arable. In areas where agriculture was no longer profitable, agriculture land that was often extensively used was abandoned, with secondary succession as a consequence. Alternatively, agricultural land has been afforested to a great extent throughout the whole of Europe. These changes have led to a more homogeneous agricultural landscape with fewer boundary features and a smaller proportion of extensively used land. For plants and animals living in the agricultural landscape, these changes have meant loss of habitat, habitat fragmentation and the deterioration of habitat quality, which in turn has resulted in species decline (Stoate *et al*., 2001). Since a large proportion of species inhabit agricultural areas, many species are concerned.

Sweden has been no exception to these general trends of land-use changes (Ihse *et al*., 1991; Ihse, 1995), even though agriculture is still carried out less intensively compared to in some parts of Central Europe. One of the major problems with the agricultural changes in Sweden is the loss of semi-natural grasslands. Semi-natural grasslands are one of the most species-rich habitats in Sweden, but cover only about 0.5 % of the area (Naturvårdsverket, 1987). Since 1850, about 90% of semi-natural grasslands have been lost; especially dramatic has been the decline of meadows, with only 3,300 ha meadows remaining in the whole of Sweden (Naturvårdsverket, 1987). To investigate biological, cultural and social aspects of semi-natural grasslands in Sweden, a research programme at the Swedish University of Agricultural Sciences called "The Pastoral Landscapes" was carried out from 1995 to 2000 (Gustavsson, 1995). One of the biologically orientated aims of the programme was to study the effect of management practices and/or landscape structure on selected species groups. As part of this research programme, this thesis examines the influence of habitat characteristics and landscape structure on butterflies in semi-natural grasslands in Sweden. The main aspect of butterfly ecology studied was variation in species richness and species movement in relationship to site quality and landscape pattern.

Aims

The overall aim of this study was to investigate the influence of habitat characteristics and landscape structure on butterfly diversity in grasslands and movement between grasslands. The objective was to provide management recommendations at site and landscape level to conserve/improve butterfly diversity in grasslands.

The specific objectives of this study were:

- to identify habitat and landscape factors that influence butterfly diversity in grasslands by comparing two study areas with different landscape structure (*Paper I*)
- to quantify the movement pattern of two grassland butterflies in a landscape with a high amount of habitat (*Paper II*)
- to investigate the influence of landscape structure on butterfly movement by comparing movement of a grassland butterfly in two different landscapes with different landscape structure (*Paper IV*)
- and to give an example of how the knowledge obtained in *Papers I*, *II* and *IV* could be applied in a management/planning context (*Paper V*).

In *Paper III,* the influence of spatial scale on quantifying butterfly dispersal using mark-release-recapture experiments is highlighted. This paper was an unplanned result of comparing data from published mark-release-recapture studies on the two butterflies investigated with the data obtained in the experiments (*Paper II*).

Semi-natural grasslands in Sweden

Domestic animals have been kept in Southern Sweden since Neolithic times (*ca.* 3000 BC), which resulted in the creation of semi-natural vegetation, grass swards and grazed woods (Olsson, 1991). Hay meadows for fodder production probably became more common around 500 AD, when iron tools for harvesting became available (Olsson, 1991). Grasslands were a very important part of the farm since they provided food for domestic animals. During spring, summer and autumn the animals grazed on pastures both near the farm (infield, Swedish: *inmark*) and outside the enclosed farm area (outland, Swedish: *utmark*) including forests. In winter the animals were fed by hay produced on meadows and leaves from trees. Winter fodder was a limiting factor on the number of domestic animals that could be kept and was thus very important to the farmer. A farm had often much more area covered with hay meadows than arable (Ekstam *et al*., 1988).

Compared to Central European grasslands, for example, Swedish semi-natural grasslands that were traditionally managed have some special features, as they are often more wooded with both bushes and tress (Fig. 1). Trees were both pollarded and coppiced. Due to geological reasons, Swedish grasslands are often very stony. With the introduction of artificial fertilizers and the availability of large machinery that could remove stones, the possibility of intensifying fodder production was created.

Fig. 1. Typical pasture in South Sweden (Bråbygden, Östantorp).

However, the possibility of improving the production of the traditional hay meadows was rather limited since most meadows could only be harvested by scythe due to trees, bushes and stones. Meadows were therefore either converted to ley, (Swedish: *vall*), pasture or forest. This explains the dramatic loss of almost all semi-natural meadows in Sweden, with only 3,300 ha remaining (Naturvårdsverket, 1997). Fodder is now instead produced in high intensity on leys. Pastures have been either improved with the help of fertiliser or converted to ley or forest. The results of a grassland inventory (*ängs- och hagmarksinventering*) showed that there were about 200,000 ha of semi-natural pastures left in 1992 (Naturvårdsverket, 1997) of the approx. 2 million ha that existed in 1850. This is about one third of all pastoral land in Sweden (575,000 ha). The decline in semi-natural grasslands was not only caused by intensification, which allowed higher production on smaller areas, but also by a decrease in grazing animals (30% for cattle, 65% for milk cows since 1950, Naturvårdsverket & Statistiska Centralbyrån, 2000). In addition to the loss of grassland and the change in their quality, grasslands have also become fragmented (Ihse *et al*., 1991; Ihse, 1995; Skånes, 1996).

Semi-natural grassland is one of the most species-rich biotopes in Sweden (Bernes, 1994) for both plant and animal species, but covers only about 0.5% of Sweden. The loss of habitat and the decline in habitat quality due to changed management practices (*e.g.* fertiliser) have caused the decline of species, which is particularly well documented for plants (for example Svensson, 1988; Svensson & Ingelög, 1990; Ingelög *et al*., 1993; Lennartsson & Svensson, 1995). The problem of species loss in agricultural landscapes and especially in semi-natural grasslands was increasingly acknowledged during the 1980s. The inventory of "ancient pastures and meadows" (*ängs- och hagmarksinventering*) initiated in 1985 was seen as a first step towards preventing further deterioration of grasslands and their flora and fauna (Naturvårdsverket, 1997). Today, the preservation of species diversity in Sweden is an explicit aim of the Swedish environmental policy, which has also been confirmed by Sweden signing the Rio convention of 1992. One of the 15 declared objectives concerning the quality of the environment (*15 miljökvalitetsmål*) relates to species diversity in the agricultural environment (*Ett rikt odlingslandskap*). The aim is to preserve or enhance the quality of the environment, biodiversity and cultural values of agricultural areas. To reach these objectives, a system of subsidies for particular agricultural activities has been developed, which also includes the extensive management of semi-natural grasslands (Jordbruksverket, 2002). The subsidies paid to farmers in Sweden in 2001 were about 8,500 million SEK (≈935 million Euro), of which about 600 million SEK (≈65 million Euro) was paid for extensive management of semi-natural grassland and 500 million SEK (≈55 million Euro) to support a diverse agricultural landscape (Statistiska Centralbyrån, 2002).

However, the threat of abandonment of farms still remains in areas where farming is unprofitable – even with subsidies - as the possibilities for farmland improvement are limited due to climate and geological constraints. In these areas, abandonment mostly results in afforestation or to a lower extent in secondary succession. On the other hand in areas, where farming is still profitable, pastures are even today threatened by improvement measurements.

Why study butterflies in grasslands?

In 1997, when this study was started, it became obvious that plants in grasslands and the effects of management on plant diversity in semi-natural grasslands have been comparatively well studied in Sweden (*e.g.* Olsson, 1975; Glimskär & Svensson, 1990; Hansson, 1991; Steen, 1991; Fogelfors, 1997). The influence of landscape pattern on plant diversity in grasslands had also been investigated (Bengtsson-Lindsjö *et al*., 1991; Eriksson *et al*., 1995). Accordingly many management recommendations have been given on the basis of floral investigations. On the other hand, there seemed to be a lack of regard for zoological aspects (apart from birds) in grassland management. Since there seemed to be a particular lack of knowledge about insects in grasslands in Sweden and factors affecting their occurrence, butterflies were chosen as one of the most easy to study insect groups. Butterflies are not only easy to study, but have been shown to react comparatively quickly to environmental changes (Erhardt, 1985). In addition, butterflies have often been used to study movement at a landscape level, and thus seemed to be an appropriate species group to address questions about influences of landscape structure on animal movement at the chosen scale. Since 1997, the problems of focusing grassland management solely on plant diversity have been pointed out (Götmark *et al*., 1998) and since the start of this thesis other studies have been carried out addressing this issue (*e.g.* Söderström *et al*., 2001).

The Swedish butterfly fauna

The taxa considered in this thesis are the Rhopalocera (butterflies), which include the Papilionoidea (true butterflies) and the Hesperioidea (skippers). In Sweden there exist about 127 butterfly species (Gärdenfors, 2000) of which about seven are rare immigrants. According to the distribution maps of Henriksen & Kreutzer (1982), about 75 species could possibly occur in the two geographical regions where butterflies were studied within this thesis (73 in Scania and 69 in Småland). Generally it can be stated that the distribution of butterfly species in Sweden is not very well documented. There is, for example, no current nation-wide distribution map of butterflies in Sweden. The only nation-wide distribution maps I know of are Nordström (1955) and Henriksen & Kreutzer (1982), which both consider the whole of Scandinavia.

In the year 2000 there were 31 butterflies (Rhopalocera) on the Swedish red data list (Gärdenfors, 2000). Of these 31 species, one was classified as *regionally extinct*, 6 as *critically endangered* or *endangered*, while 24 were classified as *near threatened* or *vulnerable*. For 25 of the 29 butterfly species that were on the red data list in 1993, *agriculture activities* were given as a reason for the threat (Ehnström *et al*., 1993). Cessation or change of grazing was the reason most often cited for the threat (18 times) among agriculture activities. Compared to other countries like Great Britain, The Netherlands or Finland, which have national monitoring schemes for butterflies (Pollard & Yates, 1993; Van Swaay *et al*., 1997; Marttila *et al*., 1999) changes in the butterfly fauna in Sweden are not well documented. However, for some areas in Southern Sweden a second recording of sites investigated in the 1980s (Hammarstedt, 1996) is ongoing (Erik Öckinger, pers. communication). There also exist examples from other Scandinavian countries, where changes in butterfly fauna in agricultural landscapes have been investigated (Kaaber & Nielsen, 1988; Saarinen, 2002a).

Landscape – some definitions

The term landscape is used in this thesis in a broad sense, which could be described as a "heterogeneous land area composed of a mosaic of different land covers or land-uses" using in the first part the definition by Forman & Gordon, (1986). The terms landscape structure and landscape pattern are used synonymously in this thesis and describe the amount of different land covers (=landscape composition) and their spatial arrangement (=landscape configuration; Fahrig, http://www.carleton.ca/lands-ecol/whatisle.html; 4th March 2003). Grain size is used according to Forman (1995, p. 10) where a "fine-grained landscape has primarily small patches, and a coarse-grained landscape is mainly composed of large patches". Fragmentation is defined as the "breaking up of habitat, ecosystem, or land-use type into smaller parcels" (Forman, 1995, p. 39).

Factors studied in relation to butterfly diversity in grasslands and other grass-dominated biotopes of the agricultural landscape

In this thesis, the term diversity is used as a synonym for species richness and number of species. Sometimes the term species composition is used when not only species numbers, but also the abundance of individuals, is being considered. To study factors influencing butterfly diversity in grasslands, in this study as in others, a distinction was made between habitat variables and landscape variables. Habitat variables are features of the investigated grassland patch such as vegetation height, flower abundance as well as bush and tree cover. Landscape variables are variables concerned with the spatial arrangement of the investigated grasslands in relation to other land-uses and landscape elements. Landscape variables are either studied only in the immediate surroundings of the investigated grassland areas or for the whole study area.

The ecology of many butterfly species has been intensively studied over recent decades and thus there exists quite detailed knowledge about the habitat needs of many butterfly species. The results of these studies are summarised in quite comprehensive books about butterflies such as Emmet & Heath (1990), Ebert (1993) and Asher *et al*. (2001) or in reports about the management of grassland butterflies (BUTT, 1986). The relationship between habitat characteristics and butterfly species richness in certain biotopes such as grasslands and other agricultural biotopes (uncultivated areas, field margin) has been less well studied. However, the number of studies has been rapidly increasing in recent years and by 2003, many different habitat variables have been investigated in relation to butterfly diversity or numbers.

Nectar or flower abundance has been one of the most studied variables and has been shown to have an important impact on butterfly species and individual numbers (Munguira & Thomas, 1992; Holl, 1995; Lörtscher *et al*., 1995; Dover, 1996; Feber *et al*., 1996; Dover, 1997; Gerell, 1997; Steffan-Dewenter & Tscharntke, 1997; Dover *et al*., 2000; Clausen *et al*., 2001; Hanssen, 2001). Sparks & Parish (1995) found an influence of the floral composition on butterfly diversity. Several studies have found a positive correlation between butterfly and plant diversity (Erhardt, 1985; Jeanneret *et al*., 1999) others no relationship (Hawkins & Porter, 2002; Weibull, 2002). Butterflies prefer species-dependent different nutrient levels of grasslands, but high nutrient levels are related negatively with butterfly species numbers (Oostermeijer & van Swaay, 1998). Söderström *et al*. (2001) investigated more closely the effect of trees and bushes on grassland. They found that tree species diversity and cover had a positive effect while a high proportion of deciduous and large trees had a negative effect on butterfly numbers. Apart from flower abundance, shelter is another important factor influencing butterfly numbers (Dover, 1996; Dover *et al*., 1997; Dover *et al*., 2000; Clausen *et al*., 2001). Vegetation height (Clausen *et al*., 2001), mowing and time of mowing (Feber *et al*., 1996) have been shown to affect butterfly species numbers in margins. Studies investigating the management influence on grasslands and margins found all that butterfly numbers decrease with management intensity or high human disturbance (Erhardt, 1985; Dolek & Geyer, 1997; Bak *et al*., 1998;

Swengel, 1998; Kitahara *et al*., 2000; Hanssen, 2001; Kitahara & Sei, 2001; Söderström *et al*., 2001; Kruess & Tscharntke, 2002; Saarinen, 2002b) and that intermediate succession stadia have high butterfly numbers (Erhardt, 1985; Berglind, 1990; Beinlich, 1995; Oates, 1995; Hammarstedt, 1996; Steffan-Dewenter & Tscharntke, 1997; Götmark *et al*., 1998; Balmer, 1999; Balmer & Erhardt, 2000; Kruess & Tscharntke, 2002). Reafforestation, on the other hand, leads to species decline (Berglind, 1990; Martin-Cano & Ferrin, 1998; Gurrea *et al*., 2000). The effect of management history has been studied by Saarinen & Jantunen (2002) and Weibull (2002). In linear elements of the agricultural landscape insolation (Dover, 1996; Clausen *et al*., 2001) and width (Munguira & Thomas, 1992; Clausen *et al*., 2001) affected species richness. Sprayed margins have lower numbers of butterflies or non-pest butterflies than unsprayed ones (Feber *et al*., 1996; Dover, 1997; Feber *et al*., 1997; Longley & Sotherton, 1997; de Snoo *et al*., 1998). Weibull (2002), on the other hand, could not find higher species diversity on organic farmland compared to farmland managed conventionally. Comparing non-linear versus linear elements, Clausen *et al*. (1998) found fewer butterfly species in linear elements of an agricultural landscape. However, Ouin & Burel (2002) emphasised the importance of margins in the agricultural landscape for butterflies as did Tscharntke *et al*. (2002) for small grassland remnants.

The influence of landscape structure on butterfly diversity in an investigated patch has also received increasing attention (Steffan-Dewenter & Tscharntke, 1997; Jeanneret *et al*., 1999; Weibull *et al*., 2000; Appelqvist *et al*., 2001; Debinski *et al*., 2001; Kerr, 2001; Söderström *et al*. 2001; Collinge *et al*., 2003). Some of these studies show that the surrounding land-use type influences species numbers of a studied biotope (Dover, 1996; Steffan-Dewenter & Tscharntke, 1997; Jeanneret *et al*., 1999; Dover *et al*., 2000; Söderström *et al*., 2001) as was the case in the present study (*Paper I*), where the presence of forest near the investigated grasslands had a positive effect on butterfly species numbers. Collinge *et al.* (2003), however, found no correlation between landscape context and butterfly species richness. Surrounding habitat heterogeneity (Jeanneret *et al*., 1999), small-scale landscape heterogeneity (Weibull *et al*., 2000) and regional habitat heterogeneity (Kerr, 2001) have been shown to be positively correlated with butterfly diversity. Habitat complementation is the most frequently cited explanation for higher butterfly diversity in landscapes with a small-scale mosaic (Jeanneret *et al*., 1999; Weibull *et al*., 2000; Appelqvist *et al*., 2001; Debinski *et al*., 2001), while Debinski *et al*. (2001) also discusses the possibility of *spillover* (=invading species from the adjacent biotope). The results of these studies show that successful species conservation is dependent on the surrounding landscape. Butterfly species conservation limited to single patches will therefore only have limited success.

The influence of the degree of patch isolation on the absence/presence of single species has been relatively long known (Harrison *et al*., 1988; Harrison, 1989). It has been observed that a species is more often absent on isolated patches compared to less isolated patches (Thomas *et al*., 1992; Thomas & Jones, 1993; Hanski, 1994a; Hanski, 1994b; Ebenhard, 1995; Dennis & Eales, 1999; Bergman & Landin, 2001; Cassel, 2002). An explanation for this observation is that species can become extinct on patches due to stochastic and other causes and that the recolonization of isolated patches is more difficult compared to less isolated patches if movement ability is limited. Thus movement ability has an influence on patch occupancy and therefore it influences the species diversity on patches.

Butterfly movement

Butterflies move to reach or to search for the different resources they need. Food resources, mating areas, egg-laying and roosting sites can be spatially separated, which makes it necessary for the butterfly to move between the different areas that provide these various resources. There are usually two terms used to describe that a butterfly moves from one place to another: *movement* and *dispersal*. The terms are used in this thesis according to the definitions by Shreeve (1990), in that movement can occur between any places, while dispersal is a particular movement between habitat patches. Thus the term movement usually includes within (=intra) and between (=inter) patch movement, while the term dispersal is only used for between (=inter) patch movement. Migration, which was not studied in this thesis, is the predictable movement of a butterfly (Shreeve, 1990) often over larger areas. However, many authors use the term 'migration rate' as synonym for 'dispersal rate' when describing inter patch movement. There are mainly two methods used to study butterfly movement: mark-release-recapture experiments and observations, either by following a butterfly or by observing it from one point as long as it is visible. These methods are described further in the Methods section.

Butterfly movement has been intensively studied during the last decade especially since the development of Levins' metapopulation concept by Gilpin & Hanski (1991) and others such as Harrison *et al*. (1988). A metapopulation is defined as a "set of local populations which interact via individuals moving among populations" (Gilpin & Hanski, 1991). The metapopulation concept is applicable in landscapes with fragmented habitat, where all (or most) habitat patches are prone to species extinction due to demographic or environmental stochasticity. Since (nearly) each patch is prone to extinction, species survival is not guaranteed at patch level, but possibly at a landscape level if patches where a species became extinct can be recolonized. Dispersal is therefore seen as a key factor for a species' survival at the landscape level.

Within the framework of the metapopulation concept an increasing number of butterfly movement studies have been carried out, and butterflies have become a kind of key-species in metapopulation research. Even if this thesis was carried out with the metapopulation concept as a theoretical background and many of the studies referred to are metapopulation studies, it was not the intention of this thesis to carry out a metapopulation study as such. There are two basic reasons for this: (a) one of the study areas was so little fragmented that patches could not have been defined as in metapopulation studies, where there is always a certain amount of non-habitat area between patches and (b) data were not collected in more than one year, so that neither colonization nor extinction processes could have been observed.

The focus in butterfly movement studies has been on quantifying butterfly dispersal between patches, identifying factors influencing dispersal and in some cases using these data for modelling survival probability in a landscape. Factors that have been investigated in relation to different aspects of butterfly movement are sex, population and life history, age, body size, density, variation between years, type of species, landscape factors and habitat quality. Many butterfly movement studies analyse movement data separately for the two sexes.

Sex has been shown to both influence movement distances (Baguette & Nève, 1994; Väisänen *et al*., 1994; Lörtscher *et al*., 1997; Fischer, 1998; Fjellstad, 1998; Fischer *et al*., 1999; Konvička & Kuras, 1999; Mousson *et al*., 1999; Bergman & Landin, 2002) and to have no effect on them (Dover *et al*., 1992; Lörtscher *et al*., 1997; Munguira *et al*., 1997; Sutcliffe *et al*., 1997; Brommer & Fred, 1999; Roland *et al*., 2000; Cassel, 2002). In some studies it was females that moved longer in average, in others males. Differences in movement rates between sexes have been found by *e.g.* Baguette & Nève (1994) and Kuussaari *et al*. (1996), where females had higher movement rates and Lörtscher *et al*. (1997), who found higher movement rates for males. Hanski *et al.* (2002) identified population history and life history as factors influencing butterfly dispersal rates. Age indicated by wing wear (Fjellstad, 1998) and flying period have also been shown to influence butterfly movement (Hanski *et al*., 1994; Ouin, 2000). Body size has been shown to both affect butterfly dispersal rates (Kuussaari *et al*., 1996) and to have no effect on them (Hanski *et al.*, 2002). How far density affects immigration and emigration has been discussed for butterflies by for example Kuussaari *et al*. (1996), Baguette *et al*. (1998), Brunzel (2002) and more generally by Bowman *et al*. (2002). The relationship between density and butterfly emigration or immigration rates does not seem to be straight forward, but is dependent on other factors such as sex ratio in a population, flight behaviour or habitat quality. Movement rates or distances can vary for the same species between years (Brakefield, 1982a; Nève *et al*., 1996; Munguira *et al*., 1997; Petit *et al*., 2001). Movement or dispersal ability is species-specific and comparative studies have been carried out with two to three butterfly species in the same study area (Dover *et al*., 1992; Lörtscher *et al*., 1997; Baguette *et al*., 2000; Merckx & Van Dyck, 2002; Wahlberg *et al*., 2002).

The importance of patch and landscape factors on butterfly dispersal has become more and more acknowledged, especially within metapopulation studies. Patch size is one factor that has often been investigated in relation to patch emigration and immigration (Hill *et al*., 1996; Kuussaari *et al*., 1996; Sutcliffe *et al*., 1997; Brommer & Fred, 1999; Baguette *et al*., 2000; Roland *et al*., 2000; Fleischman *et al*., 2002). Emigration rates have shown to be higher in smaller patches (Hill *et al*., 1996; Sutcliffe *et al*., 1997; Brommer & Fred, 1999; Baguette *et al*., 2000). Immigration rates can be both higher (Sutcliffe *et al*., 1997) and lower (Cassel, 2002; Wahlberg *et al*., 2002) on small patches compared to larger ones. Habitat quality, and in particular nectar source, has been shown to influence butterfly movement (Brommer & Fred, 1999; Cassel, 2002; Matter & Roland, 2002). Fleischman *et al*. (2002) pointed out the importance of considering habitat quality in addition to patch geometrics when studying butterfly dispersal. Patch distance or isolation between patches has been shown to influence exchange between patches negatively (Hill *et al*., 1996; Fjellstad, 1998). There are also indications that patch isolation can affect butterfly morphology, which in turn has consequences for the butterfly's dispersal ability (Thomas *et al*., 1998; Hill *et al*., 1999; Van Dyck & Matthysen, 1999).

While the quality of the area between patches has been less considered in previous studies, the influence of matrix on butterfly movement has been taken more into account recently (Fjellstad, 1998; Ricketts, 2001; Cassel, 2002; Sutcliffe *et al*., 2003). Since landscapes with a low permeability of the matrix can inhibit movement, the role of corridors for butterfly dispersal has been investigated. Sutcliffe & Thomas (1996), Haddad (1999a) and Pryke & Samways (2001) were able to show that corridors facilitate butterfly dispersal. Fry & Robson (1994) demonstrated how different types of field margins acted differently on butterfly movement. It is not only open linkages and corridors that affect butterfly movement in areas predominated by non-habitat, since other components (windbreak, tape) have also been shown to have an impact on movement behaviour (Fry & Robson, 1994; Dover & Fry, 2001). The study of behaviour at patch boundaries (Schultz, 1998; Haddad, 1999b; Schultz & Crone, 2001) can provide indications about the inclination of a butterfly species to leave its habitat patch. Other behavioural studies have been carried out to question the precondition of many metapopulation models of random butterfly movement (Conradt *et al*., 2000, 2001).

While single patch and landscape factors have been tested on various aspects of butterfly movement, only recently was the approach of comparing the same species in different landscapes chosen to study the effect of landscape factors on butterfly movement (Mennechez *et al*., *in press*; Ouin, 2000). Both studies showed that butterfly movement differed between landscapes. In recent years spatially explicit dispersal models for butterflies have been developed, which aim to predict dispersal and the survival chances of a species at a landscape level. For example the virtual migration (VM) model by Hanski *et al*. (2000) has been tested for several species (Petit *et al*., 2001; Wahlberg *et al*., 2002) and allows the effects of landscape changes on species survival to be modelled.

In addition to experimental and behavioural butterfly studies, there are studies using simulation models, which investigate the relationship between landscape pattern (habitat amount, habitat configuration) and movement in a more general approach (*e.g.* Fahrig, 2001; King & With, 2002). King & With (2002) investigated the question "When do spatial pattern and dispersal behaviour really matter" and concluded that both factors affect dispersal success in landscapes with <30-40% habitat, while spatial pattern is not important in landscapes with more than 40% habitat. Fahrig (2001), on the other hand, showed that changing the emigration rate from very low to very high led to a change in habitat threshold for a species' extinction from 4 to 66%.

Applications in management and planning

To be able to preserve natural resources and biodiversity, there is a recognised need to integrate landscape ecological research and spatial planning (*e.g.* Skage, 1984; Forman, 1995; Forman & Collinge, 1997; Agger, 1998; Leitão & Ahern, 2002; Opdam *et al*., 2002). For example Golley & Bellot (1991), Selman (1993), Hersperger (1994), Fry (1996) Raymarkers & Skage (1996) and Jongman (1999) have discussed the possibilities and potential of an integration of landscape ecology into planning. However, recently it has been pointed out that there is still a gap between ecology and spatial planning both concerning the applicability of ecological research in design and evaluation (Opdam *et al*., 2002) and between the language/terminology used by ecologists and planners (Antrop, 2001). An idea of the difficulties involved working across the different disciplines in landscape research is given by Fry (2001).

The statement of Opdam *et al*. (2002) that there is quite a wide range of empirical case studies of different scales, organisms and processes is also true for butterfly studies. Most of these studies investigating the ecology of a single butterfly species give some kind of management recommendation of how to preserve the studied species in its habitat (site level). Though the importance of landscape factors for butterfly diversity has been acknowledged in several studies (Jeanneret *et al*., 1999; Söderström *et al*., 2001; Weibull, 2002), spatial management advice for butterfly diversity conservation is rarely given at a landscape scale. Smallidge & Leopold (1997) give an example of how general guidelines for butterfly conservation at a landscape level could be formulated. In the case of butterflies, single species might be rarely of interest in a planning context in the agricultural landscapes, but as a species group they could be taken into account as an indicator group together with, for example, birds and plants (Dramstad *et al*., 2001).

In movement studies, recommendations for conservation include either spatially explicit advice (*e.g.* Bergman & Landin, 2002) or can be derived indirectly from the Result and Discussion section, for example in the form of movement rates and distances moved. A further step on the way to applying ecological data in a planning context according to Opdam *et al*. (2002) would be an extrapolation in space and time with the help of modelling. There are studies where this step has been carried out; the butterfly studies using the VM model are an example (Hanski *et al*., 2000). The difficulties and errors that can arise here are discussed by Moilanen & Hanski (1998) and Ruckelshaus *et al*. (1997), who show that the prediction errors can be high. What would also be needed according to Opdam *et al*. (2002) to close the gap between landscape ecology research and spatial planning are “modelling studies to produce guidelines and standards for landscape conditions” and “methods and tools for integration to the landscape level, which can be built into multidisciplinary tools for design and evaluation”.

An example of how butterfly movement data can be applied to planning of agricultural areas is the study by Sutcliffe *et al*. (2003). The approach chosen there was a mapping of the whole study area and an allocation of friction values to the different land use types, which were based on the results of a mark-release-recapture study. In this way it is possible to model landscape changes and the effect on butterfly movements can be tested. It is also possible to produce guidelines and standards for landscape conditions as suggested by Opdam *et al*. (2002). The approach developed by Sutcliffe *et al*. (2003) has been applied in *Paper V*, where effects of landscape changes on butterfly diversity and movement are estimated.

Another example of how to use butterfly data in a planning context is given in Kleyer & Settele (1999).

Methods

Study areas

To investigate the influence of landscape pattern on butterfly movement in grasslands the approach was chosen of comparing two study areas with a very different landscape pattern regarding field size and amount of semi-natural grasslands (see p. 164 *Paper I*). The confinement to two areas was due to practical reasons. It was not possible within this PhD thesis to cover more areas of the chosen size. One of the study areas, area A, was situated in the most southernly province of Sweden, in Scania (Swedish: *Skåne*) about 10 km east of Lund (Fig. 2). The other study area, area B, was situated in Småland, *ca.* 20 km west of Oskarshamn.

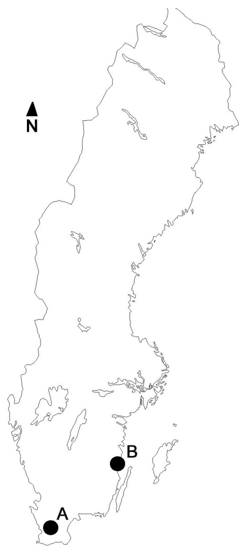

Fig. 2. Situation of the two study areas A in Scania near Lund, and B in Bråbygden near Oskarhamn (Sweden).

Area B in Småland covers parts of the settlement of Bråbygden, which consists in total of 14 small hamlets. This settlement was one of the study areas of the "Pastoral Landscapes" Faculty Programme. The area investigated in this thesis had a size of 172 ha (mostly open parts) respectively 266 ha when some parts of the surrounding forest were included. Bråbygden represents a remnant of the agricultural landscape, as it was typical in Sweden until the 1950s. Fields have kept their small size, and both stone walls and traditional wooden fences (Swedish: *gärdesgårdar*) surround the fields. The landscape has a fine-grained pattern with an average patch size of 0.9 ha (agricultural areas). Many trees have been pollarded, even during the past decade. Though many areas were cleared of stones with the help of large machinery after the Second World War, the amount of semi-natural grasslands is still very high. The meadows, however, have nearly all gone. The main agricultural production is beef production. Few farms or other houses have been abandoned, even though the people living there today are not employed not within agriculture. As Småland is one of the Swedish landscapes known for it' s extensive tree cover, many of the smaller settlements are surrounded by forest. They are called "forest hamlets" (Swedish: *skogsbygd*). This is also the case for Bråbygden.

In the 1960s, Bråbygden was identified as one of eight areas in Sweden best representing agricultural landscapes of high cultural and natural value (Statens Offentliga Utredningar (SOU), 1971) and has been described as such (Aronsson, 1979). Two PhD-theses within the research programme have been carried out in Bråbygden: "The Experience of Pastoral Landscapes" (Hägerhäll, 1999) and "Coppicing in Sweden and on Åland" (Slotte, 2000). Two further PhD theses are ongoing ("Trees and Shrubs in the Cultural Landscape - History and Future", A. Peterson, and "Dynamic and continuity in land-use in Bråbygden from 1700 until today", M. Aronsson). In 2000, the Swedish WWF yearbook for that year was devoted to Bråbygden and the neighbouring settlement Krokshult, where the beautiful environment and the farmers creating it were in focus (Gerdehag & Aronsson, 1999). The area, however, is not protected by any specific legislation.

Fig. 3. Pasture in Bråbygden (in study area B).

The other study area, area A, is situated in the south-western part of Scania. This part of Sweden is one of the most intensively used agricultural areas of Sweden due to its very fertile soils. Fields have become enlarged as a result of rationalising agricultural practices. The landscape pattern is coarse-grained; the average field size of the agriculturally used areas is 6.4 ha. The dominant agricultural activity is cereal production, while animal husbandry (cattle) plays a minor role. The proportion of forest is relatively small, since forest was cleared early on to enable the fertile soils to be used for agriculture. The study area covers 1800 ha (1200 ha in the movement study). It was chosen on the basis of the results of the inventory for semi-natural grasslands (*ängs- och hagmarksinventering*). The following criteria were met: the grasslands should be more isolated than in area B, but the quality of the grassland should be comparable. The Swedish recording scheme for semi-natural grassland classifies grassland into four categories according to their quality. The area west of Lund contained a larger number of grasslands of the highest quality category, while at the same time distances between some of the grasslands were large. This area was chosen even though this led to different grain sizes for the two study areas and area A became much larger in size than area B. Today the semi-natural grasslands in this area are almost all protected as nature reserves. Most woodlands in the study area are small, an exception is the *Dalby Söderskog* of about 40 ha, which borders the study area in the south and is Sweden's oldest National Park. A more detailed description of the land-use proportions can be found in *Paper I* (Table 1 on page 165).

Fig. 4. Pasture in Study area A, west of Dalby.

The comparison of two study areas with the aim of investigating differences in butterfly diversity and movement involves problems in relating any observed differences to the landscape pattern, especially being able to exclude other factors that might affect differences. Thus, it is important to know in which ways the two areas are similar and in which they differ. The following factors were considered: species pool, climate (July, summer months), vegetation and management.

The species pool is about the same in both study areas, where theoretically about 69 (Småland) to 73 (Scania) butterfly species could have been expected at the regional level (Henriksen & Kreutzer, 1982). Due to the southerly situation of Scania, there are a few species that only occur in this part of Sweden. None of these species were recorded within this thesis. Climate data were compared for July, when most butterflies were recorded. The normal July temperature and precipitation are quite similar, with 16.8 °C and 70 mm rainfall in Lund and 16.3 °C in Oskarshamn and 66 mm rainfall in Krokshult (which is the nearest weather station to Bråbygden, but temperature is not recorded here; all data from the Swedish Meteorological and Hydrological Institute, SMHI). In both study areas, the most common vegetation types are "common bent meadow" (*rödvenäng*, Agrostis capillaris-Alchemilla spp.-Trifolium repens-typ) and "sheep's fescue dry meadow" (*fårsvingeltorräng*, Festuca ovina-Lychnis viscaria-typ) (Länsstyrelsen Kalmar Län, 1989; Länsstyrelsen Malmö Län, unpublished). Management was similar in both study areas through extensive grazing. In both areas, there are a few meadows left, which are managed for nature conservation. One difference was the higher number of abandoned grasslands in area B. More information about grassland characteristics in the two study areas is given in *Paper I* (Table 3, page 166).

Field Methods

Transect walks

To survey butterfly species numbers and abundance (*Paper I*) an adjusted method of the Pollard recording method was used (Pollard & Yates, 1993; Pollard & Eversham, 1995). Butterflies were recorded along transects 5 m to each side of the transect (instead of 2.5 m according to Pollard & Yates, 1993) and 5 m ahead of the recorder. Transects were divided into transect sections, where each section represented a more or less homogeneous grassland area. Transects were selected to represent grassland variation and were representative for each study area. The temperature was at least 17 °C irrespective of sunshine, with the wind speed not exceeding 5 on the Beaufort scale. Recording was carried out between 09.00 and 16.00 h (CET). Transect walks were carried out five times between June and August 1997. Species were identified to species level where possible; otherwise they were recorded as species groups. Certain species were always recorded as species groups: *Pieris* spp., skippers and *Plebejus idas* and *Plebejus argus* (further details on page 165 of *Paper I*).

The species chosen for the mark-release-recapture experiments

On the basis of the results of the butterfly recording in 1997, the aim was to choose two typical grassland species that:

- occurred in both study areas in sufficient numbers to allow mark-release-recapture experiments
- were known to be able to move between habitat patches.

Typical grassland butterflies with high abundance in both study areas were *Maniola jurtina, Coenonympha pamphilus* and the two skipper species *Ochlodes venatus* and *Thymelicus lineola* (considering *Aphantopus hyperantus* rather as a forest edge species). Since the movement abilities of *Coenonympha pamphilus* and the two skippers were rather unsure, the only species that seemed to match these criteria was the meadow brown *Maniola jurtina*. In addition to the meadow brown, the scarce copper *Lycaena virgaureae* was chosen for mark-release-recapture experiments to study possible differences between two grassland butterflies in at least one study area. *Lycaena virgaureae* was one of the more abundant grassland butterflies in study area B, and was shown to move up to 1450 m (Fjellstad, 1998). In study area A, only a few individuals of the scarce copper have been observed during the years in which this thesis was carried out.

The meadow brown, *Maniola jurtina* L.

The meadow brown is common and widespread. It is distributed throughout the whole of Europe south of 63° North (Tolman & Lewington, 1997) and occurs in all types of grassland habitats (Henriksen & Kreutzer, 1982; Ebert, 1993). In Southern Sweden, it flies in one generation from the end of June until August, with its peak in the middle of July (Henriksen & Kreutzer, 1982). The larvae of the meadow brown feed on grass species such as *Poa* (Henriksen & Kreutzer, 1982; Svensson, 1993). Adults were observed during this study feeding mainly on *Knautia arvensis*, *Succisa pratensis*, *Centaurea scabiosa*, and *Cirsium* spp., but occasionally also on other flowers such as *Trifolium* spp. Even though the meadow brown is one of the most common grassland butterflies in Central Europe, it has been reported as declining in areas with intensive agriculture (Ebert, 1993).

The meadow brown is a well-studied butterfly species where the investigation of spot-distribution on the hind-wings has been in focus (*e.g.* Bengtson, 1978; Owen & Smith, 1990; Goulson, 1993b; Shreeve *et al*., 1998). The ecology of the meadow brown have been investigated by Brakefield (1982a, b) and Dover (1996). Feber *et al*. (1994) looked at the effect of field margin restoration on the meadow brown. Its phenology has been studied in Sweden by Wickman *et al*. (1990). In addition several behavioural studies have been carried out, for example by Goulson (1993a) studying emergence and Merckx & Van Dyck (2002) investigating habitat use.

Movement has been investigated by Brakefield (1982a, b) and Lörtscher *et al*. (1997) focusing on within-habitat movement and Dover *et al*. (1992) and Ouin (2000) studying movement at a landscape scale. Conradt *et al*. (2000, 2001) have been looking at dispersal behaviour. Wood & Pullin (2002) have studied the distribution and the genetic similarity between populations of the meadow brown and three other common grassland butterflies in an urban landscape. They concluded that habitat availability in an urban area with fragmented habitat is probably more important for the distribution of the grassland butterflies studied than dispersal ability, since they could not find any relationship between genetic similarity and geographic proximity of populations.

The scarce copper *Lycaena virgaureae* L.

The distribution of the scarce copper covers Northern Europe up to the polar circle and most of Central and Eastern Europe (Tolman & Lewington, 1997). Its habitat is flower-rich grasslands and also margins (Henriksen & Kreutzer, 1982). The preference for damp terrain as reported by Henriksen & Kreutzer (1982) has not been observed in this study, on the contrary the scarce copper seemed to be more common on mesic grasslands and also on drier outcrops. The larvae of the scarce copper feed on *Rumex acetosa* or *Rumex acetosella* (Douwes, 1976a). The scarce copper flies in Southern Sweden in one generation between July and August and has its highest abundance around the middle of July (Henriksen & Kreutzer, 1982). Adult distribution has been related with the presence to Tubuliflorae (*Achillea* spp. and *Matricaria indora*; Douwes, 1975a). This has been also observed in agricultural landscapes in Southern Norway, where white *Asteraceae* (*Matricaria, Camomilla)* were the single largest nectar source in field margins (Fry & Dramstad, 1998). In the present study, however, the number of Tubuliflorae was not dominant and most adults were observed visiting *Knautia arvensis*, *Achillea* spp. and *Centaurea scabiosa*.

The scarce copper was a common grassland species and can be locally abundant. However, it now seems to be confined to areas with less intensive agriculture. An ongoing study comparing butterfly abundance on grasslands in Southern Sweden in the 1980s and today has found that the scarce copper is one of the species with the most dramatic decline (Erik Öckinger, pers. communication). The ecology of the scarce copper has been intensively studied by Douwes in the 1970s (Douwes, 1970, 1975a, 1975b, 1976a, 1976b). Fjellstad (1998) investigated movement of the scarce copper between hay meadows and abandoned grasslands in Central Norway. Movement behaviour has been also investigated by Dover & Fry (2001). Sutcliffe *et al*. (2003) have used the scarce copper for modelling the benefit of farmland restoration, a method that has been applied in this thesis in *Paper V*.

Mark-release-recapture experiments

To study butterfly movement three different methods can be used: observation from one point (by eye or with the help of binocular), following flying butterflies (=individual tracking) and mark-release-recapture experiments. Observation from a fixed point can only be used to follow individual butterflies up to the distance where they can be seen by eye or binoculars (*e.g.* Pryke & Samways, 2001). To study longer movements, following of individuals or mark-release-recapture experiments are used. Following individuals means following butterflies as long as possible. In some studies, when an individual is lost one waits at that point until a new individual of the same species passes and starts to follow the new individual (*e.g.* Baker, 1984). In mark-release-recapture experiments, butterflies are marked on their hind wings, often with an individual code. Afterwards, the butterflies are released either at the place of their capture or somewhere else. The location and other information (time, sex, wing wear, behaviour) are recorded. By repeatedly capturing butterflies at the marking locations (or somewhere else), it is expected to eventually capture a butterfly that has been previously marked. By calculating the distance between the first and second recapture, a statement can be made about the minimum distance the butterfly has flown.

The advantages and disadvantages of studying butterfly movement by follow-ups or mark-release-recapture experiments have been discussed for example by Shreeve (1992). One of the main disadvantages of mark-release-recapture experiments is the underestimation of movement. Wilson & Thomas (2002) have discussed thoroughly the problems of underestimation of butterfly movement in mark-release-recapture experiments. In addition, no statement about the flight path can be given (where the butterfly actually moved). Follow-ups on the other hand have the major problem that it is very difficult to follow butterflies. The method is labour-intensive and thus only a few individuals can be sampled.

In this study, mark-release-recapture experiments were chosen to study butterfly movement, because of the possibility they provide to study a larger number of individuals. In addition, most butterfly movement studies are carried out with mark-release-recapture experiments, which allows a better comparison of results. Mark-release-recapture experiments were carried out in the years 1999 and 2000. In 1999, the meadow brown and the scarce copper were studied in area B (5^{th} – 30^{th} July), in 2000 the meadow brown was investigated in area A (28^{th} June – 24^{th} of July). Individuals of these species were caught in nets, individually marked and immediately released at the place of their capture. For every marked and released butterfly the location of capture, date and sex were recorded. Marking was carried out on 13 patches in area A and 41 patches in area B. The higher number of patches in area B is caused by the fact that larger grasslands here were subdivided into smaller units. For comparison of movement data on the meadow brown in both study areas, these sub-units were clustered in the analysis to 19 patches. The reason for the subdivision was that at the beginning of the experiment, it was not clear how far both species would move in a study area of a comparable large size (172 ha). To avoid risking very low recapture data of moved individuals, within-grassland movement was also recorded in case butterflies would not move far. Due to the rather large study areas, not all investigated patches could be sampled every day. Instead a rotational system was used, where each patch was visited every fourth day (if weather conditions were good) or at latest every sixth day (if there were cold/rainy days in between). In area B all patches were visited five times, in area A seven times. The higher number of visits in area A was to compensate for the lower labour force available in this area, so that the sampling extent in both study areas was about the same. Sample intensity depended on area and butterfly abundance. In area A, nearly all semi-natural grasslands were sampled, while in area B only a subset of patches was investigated due to the high percentage of grassland. Here, the patches were chosen randomly ensuring spatial coverage of the area.

Recording habitat variables

To be able to relate butterfly diversity and abundance to habitat characteristics, several habitat variables were recorded for each grassland unit (transect section) (*Paper I*). The variables chosen could hypothetically influence, or have influenced, butterfly numbers in other studies. Recorded variables were cover of bush layer (BUSH), cover of tree layer (TREE), estimated nutrient level (NUTRIENT), vegetation height (HEIGHT) and flower abundance (FLOWER). For further details about the recording of habitat variables see Methods, *Paper I*, page 165.

For the movement studies, flower density and in area B the abundance of the larval food plant *Rumex acetosa* and *Rumex acetosella* were recorded for the investigated marking patches. Flower density was recorded in three classes on every occasion the patch was visited to carry out mark-release-recapture experiments. The abundance of *Rumex acetosa* and *Rumex acetosella* was recorded on a scale from 1 (rare) to 3 (abundant). (For further details see Method section of *Paper II*).

Surveying land-use

Land use was surveyed in 1998 in both study areas by field surveys and with the help of rectified aerial photographs (orthophotographs, scale 1:10.000). Where field use changed between years, this was recorded and taken into account in the study concerned.

Analysis

Movement data

The data obtained from the mark-release-recapture experiments were used to calculate distance decay curves, the fractions of residents, emigrants and immigrants and exchange rates between patches. The distance decay curves were calculated according to the method described by Hill *et al*. (1996), in which the inverse cumulative proportion of individuals moving certain distances was fitted to a negative and an inverse power function. The resident fractions were calculated according to Sutcliffe & Thomas (1996). The fraction of residents was here the number of residents (R) divided by the sum of R+E+I, where E was the number of emigrants and I the number of immigrants. The emigrant fraction was E/E+R and the immigrant fraction I/I+R. Exchange rates between pairs of recaptures were calculated according to Sutcliffe and Thomas (1996), in which the exchange rate between a pair of patches is the number of individuals marked in one patch and recaptured in the other (movement in both directions is considered) divided by the number of individuals marked in the two patches and recaptured in any other patch, including the selected pair of patches.

Estimating consequences of land-use changes on butterfly diversity

The estimations of effects on butterfly diversity were based on the butterfly recording data of *Paper I*. The findings on the grasslands investigated were generalised and expanded to other grasslands of the study area that were not investigated. This was done by classifying butterfly diversity into three degrees of diversity (low, medium and high). These classes were then related to the different land-use types in the study area (for details see Table 1 in *Paper V*). Each single patch in the study area was thus allocated one of the three diversity classes. The effects of possible land-use changes on butterfly diversity were then calculated for each scenario in the form of number and area of land-use patches with low, medium and high diversity.

Geographic information systems (GIS)

Geographic information systems (GIS) were used to produce land-use maps of the study area (including possible scenarios), to calculate landscape variables, transect lengths, movement distances and for a least-cost analysis of movement between patches. Landscape variables calculated were field size (FIELD SIZE) and percentage of forest in 100 m buffers around transect sections (FOREST). The geographic information systems used were both ArcView (ESRI, 2000) and MapInfo 4.5 (MapInfo Corporation, 1998). Land-use maps were produced on the basis of the field surveys and digital rectified photographs (orthophotographs, scale 1:10.000).

Distances to the 10 nearest patches were calculated using the ArcView Extension "Nearest features" V. 3.5 (Jenness, 2001). Movement distances were calculated from mid-point to mid-point of the marking patches. The least-cost analysis was carried out according to the method described in Sutcliffe *et al*. (2003) using an ArcView script written by Ray (1999). (For further details of the least-cost analysis, see Methods in *Paper V*).

Statistical methods

To analyse the butterfly diversity on different grasslands, the ordination method Detrended Correspondence Analysis was chosen using CANOCO (ter Braak & Smilauer, 1998). For analysing correlations, Spearman rank and Kendall's tau_b were used. Forward multiple regression was applied to analyse the variance in species diversity in relation to the recorded habitat and landscape variables. For the analysis of correlations and multiple regressions, Statistica 5.0 (StatSoft, 1997) was used. A Mantel test was carried out using "The R-Package" (Legendre, 2000) to analyse the dependence of exchange rates to distance. The Mantel test is further described in Sutcliffe & Thomas (1996).

Results and discussion

In this study, it was shown that landscape structure is important for both butterfly diversity within grasslands and butterfly dispersal between grasslands. In addition, the importance and difficulties of applying the ecological knowledge obtained in this thesis are pointed out.

The influence of landscape structure on butterfly diversity in grasslands (*Paper I*)

The results of studying butterfly species richness in grasslands in the two study areas showed that both habitat variables and landscape variables influenced species composition. The results of the Detrended Correspondence Analysis (DCA) showed clearly a separation in species composition between the two study areas (Fig. 5). The axes of the DCA had a significant correlation with both habitat variables (BUSH, TREE, NUTRIENT, FLOWER and HEIGHT) and landscape variables (FIELD SIZE, FOREST). The multiple regression analysis showed that the variables FOREST, FLOWER and FIELD SIZE explained most of the variation in species composition (Table 1).

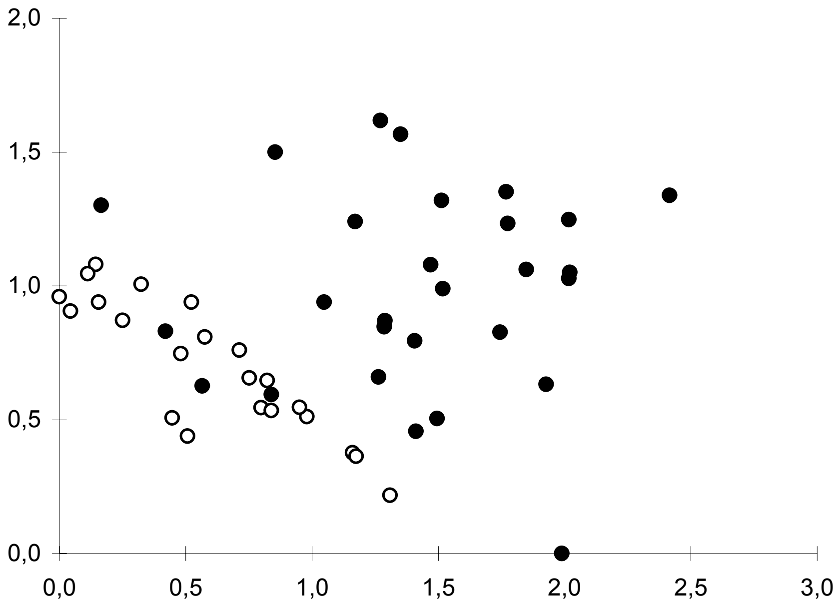

Fig. 5. An ordination plot of the first two axes of the Detrended Correspondence Analysis (DCA) showing a clear separation of the transect sections in the two study area. Open circles area A, full circles area B. (from *Paper I*).

Table 1. *Results of the stepwise forward multiple regression analysis between habitat and landscape variables of the first two axes of the DCA (from Paper I)*

Variable	Beta	Multiple R^2	F
Axis 1			
FOREST	0.499***	0.315	22.0***
FLOWER	0.421***	0.490	16.2***
FIELD SIZE	-0.318**	0.605	13.3***
HEIGHT	0.129 n.s.	0.618	2.9 n.s.
Axis 2			
NUTRIENT	0.341*	0.116	6.3*

* p< 0.05, ** p<0.01, *** p< 0.001

The study area A, with a large mean field size – a coarse-grained landscape - had only about half the number of species of the fine-grained landscape (study area B). The individual numbers, on the other hand, in area A were double those in area B. In area A, 96 % of all recorded individuals belonged to the very abundant species/species groups skippers, whites (*Pieris*), the meadow brown (*Maniola jurtina*), ringlet (*Aphantopus hyperantus*) and common heath (*Coenonympha pamphilus*). In area B, however, the numbers of fritillaries, coppers and blues were much higher, making up 32% of all butterflies observed.

The strong influence of landscape pattern was not expected. The study was originally designed to test which habitat variables in grasslands are related to species numbers and abundance. The study was carried out in two study areas to gain knowledge about species that might be abundant enough to allow mark-release-recapture studies to be carried out in the following years. The large differences in species numbers between the two study areas was even more striking, as most of the investigated grasslands in area A (low species numbers) were nature reserves.

Since 1997, an increasing number of articles have been published emphasising the influence of landscape pattern on butterfly diversity (Steffan-Dewenter & Tscharntke, 1997; Jeanneret *et al*., 1999; Weibull *et al*., 2000; Appelqvist *et al*., 2001; Debinski *et al*., 2001; Kerr, 2001; Söderström *et al*., 2001). The reason for a positive relationship between habitat heterogeneity, landscape heterogeneity or a small-scale landscape mosaic can be explained by a *spillover effect*, which can mean that individuals invade from the adjacent biotopes (Debinski *et al*., 2001). Habitat complementation is another explanation offered for higher butterfly diversity in landscapes with a small-scale mosaic (Jeanneret *et al*., 1999; Weibull *et al*., 2000; Appelqvist *et al*., 2001; Debinski *et al*., 2001). Many butterfly species need different biotopes to complete their life-cycles or might need even different biotopes within one life-cycle.

The habitat variables, that were significantly correlated with the same axis of the DCA as species numbers (TREE, FLOWER and HEIGHT) have also been shown to affect species numbers in other studies (Munguira & Thomas, 1992; Holl, 1995; Lörtscher *et al*., 1995; Dover, 1996; Dover, 1997; Gerell, 1997; Steffan-Dewenter & Tscharntke, 1997; Dover *et al*., 2000; Clausen *et al*., 2001; Söderström *et al*., 2001). This study emphasises once more the importance of flower abundance for butterflies. Individual numbers were positively correlated with the same axis as BUSH and negatively with NUTRIENT. The positive effect of the presence of bushes can be explained by their sheltering effect (Dover *et al*., 1997; Dover & Sparks, 2000), while high nutrient levels (caused by artificial fertilising or intensive grazing) lead to a reduction in flower abundance, which in turn affects butterfly numbers (Oostermeijer & van Swaay, 1998).

The influence of landscape structure on the movement of two grassland butterflies (*Papers II* and *IV*)

Butterfly movement in a landscape with a high amount of habitat and little habitat fragmentation (Paper II)

Butterfly movement has predominantly been studied in either landscapes with very fragmented habitat or with more continuous habitat in small study areas. Both types of studies often concluded that butterfly movement is limited. However, Shreeve (1995) pointed out that these results might be caused by the butterfly's reluctance to cross an unfavourable matrix rather than a lack of dispersal ability. Recently Fahrig (2001) has discussed this issue and criticised the approach of many metapopulation studies in using the term dispersal ability as this would "determine the probability of colonisation, and is considered to be a species trait". Fahrig (2001) argues that a species with good dispersal ability can be a good disperser in its optimal habitat, but a bad one in a fragmented habitat.

To study butterfly movement in a less fragmented landscape, but in a comparatively large area seemed therefore to be an appropriate approach to see whether movement would still be evaluated as rather limited. Two grassland species were chosen to demonstrate possible specific differences in butterfly movement. Patch area and flower density were selected as factors possibly influencing movement. The results (*Paper II*) of studying movement of the meadow brown and the scarce copper by mark-release-recapture experiments in the study area with a high amount of habitat (area B) showed that:

- butterfly movement was evaluated as less limited in this study compared with other studies regarding movement frequency (*Maniola jurtina*) and mean movement distances (*Lycaena virgaureae*),
- there were differences between the two species regarding movement frequency, but not movement distances,
- flower density (adult resource density) could be related to numbers and fractions of residents, emigrants and immigrants, while patch area and larval food plant abundance could not,
- the size of the study area in which mark-release-recapture studies are carried out influences the recorded movement parameters.

Compared to other mark-release-recapture studies (Table 3, *Paper II*) mean movement distances were not higher for the meadow brown than reported in other studies, but were for the scarce copper. The percentage of recaptures taking place at a different patch to before were much higher in this study compared to those of Dover *et al*. (1992), who worked in a landscape with a low percentage of habitat where only 9% of recaptures were observed at a different patch. However, the comparison of results of different mark-release-recapture studies is difficult due to different methods used (for example sampling intensity). Therefore, such comparisons are rarely made, a factor pointed out by Wahlberg *et al*. (2002), who compared different movement studies of five fritillary butterflies. In the case of this thesis, it became apparent that the size of the study area influences the parameter *mean distance* that was used to evaluate species-specific movement ability (*Paper III*).

The distances moved between recaptures were not significantly different for the two species studied (meadow brown n=190, mean 322±21 m, scarce copper n=104, mean 272m±24 m; Mann-Whitney z=1.6, p>0.05, see also Table 2), which one might have expected from previous studies (Fjellstad, 1998) or from the different life history features of the two species. Movement frequencies, however, were significantly different (χ^2=9.59, p<0.01).

Of the two factors investigated patch area and flower density, only flower density was correlated with the number or fractions of residents, emigrants or immigrants (Table 2, *Paper II*). Flower density has previously been shown to influence residency of butterflies (Kuussaari *et al*., 1996; Brommer & Fred, 1999; Matter & Roland, 2002).

Table 2. *Movement parameters obtained from the mark-release-recapture experiments for Maniola jurtina and Lycaena virgaureae in study area B*

Species	*Maniola jurtina*			*Lycaena virgaureae*		
Sex	m	f	m+f	m	f	m+f
Number marked	800	443	1243	530	116	646
Recapture events	220	134	354	241	13	254
Recapture rate (% of marked indiv. recaptured)	22	26	24	33	11	29
Mean distance (metres) between recaptures ± SE	326 ± 26	319 ± 34	323± 21	275 ± 25	220 ± 91	271 ± 24
Mean distance (metres) between first and last recapture ± SE	369 ± 33	343 ± 36	359 ± 24	317±30	220 ± 91	312 ± 29
Maximum distance (metres) covered by an individual	2100	1110	2100	1460	660	1460
Movement frequency (% of recaptures caught on a different patch to previous capture)	55	52	54	41	54	41

m=males, f=females

The comparison of butterfly movement in two landscapes with different amounts of habitat and different degrees of habitat fragmentation (Paper IV)

One of the main hypotheses of this thesis was that the amount of habitat and spatial arrangement of habitat patches have an influence on butterfly movement. The influence of the spatial arrangement of patches on butterfly movement has been observed in many experimental studies and the expected influences have also been addressed with theoretical approaches. Most experimental butterfly studies have worked in one study area that covers a variation in patch isolation, while for other species groups there are studies where movement has been studied in different areas with different amounts of habitat (*e.g.* Andrén, 1994). The only studies I know of that study butterfly movement of the same species in relation to the landscape pattern in different study areas are Ouin (2000) and Mennechez *et al*. (*in press*). Ouin (2000) has studied the meadow brown in landscapes with varying amounts of habitat and found that mobility measures differed significantly among landscapes. However, the differences could also have been influenced by differences in the size of the study areas. Mennechez *et al*. (*in press*) show that fragmentation affected dispersal rates of the bog fritillary negatively. Working in different study areas has the advantage that movement can be compared between different landscapes rather than different parts (*e.g.* more or less isolation, amount of habitat) within one landscape. According to Fahrig (http://www.carleton.ca/lands-ecol/whatisle.html; 4th March 2003) this is the only way to conduct a landscape-scale study that investigates the effect of a larger landscape context. The disadvantages are a series of methodological problems, which will be discussed further on page 32.

The comparison of the results of the two mark-release-recapture experiments (*Paper IV*) in study areas A and B showed that

- movement rate was much lower in the landscape with a low cover of habitat and higher patch isolation (area A) than in the less fragmented landscape with a high amount of habitat (area B),
- mean movement distances were not significantly different between the two study areas,
- the mathematical functions that best fitted the inverse cumulative proportions of individuals moving certain distances differed between the two study areas,
- patch area influenced patch immigration in area A, while in area B it was patch isolation that influenced patch immigration.

In area B, the area with little patch isolation, the percentage of recaptures made on a different patch than the previous one was 36% compared to 10% in area A (χ^2=68.7, p<0.0001). The mean movement distance was higher in area B, but not significantly (A: 323±50 m, n=35, B: 428±27 m, n=127; Mann-Whitney z=-1.5, p=0.13). Mennechez *et al.* (*in press*), on the other hand, found longer moved distances in the study area with higher habitat fragmentation. Maybe most interesting was the result that the mathematical functions best fitting the inverse cumulative proportions of individuals moving certain distances differed between the two study areas. While the data from area A better fitted an inverse power function the data from area B better fitted a negative exponential function (A: inverse power: R^2=0.91, $F_{1,21}$=215.4, p<0.001; negative exponential: R^2=0.73, $F_{1,21}$=57.5, p<0.001; B: negative exponential: R^2=0.90, $F_{1,19}$=178.2, p<0.001; inverse power function: R^2=0.72, $F_{1,19}$=48.3, p<0.001). This result is important because the different functions will predict differently the amount of long distance dispersal. An inverse power function would predict more long distance dispersers than a negative exponential function. In metapopulation models, negative exponential functions have been applied and it has been suggested that they be replaced by inverse power functions for species where suitable (Hill *et al.*, 1996). However, the results of this study indicated that the type of function is not only species dependent, but also landscape dependent.

As described in the introduction, several factors have been shown to influence patch immigration and emigration. In this study it was shown that factors could vary between landscapes for the same species. Patch area was negatively correlated with the immigration fraction in area B (Spearman rank: –0.70, p<0.001, Table 3 in *Paper IV*), but not correlated in area A. A negative correlation between immigration rate and patch area has also been found by Sutcliffe *et al.* (1997), but Wahlberg *et al.* (2002) found on the contrary that immigration rates were higher on large patches. Both results are plausible, since large patches might just by chance be more often detected by immigrants, which would result in higher immigration rates. In this study, however, small patches had often only a few residents; thus only one or two immigrants resulted in very high immigration rates.

The influence of patch area on immigration was found to be different in *Paper II* than in *Paper IV* for the same study area (B) and species (*Maniola jurtina*). While in *Paper II* no correlation between patch area and immigration fraction could be found, a significant negative correlation was found in *Paper IV*. The differences can be explained by the fact that in *Paper II* patches belonging to the same grassland units were also considered, while for *Paper IV* these were clustered (see also Methods, mark-release-recapture experiments). That means that factors influencing emigration and immigration are also dependent on the scale at which they are investigated. Distance to the nearest patch was negatively correlated with the immigration fraction in area A (Spearman rank: -0.77, $p<0.002$), but not in area B. This result confirms the findings of other studies, that distance between patches is negatively correlated with exchange of individuals between patches (Hill *et al*., 1996; Sutcliffe *et al*., 1997; Fjellstad, 1998).

The comparative study of movement of the same species in two different landscapes involves a series of methodological problems, which are discussed in detail in *Paper IV*. The problems concern among others the number of replications and working in two different years. Since these types of landscape studies involving mark-release-recapture experiments are labour intensive, the number of study areas (two, one representative of each landscape type) is not to be seen as an optimum, but as a result of constraints – especially given the limits of a PhD thesis. The problem of replication in landscape studies has recently been discussed by Oksanen (2001) and Wu & Hobbs (2002). Oksanen (2001) concluded that replication in landscape studies is not an absolute necessity.

Comparing results from two different years is problematic, but maybe not more problematic than the approach selected by Mennechez *et al*. (*in press*). These authors chose instead to carry out their mark-release-recapture experiments within the same year, but in two different countries (Belgium and Finland), where the studied butterfly has different emergence times (so the experiments were carried out first in Belgium and afterwards in Finland). Ideally the movement studies should be carried out in the same geographical region, in the same year, under same weather conditions, to be able to exclude temporal and regional variation. A general issue worth further exploration would be the influence of the spatial constraints (spatial arrangement of habitat) on the observed mark-release-recapture results.

The influence of spatial scale on studying butterfly movement (*Paper III*)

By comparing the mark-release-recapture results of the two studied butterfly species *Maniola jurtina* and *Lycaena virgaureae* (*Paper II*) with other mark-release-recapture studies of the same species (Brakefield, 1982a; Douwes, 1975a; Dover *et al*., 1992; Lörtscher *et al*., 1997; Ouin, 2000) it became obvious that the movement parameters derived from the mark-release-recapture data differed greatly. In particular, the recorded mean movement distance, which is often calculated in this context and was earlier also used to evaluate the dispersal ability of a species, varied between the different studies and for the same species. It could be shown that the size of the study area had an overriding impact on the mean movement distance (Fig. 6).

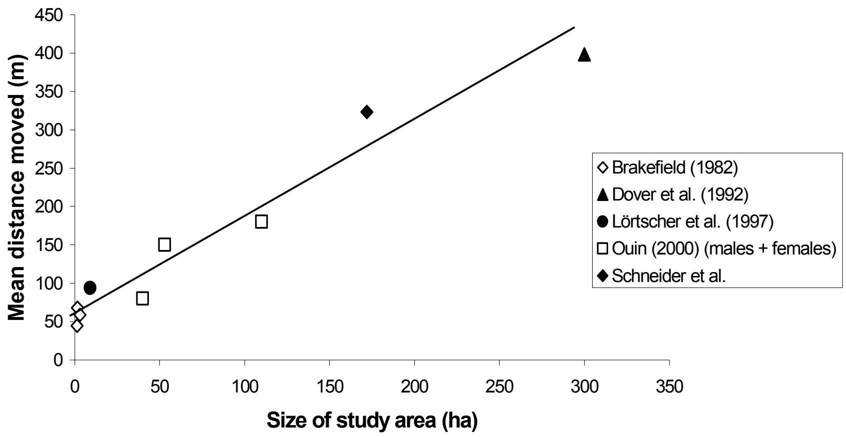

Fig. 6. Recorded mean distance moved by the meadow brown (males) in relation to the size of the study area (R^2 = 0.95, $F_{1,7}$ = 138.0, p < 0.001); from *Paper III*.

An enlarged literature search revealed that this is true not only when comparing different data sets for the same species, but also when comparing several species together (see Table 2 in *Paper III*). Most of the variation in mean distance moved between the species could be explained by the size of the area in which they were studied (R^2=0.81, $F_{1,25}$=106.6, p<0.001, without the *Maniola* studies). However, if more studies of the same species at different study area sizes had been available, differences between species would be expected. It is known from previous studies that mark-release-recapture data are biased towards shorter movements because these are more detectable by sheer chance (*e.g.* Koenig *et al.*, 1996). Wilson & Thomas (2002) demonstrated the underestimation of long distance dispersal in mark-release-recapture studies analysing movement data of the brown argus by taking into account detectability.

The mark-release-recapture data obtained from study area A (*Paper IV*) do not fit in this general trend. In study area A, with a size of about 1200 ha, the meadow brown had an observed mean movement distance which was slightly lower than in study area B (172 ha). A likely explanation for this is that the distance between habitat patches was so large that the patches were beyond the dispersal ability of the species – at least over unfavourable matrix. A positive correlation between the size of the study area and observed mean movement distances is thus only to be expected where the species is able to move between large parts of the study area.

How can the results of this thesis be applied in a planning context? (*Paper V*)

A need has been expressed for integration of landscape ecological data within spatial planning (Forman & Collinge, 1997; Opdam *et al*., 2002). *Paper V* of this thesis gives an example of how the ecological data presented in *Papers I* and *II* could be applied in a planning or management context. One of the major threats to butterfly diversity is abandonment and subsequent afforestation in landscapes like study area B. Therefore different alternatives (=scenarios) of this type of land-use change were created and the effects on butterfly diversity and butterfly dispersal were estimated. The focus of this study was rather on the comparison between the three scenarios than creating the scenarios them selves. Thus no detailed analysis of socio-economic conditions was carried out; instead, the scenarios were based on rough assumptions about possible future landscape changes. In addition, a land-use map of 1939 was used to identify trends of abandonment that have taken place in the last 60 years. The land-use maps of 1939 and 1999 and the three scenarios can be seen in Figs. 2a-2e in *Paper V*. Figs 7 and 8 illustrate landscape changes in one part of Bråbygden (Bjälebo) between the 1972 and 2001.

In this study two different approaches were used separately: One was based on species distribution, the other was a least-cost analysis (Sutcliffe *et al*. 2003). The results showed that different land-use scenarios, which varied in the grade and spatial distribution of abandonment and subsequent afforestation, affected butterfly diversity differently. If full-time farming were to cease and part-time farming to be reduced, most grassland valuable for butterflies would be expected to vanish (scenario 1, see Fig. 9). Even in the case of abandonment taking place to a lesser extent, the areas with the highest butterfly biodiversity would be most threatened if abandonment continued to progress from the periphery of the settlement (scenario 2). It was assumed that only a directed management strategy could prevent the most valuable areas from abandonment (scenario 3). While this estimation of the effects of abandonment can give a rough idea about possible effects on butterflies due to habitat loss, it does not include possible fragmentation effects.

The results of the least-cost analysis (Table 3) made evident the increase in travel costs for a grassland butterfly in the case of further abandonment and afforestation compared to 1999. Travel costs for a butterfly between habitat patches (=patches of semi-natural grasslands) increased multifold in all scenarios. This was true not only when all habitat patches were taken into account, but also considering only the 10 nearest (in cost terms). This means that butterflies will have a several times higher travel cost even if they use only a small habitat network of 11 patches.

Foto: Mårten Aronsson

Fig. 7. View southwards from Bjälebo, Bråbygden (a) in the year 1972, (b) in the year 2001.

Foto: Mårten Aronsson

Fig. 8. South of Bjälebo, Bråbygden (a) in the year 1972, (b) in the year 2001. The meadows have been abandoned.

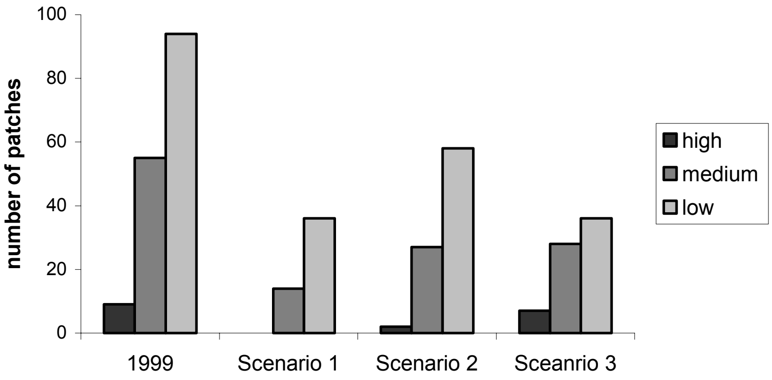

Fig 9. Number of patches with high, medium and low diversity (agricultural areas only) in the different scenarios (from *Paper V*).

Table 3. *Results of the least-cost analysis. Average means of least-costs between each habitat patch to all other habitat patches in 1999, scenario 1, 2, and 3 and the average mean least-costs between each patch and the 10 ecological nearest (least-cost) patches (from Paper V)*

	Average mean least-cost between each habitat patch to all others	Factor increase (compared to 1999)	Average mean least-cost between each habitat patch and the 10 nearest (in cost terms)	Factor increase (compared to 1999)
1999	13770		2786	
Scenario 1	49379	3.6	24397	8.8
Scenario 2	31620	2.3	8484	3.0
Scenario 3	33254	2.4	9298	3.3

Interestingly travel costs in scenario 3 were slightly higher than in scenario 2, even if in scenario 3 certain patches were managed as grasslands for the purpose of keeping movement paths open. This means that it might be difficult to find a satisfactory solution regarding which grasslands to prevent from abandonment considering species diversity and dispersal at the same time – at least if habitat area is reduced by more than 50 percent.

The need to be able to predict the effect of landscape changes on species diversity has been stated by several authors (for example Burel & Baudry, 1995; Burel *et al.*, 1998; Opdam *et al.*, 2002; Schmiegelow & Mönkkönen, 2002). The approaches used so far are varying and range from single species studies using for example a metapopulation model (Hanski *et al.*, 1994; Sawchik *et al.*, 2002; Baguette & Schtickzelle, *in press*) to considering several species (Swetnam *et al.*, 1998; Pearson *et al.*, 1999; Schmiegelow & Mönkkönen, 2002) and simulation approaches (Fahrig, 2001; King & With, 2002). The methods used in this field seem to be under development and both more field and simulation studies have been requested.

Conclusions and guidelines

The major conclusions of this thesis are that:

- landscape structure and habitat factors influence butterfly diversity in grasslands,
- landscape structure influences butterfly dispersal between grasslands and thus dispersal parameters can vary between landscapes for the same species,
- the scale chosen for dispersal studies has a major impact on the results of species' dispersal ability,
- it is necessary to take landscape factors into account for a successful species conservation,
- planning for land-use changes in the agricultural landscape can reduce the negative effects on butterfly diversity.

For semi-natural grassland in Sweden the following guidelines and measurements are suggested for butterfly conservation. They are based on an integration of the results of this thesis with existing literature.

At the site level

Pastures

Very extensive grazing seems to be one of the most suitable methods of grassland management for many grasslands areas in Sweden. Extensive grazing still guarantees a high numbers of flowering plants (adult nectar source) and might also allow for patches with high vegetation (needed by some species). If the establishment of trees and shrubs becomes a problem, manual clearing at larger intervals could be a better solution than constant high grazing pressure, which is unfavourable for many species. The best situation is a within-grassland variation where all different vegetation heights exist next to each other. In Sweden it is often difficult to have enough grazing animal available to graze all semi-natural pastures worth conserving in a region. Rotational grazing over years could be a solution that I would expect to favour butterfly species richness. Grasslands would be grazed one year and not be grazed for the following 1-3 years.

From a floral perspective, high grazing pressure is often recommended. It might be better to decide individually for each grassland if high grazing pressure is really needed to preserve a certain plant community present. A variation in grazing intensity between grasslands is absolutely preferable to earlier recommendations of a generally targeted short grass sword.

Meadows

Meadows are very rare in Sweden and it is of course important to try to preserve all meadows remaining (and also not convert them to pasture). At the end of July meadows are the largest, and sometimes only, flower source left (due to continuous cutting of road verges). In this study, the meadows in both study areas were cut at the end of July. Cutting at least two weeks later would be preferable keeping nectar sources a little longer than the peak of butterfly abundance. To increase the nectar source in intensively used agricultural areas, a solution could be to extensify the grass production on leys by going over to permanent grasslands, lower fertiliser application and fewer cuttings. Over time, this management could produce more flower-rich grasslands, but would still permit fairly rational management (cutting with the help of large machinery).

Margins

Extensive management of field margins and road verges would favour butterflies by increasing flower abundance. Wide margins, with few cuttings a year and little or preferably no influence of fertilizer/pesticides would increase resources for butterflies.

The role of bushes and trees

The presence of bushes and trees seems to be favourable for butterfly diversity by creating shelter and offering other resources. Half-open pastures were the most species-rich areas investigated in this study, since there were habitats both for grassland and woodland butterflies. In this thesis, it was shown for example that grasslands with a certain amount of bushes had more butterfly individuals. Probably not all butterfly species prefer half-open conditions, but this type of grassland is very valuable from a butterfly conservation perspective and should be present in a pastoral landscape. This type of habitat is even more important since it is probably drastically declining in forests managed for timber production. The establishment of bushes is favourable to a certain extent. For butterflies, large open grasslands without any bushes are less attractive due to the lack of shelter.

At the landscape level

Adjacent land-use

Grasslands with adjacent woodlands are more species-rich than grasslands that are surrounded by arable. This is a factor that should be considered in cases where landscape changes are taking place. It would therefore always be preferable to keep an existing border line between woodland and grassland instead of separating those two land uses from each other. In cases where large grassland can not be kept open, the best solution might be to let secondary succession take place in one part of the grassland and to keep the rest open, thus creating an ecotone between woodland and grassland.

Landscape pattern

A fine-grained landscape pattern supports more butterfly species than a coarse-grained landscape. Since landscape pattern is often developed over long periods of time, this is not something that can be easily influenced. It has long been known that the enlargement of fields and the removal of margin vegetation has a negative effect on many species. There are two conclusions that can be drawn from this study:

- a fine-grained mosaic landscape as in Bråbygden supports high butterfly species richness and is therefore valuable as a whole landscape; changes in the landscape pattern are expected to affect the diversity,
- where possible the reintroduction of a fine-grained landscape pattern should be promoted.

Spatial arrangement of grasslands

As shown, some butterfly species can move freely within comparatively large areas if the conditions are favourable (large amount of habitat, permeable matrix). It is therefore important to conserve areas with less fragmented grassland as whole landscapes. In areas with more than 50% habitat, the spatial configuration of habitat seems to be less important for movement. A reduction in the total amount of habitat or a change in matrix quality reduces dispersal rates and thus can lead to extinction, especially where habitat patches are small. If land-use changes that lead to a reduction in dispersal ability cannot be prevented, careful planning can mitigate the negative effects. In such cases it is important to a) preserve the most valuable patches, b) maintain movement possibilities *e.g.* by keeping corridors, c) take into account dispersal distances of the species concerned, and d) manage other biotopes valuable to butterflies (*e.g.* margins) optimally.

Concerning recommended distances between grasslands, it is important to consider the matrix. Woodland acts as a strong barrier for many butterfly species and therefore it cannot be expected that butterflies will cross woodlands even for short distances. The meadow brown butterfly can cross several hundred metres of arable field and can thus be expected to disperse even in highly fragmented landscapes with a distance of 500-800 meters between grasslands (but note that dispersal rates here are much reduced compared to a non-fragmented landscape). The scarce copper frequently moves distances up to 500 m in an open landscape with a high amount of habitat. On the other hand, it seems not to be able to cope with either the landscape or habitat conditions or both as represented by study area A.

References

Agger, P. 1998. Dispersal ecological considerations in rural planning. *Roskilde University - Landscape Ecological Papers 11*, 11-27.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos 71*, 355-366.

Antrop, M. 2001. The language of landscape ecologists and planners - A comparative content analysis of concepts used in landscape ecology. *Landscape and Urban Planning 55*, 163-173.

Appelqvist, T., Gimdal, R. & Bengtson, O. 2001. Insekter och mosaiklandskap. *Entomologisk Tidskrift 122*, 81-97.

Aronsson, M. 1979. Det relikta odlingslandskapet i mellersta Kalmar län. *Svensk Botanisk Tidskrift* 73, 97-114.

Asher, J., Warren, M. & Fox, R. 2001. *The millennium atlas of butterflies in Britain*. Oxford University Press. Oxford. 433 pp.

Baguette, M. & Nève, G. 1994. Adult movements between populations in the specialist butterfly *Proclossiana eunomia* (Lepidoptera, Nymphalidae). *Ecological Entomology 19*, 1-5.

Baguette, M. & Schtickzelle, N. *in press*. Local population dynamics are important to the conservation of metapopulations in highly fragmented landscapes. *Journal of Applied Ecology*.

Baguette, M., Petit, S. & Quéva, F. 2000. Population spatial structure and migration of three butterfly species within the same habitat network: consequences for conservation. *Journal of Applied Ecology 37*, 100-108.

Baguette, M., Vansteenwegen, C., Convi, I. & Nève, G. 1998. Sex-biased density-dependent migration in a metapopulation of the butterfly *Proclossiana eunomia*. *Acta Oecologica 19*, 17-24.

Bak, A., Oorthuijsen, W. & Meijer, M. 1998. Vlindervriendelijk wegbermbeheer langs de A58 in Zeeland. *De Levande Natuur 99*, 261-267.

Baker, R.R. 1984. The dilemma: When and How to Go or Stay. In: *Symposia of the Royal Entomological Society of London No. 11 (The Biology of Butterflies)*. Academic Press. London. pp. 279-296.

Balmer, O. 1999. Die Schmetterlingsfauna an mageren Standorten des Jura in verschiedenen Stadien der Verbrachung. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft 72*, 303-314.

Balmer, O. & Erhardt, A. 2000. Consequences of succession on extensively grazed grasslands for Central European butterfly communities: rethinking conservation practices. *Conservation Biology 14*, 746-757.

Beinlich, B. 1995. Veränderung der Wirbellosen-Zönosen auf Kalkmagerrasen im Verlaufe der Sukzession. In: Schutz und Entwicklung der Kalkmagerrasen der Schwäbischen Alb (Ed. B. Beinlich). *Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg 83*. pp. 283-310.

Bengtson, S.-A. 1978. Spot-distribution in *Maniola jurtina* (Lepidoptera) on small islands in southern Sweden. *Holarctic Ecology 1*, 54-61.

Bengtsson-Lindsjö, S., Ihse, M. & Olsson, E.G.A. 1991. Landscape patterns and grassland plant species diversity in the 20th century. In: *The cultural landscape during 6000 years in southern Sweden*, *Ecological Bulletins vol. 41* (ed. B. E. Berglund). Munksgaard International Booksellers and Publishers. Copenhagen.

Berglind, S.-Å. 1990. Ängsfjärilar på väg att ersättas av granplantor. *Värmlandsnatur 4*, 12-17.

Bergman, K.-O. & Landin, J. 2001. Distribution of occupied and vacant sites and migration of *Lopinga achine* (Nymphalidae: Satyrinae) in a fragmented landscape. *Biological Conservation 102*, 183-190.

Bergman, K.-O. & Landin, J. 2002. Population structure and movements of a threatened butterfly (*Lopinga achine*) in a fragmented landscape in Sweden. *Biological Conservation 108*, 361-369.

Bernes, C. 1994. *Biologisk mångfald i Sverige*. Monitor. Naturvårdsverket Förlag. Solna. pp. 121-165.

Bowman, J., Cappuccino, N. & Fahrig, L. 2002. Patch size and population density: the effect of immigration behaviour. *Conservation Ecology 6*, 9 pp.

Brakefield, P.M. 1982a. Ecological studies on the butterfly *Maniola jurtina* in Britain. I. Adult behaviour, microdistribution and dispersal. *Journal of Animal Ecology 51*, 713-726.

Brakefield, P.M. 1982b. Ecological studies on the butterfly *Maniola jurtina* in Britain. II. Population dynamics: the present position. *Journal of Animal Ecology 51*, 727-738.

Brommer, J.E. & Fred, M.S. 1999. Movement of the Apollo butterfly *Parnassius apollo* related to host plant and nectar plant patches. *Ecological Entomology 24*, 125-131.

Brunzel, S. 2002. Experimental density-related emigration in the Cranberry Fritillary *Boloria aquilonaris*. *Journal of Insect Behaviour 15*, 739-750.

Burel, F. & Baudry, J. 1995. Species biodiversity in changing agricultural landscapes: A case study in the Pays d'Auge, France. *Agriculture, Ecosystems and Environments 55*, 193-200.

Burel, F., Baudry, J., Butet, A., Clergeau, P., Delettre, Y., Le Coeur, D., Dubs, F., Morvan, N., Paillat, G., Petit, S., Thenail, C., Brunel, E. & Lefeuvre, J.-C. 1998. Comparative biodiversity along a gradient of agricultural landscapes. *Acta Oecologica 19*, 47-60.

BUTT (Butterflies under Threat Team) 1986. The management of chalk grassland for butterflies. *Focus on Nature Conservation 17*. Nature Conservation Council. Peterborough.
Cassel, A. 2002. Conservation Biology and Genetic Structure of Fringe Populations of the Scarce Heath Butterfly in Sweden. PhD Thesis. *Comprehensive Summaries of the Faculty of Technology and Sciences 749*. *Acta Universitatis Upsaliensis* Uppsala University. Uppsala.
Clausen, H.D., Holbeck, B.H. & Reddersen, J. 1998. Butterflies on organic farmland: association to uncropped small biotopes and their nectar sources (Lepidoptera: Papilionidea and Hesperioidea). *Entomolgiske Meddelelser 66*, 33-44.
Clausen, H.D., Holbeck, B.H. & Reddersen J. 2001. Factors influencing abundance of butterflies and burnet moths in the uncultivated habitats of an organic farm in Denmark. *Biological Conservation 98*, 167-178.
Collinge, S.K., Prudic, K.L. & Oliver, J.C. 2003. Effects of local habitat characteristics and landscape context on grassland butterfly diversity. *Conservation Biology 17*, 178-187.
Conradt, L., Bodsworth, E.J., Roper, T.J. & Thomas, C.D. 2000. Non-random dispersal in the butterfly *Maniola jurtina*: implications for metapopulation models. *Proceedings of the Royal Society London Biological Sciences 267*, 1505-1510.
Conradt, L., Roper, T.J. & Thomas, C.D. 2001. Dispersal behaviour of individuals in metapopulations of two British butterflies. *Oikos 95*, 416-424.
de Snoo, G.R., van der Poll, R.J. & Bertels, J. 1998. Butterflies in sprayed and unsprayed field margins. *Journal of Applied Entomology 122*, 157-161.
Debinski, D.M., Ray, C. & Saveraid, E.H. 2001. Species diversity and the scale of the landscape mosaic: do scales of movement and patch size affect diversity? *Biological Conservation 98*, 179-190.
Dennis, R.L.H. & Eales, H.T. 1999. Probability of site occupancy in the large heath butterfly *Coenonympha tullia* determined from geographical and ecological data. *Biological Conservation 87*, 295-301.
Dolek, M. & Geyer, A. 1997. Influence of management on butterflies of rare grassland ecosystems in Germany. *Journal of Insect Conservation 1*, 125-130.
Douwes, P. 1970. Size of, gain to and loss from a population of adult *Heodes virgaureae* L. (Lep,. Lycaenidae). *Entomolgica Scandinavica 1*, 263-281.
Douwes, P. 1975a. Distribution of a population of the butterfly *Heodes virgaureae*. *Oikos 26*, 332-340.
Douwes, P. 1975b. Territorial behaviour in *Heodes virgaureae* L. (Lep., Lycaenidae) with particular reference to visual stimuli. *Norsk Entomologisk Tidsskrift 22*, 143-153.
Douwes, P. 1976a. Activity in *Heodes virgaureae* (Lep., Lycaenidae) in relation to air, temperature, solar radiation and time of day. *Oecologia 22*, 287-298.
Douwes, P. 1976b. Mating behaviour in *Heodes virgaureae* with particular reference to the stimuli from the female (Lepidoptera: Lycaenidae). *Entomologica Germanica 2*, 232-241.
Dover, J.W. 1996. Factors affecting the distribution of satyrid butterflies on arable farmland. *Journal of Applied Ecology 33*, 723-734.
Dover, J.W. 1997 Conservation headlands: effects on butterfly distribution and behaviour. *Agriculture, Ecosystems and Environment 63*, 31-49.
Dover, J.W. & Fry, G.L.A. 2001. Experimental simulation of some visual and physical components of a hedge and the effects on butterfly behaviour in an agricultural landscape. *Entomologia Experimentalis et Applicata 100*, 221-233.
Dover, J.W. & Sparks, T. 2000. A review of the ecology of butterflies in British hedgerows. *Journal of Environmental Management 60*, 51-63.
Dover, J.W., Clarke, S.A. & Rew, L. 1992. Habitats and movement patterns of satyrid butterflies (Lepidoptera: Satyridae) on arable farmland. *Entomologist's Gazette 43*, 29-44.
Dover, J.W., Sparks, T., Clarke, S., Gobbett, K. & Glossop, S. 2000. Linear features and butterflies: the importance of green lanes. *Agriculture, Ecosystems and Environment 80*, 227-242.
Dover, J.W., Sparks, T.H. & Greatorex-Davies, J.N. 1997. The importance of shelter for butterflies in open landscpapes. *Journal of Insect Conservation 1*, 89-97.

Dramstad, W.E., Fry, G., Fjellstad, W.J., Skar, B., Helliksen, W., Sollund, M.-L. B., Tveit, M.S., Geelmuyden, A.K. & Framstad, E. 2001. Integrating landscape-based values - Norwegian monitoring of agricultural landscapes. *Landscape and Urban Planning 57*, 257-268.

Ebenhard, T. 1995. Våtmarksfjärilar i ett fragmenterat landskap - små populationers överlevnad. *Entomologisk Tidskrift 116*, 73-82.

Ebert, G. 1993. *Die Schmetterlinge Baden-Württembergs, Vol 1 & 2*. Eugen Ulmer. Stuttgart.

Ehnström, B., Gärdenfors, U. & Lindlöw, Å. 1993. *Rödlistade evertebrater i Sverige 1993*. Databanken för hotade arter. Uppsala.

Ekstam, U., Aronsson, M. & Forshed, N. 1988. *Ängar*. LTsförlag. Stockholm. 209 pp.

Emmet, A.M. & Heath, J. 1990. *The Butterflies of Great Britain and Ireland*. Vol. 7 part 1. Harley Books. Colchester. 370 pp.

Erhardt, A. 1985. Diurnal Lepidoptera: Sensitive indicators of cultivated and abandoned grassland. *Journal of Applied Ecology 22*, 849-861.

Eriksson, Å., Eriksson, O. & Berglund, H. 1995. Species abundance patterns of plants in Swedish semi-natural pastures. *Ecography 18*, 310-317.

ESRI (Environmental Systems Research Institute) 2000. *ArcView*. Environmental Systems Research Institute Inc. Redlands, Carlifornia.

Fahrig, L. 2001. How much habitat is enough? *Biological Conservation 100*, 65-74.

Fahrig, L. 2003. When is a landscape perspective important. (An essay). http://www.carleton.ca/lands-ecol/whatisle.html#Perspective - 4th March 2003.

Feber, R.E., Firbank, L.G., Johnson, P.J. & Macdonald, D.W. 1997. The effects of organic farming on pest and non-pest butterfly abundance. *Agriculture, Ecosystems and Environment 64*, 133-139.

Feber, R.E., Smith, H. & MacDonald, D.W. 1994. The effects of field margin restoration on the meadow brown butterfly (*Maniola jurtina*). In: *BCPC Monograph No 58 (Field Margins: Integrating Agriculture and Conservation*). pp. 295-300.

Feber, R.E., Smith, H. & Macdonald, D.W. 1996. The effects on butterfly abundance of the management of uncropped edges of arable fields. *Journal of Applied Ecology 33*, 1191-1205.

Fischer, K. 1998. Population structure, mobility and habitat selection of the butterfly *Lycaena hippothoe* (Lycaenidae: Lycaenini) in western Germany. *Nota lepidopterologica 21*, 14-30.

Fischer, L., Beinlich, B. & Plachter, H. 1999. Population structure, mobility and habitat preferences of the violet copper *Lycaena helle* (Lepidoptera: Lycaenidae) in Western Germany: implications for conservation. *Journal of Insect Conservation 3*, 43-52.

Fjellstad, W.J. 1998. *The landscape ecology of butterflies in traditionally managed Norwegian farmland*. PhD Thesis. Department of Biological Sciences. University of Durham. 223 pp.

Fleischman, E., Ray, C., Sjögren-Gulve, P. & Boggs, C. L. 2002. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. *Conservation Biology 16*, 706-716.

Fogelfors, H. 1997. *Naturbetesmarker av ek- och björkhagstyp - vegetationsförändringar vid skiftande betesintensitet och upphörd beteshävd*. Swedish University of Agricultural Sciences, Department of Ecology and Environmental Research. Report 17. 2. ed. Uppsala. 89 pp.

Forman, R.T.T. 1995. *Land mosaics*. Cambridge University press. Cambridge. 632 pp.

Forman, R.T.T. & Collinge, S.K. 1997. Nature conserved in changing landscapes with and without spatial planning. *Landscape and Urban Planning 37*, 129-135.

Forman, R.T.T. & Gordon, M. 1986. *Landscape Ecology*. Wiley and Sons. New York.

Fry, G.L.A. 1996. A landscape perspective of biodiversity; indices, models and planning. In: *The spatial dynamics of biodiversity* (Eds. I.A. Simpson & P. Dennis). IALE (UK). Stirling. pp. 3-13.

Fry, G.L.A. 2001. Multifunctional landscapes - towards transdisciplinary reserach. *Landscape and Urban Planning 57*, 159-168.

Fry, G.L.A. & Dramstad, W. 1998. Dyreliv i åkerlandskapet. *Jordbrukets kulturlandskap; Forvaltning av miljøverdier* (Eds. E. Framstad & I.B. Lid) Universitetsforlaget. Oslo. pp. 106-112.

Fry, G.L.A. & Robson, W.J. 1994. The effects of field margins on butterfly movement. *BCPC Monograph No58 (Field Margins: Integrating Agriculture and Conservation)*, 111-116.

Gärdenfors, U. 2000. *The red list of Swedish species*. ArtDatabanken, SLU & Naturvårdsverket. Uppsala. pp. 185-193.

Gerdehag, P. & Aronsson, M. 1999. *Bygden där vinden vände*. Pandabok. Prisma. Stockholm.

Gerell, R. 1997. Skötseln av vägkanter och dess inverkan på tätheten och artsdiversiteten hos dagfjärilsfaunan i sydöstra Skåne. *Entomologisk Tidskrift 118*, 171-176.

Gilpin, M. & Hanski, I. 1991. Metapopulation Dynamics: Empirical and Theoretical Investigations. *Biological Journal of the Linnean Society 42*.

Glimskär, A. & Svensson, R. 1990. *Vegetationsförändring vid gödsling och ändrad hävd.* Swedish University of Agricultural Sciences, Department of Ecology and Environmental Research. Report 38. Uppsala. 71 pp.

Golley, F.B. & Bellot, J. 1991. Interactions of landscape ecology, planning and design. *Landscape and Urban Planning 21*, 3-11.

Götmark, F., Gunnarsson, B. & Andrén, C. 1998. Biologisk mångfald i kulturlandskap. Naturvårdsverket. Stockholm. 192 pp.

Goulson, D. 1993a. The evolutionary significance of bimodal emergence in the butterfly, *Maniola jurtina* (Lepidoptera: Satyrinae) (L.). *Biological Journal of the Linnean Society* , 127-139.

Goulson, D. 1993b. An experimental evaluation of the function of hindwing spots in the Meadow Brown butterfly, *Maniola jurtina* (Linnaeus) (Lepidoptera: Nymphalidae, Satyrinae). *Entomolgist's Gazette 44*, 167-171.

Gurrea, P., Ferrín, J.M., Martín, J., Pérez, F., Ruiz, M. & Simón, J.C. 2000. Loss of biodiversity due to reafforestation in Central Spain (Lepidoptera Papilionoidea; Coleoptera Curculionidae; Collembola). *Belgian Journal of Entomology 2*, 149-170.

Gustavsson. R. 1995. Faculty research program: The pastoral landscapes - perspectives for landscape planning, landscape management and grazing. Alnarp: Department of Landscape Planning, Swedish University of Agricultural Sciences.

Haddad, N.M. 1999a. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. *Ecological Applications 9*, 612-622.

Haddad, N.M. 1999b. Corridor use predicted from behaviours at habitat boundaries. *The American Naturalist 153*, 215-227.

Hägerhäll, C. 1999. The Experience of Pastoral Landscapes. PhD Thesis. *Acta Universitatis Agriculturae Sueciae 182*. Department of Landscape Planning. Alnarp. Alnarp.

Hammarstedt, O. 1996. Miljöövervakning av och med dagfjärilar. Rapport från Miljöövervakningen i Malmöhus län. *Länet i utveckling 1996:21*. Länsstyrelsen Malmöhus län. Malmö. 30 pp.

Hanski, I. 1994a. Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. *Biological Conservation 68*, 167-180.

Hanski, I. 1994b. Patch-occupancy dynamics in fragmented landscapes. *Tree 9*, 131-135.

Hanski, I., Alho, J. & Moilanen, A. 2000. Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology 81*, 239-251.

Hanski, I., Breuker, C.J., Schöps, K., Setchfield, R. & Nieminen, M. 2002. Population history and life history influence the migration rate of female Glanville fritillary butterflies. *Oikos 98*, 87-97.

Hanski, I., Kuussaari, M. & Nieminen, M. 1994. Metapopulation structure and migration in the butterfly *Melitaea cinxia*. *Ecology 75*, 747-762.

Hanssen, U. 2001. *Faunistisch-ökologische Untersuchungen als Beitrag zur Entwicklung von Naturschutzkonzepten in einer Agrarlandschaft.* Faunistisch-Ökologische Mitteilungen. Zoologisches Institut und Museum der Universität Kiel. Kiel.

Hansson, M. 1991. *Skötsel av naturliga fodermarker: Resultat av femtonåriga fältexperimen i Syd- och Mellansveriget.* Swedish University of Agricultural Sciences, Department of Ecology and Environmental Research. Report 45. Uppsala.

Harrison, S. 1989. Long-distance dispersal and colonization in the bay checkerspot butterfly, *Euphydryas editha bayensis*. *Ecology 70*, 1236-1243.

Harrison, S., Murphy, D.D. & Ehrlich, P.R. 1988. Distribution of the bay checkerspot butterfly, *Euphydryas editha bayensis*: evidence for a metapopulation model. *The American Naturalist 132*, 360-382.

Hawkins, B.A. & Porter, E.E. 2002. Does herbivore diversity depend on plant diversity? The case of California butterflies. *The American Naturalist 161*, 40-49.

Henriksen, H.J. & Kreutzer, I. 1982. *The Butterflies of Scandinavia in Nature*. Skandinavisk Bogforlag. Odense. 215 pp.

Hersperger, A.M. 1994. Landscape ecology and its potential application to planning. *Journal of Planning Literature 9*, 14-29.

Hill, J.K., Thomas, C.D. & Lewis, O.T. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. *Journal of Animal Ecology 65*, 725-735.

Hill, J.K., Thomas, C.D. & Lewis, O.T. 1999. Flight morphology in fragmented populations of a rare British butterfly, *Hesperia comma*. *Biological Conservation 87*, 277-283.

Holl, K.D. 1995. Nectar resources and their influence on butterfly communities on reclaimed coal surface mines. *Restoration Ecology 3*, 76-85.

Ihse, M. 1995. Swedish agricultural landscapes - patterns and changes during the last 50 years, studied by aerial photos. *Landscape and Urban Planning 31*, 21-37.

Ihse, M., Justusson, B. & Skånes, H. 1991. *Slättbygden i Skåne och Halland, ett odlingslandskap i förändring*. Naturvårdsverket. Rapport 3887. Stockholm.

Ingelög, T., Thor, G., Hallingbäck, T., Andersson, R. & Aronsson, M. 1993. *Floravård i jordbrukslandskapet*. SBT-Förlaget. Lund.

Jeanneret, P., Schüpbach, B., Lips, A., Harding, J., Steiger, J., Waldburger, M., Bigler, F. & Fried, P.M. 1999. Biodiversity patterns in cultivated landscapes: modelling and mapping with GIS and multivariate statistics. In: *Heterogeneity in Landscape Ecology: Pattern and Scale - 1999 annual IALE (UK) conference* (Eds. A. Maudsley & J. Marshall), Bristol. 10 pp.

Jenness, J. 2001. *Nearest Feature 3.5* (Program extension for ArcView, ESRI).

Jongman, R.H.G. 1999. *Landscape Ecology in Land Use Planning*. In: Issues in Landscape Ecology (Eds. J.A. Wiens & M.R. Moss). International Association for Landscape Ecology (IALE), Fifth World Congress. Colorado, USA. pp. 112-118.

Jongman, R.H.G. 2002. Homogenisation and fragmentation of the European landscape: ecological consequences and solutions. *Landscape and Urban Planning 58*, 211-221.

Jordbruksverket 2002. Stöd för miljövänligt jordbruk. Jordbruksverket. Jönköping.

Kaaber, S. & Nielsen, O.F. 1988. 30 års forandringer i Ry-engens dagsommerfuglefauna. *Flora og Fauna 94*, 95-110.

Kerr, J.T. 2001. Butterfly species richness patterns in Canada: Energy, heterogeneity, and the potential consequences of climate change. *Conservation Ecology 5*. 10 pp.

King, A.W. & With, K.A. 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behaviour really matter? *Ecological Modelling 147*, 23-39.

Kitahara, M. & Sei, K. 2001. A comparison of the diversity and structure of butterfly communities in semi-natural and human-modified grassland habitats at the foot of Mt. Fuji, central Japan. *Biodiversity and Conservation 10*, 331-351.

Kitahara, M., Sei, K. & Fujii, K. 2000. Patterns in the structure of grassland butterfly communities along a gradient of human disturbance: further analysis based on the generalist/specialist concept. *Population Ecology 42*, 135-144.

Kleyer, M. & Settele, J. 1999. Vom Forschungsergebnis zur integrierten Planung. In: *Die Tagfalter Deutschlands* (Eds. J. Settele, R. Feldmann & R. Reinhardt). Eugen Ulmer. Stuttgart. pp. 214-229.

Koenig, W.D., Van Vuren, D. & Hooge, P.N. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology and Evolution 11*, 514-517.
Konvička, M. & Kuras, T. 1999. Population structure, behaviour and selection of oviposition sites of an endangered butterfly, *Parnassius mnemosyne*, in Litovelské Pomoraví, Czech Republic. *Journal of Insect Conservation 3*, 211-223.
Kruess, A. & Tscharntke, T. 2002. Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conservation Biology 16*, 1570-1580.
Kuussaari, M., Nieminen, M. & Hanski, I. 1996. An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. *Journal of Animal Ecology 65*, 791-801.
Länsstyrelsen Kalmar Län 1989. *Inventering av ängs- och hagmarker. Oskarhamns kommun*. Länsstyrelsen Kalmar Län Informerar 1989:21. Kalmar.
Legendre, P. *The R-package*. (http://www.fas.umontreal.ca/BIOL/Casgrain/en/labo/R/).
Leitão, B.A. & Ahern, J. 2002. Applying landscape ecological concepts and metrics in sustainable landscape planning. *Landscape and Urban Planning 59*, 65-93.
Lennartsson, T. & Svensson, R. 1995. Patterns in the decline of tree species of *Gentianella* (*Gentianaceae*) in Sweden, illustrating the deterioration of semi-natural grasslands. *Symb. Bot. Upsala 31*, 169-184.
Longley, M. & Sotherton, N.W. 1997. Factors determining the effects of pesticides upon butterflies inhabiting arable farmland. *Agriculture Ecosystems & Environment 61*, 1-12.
Lörtscher, M., Erhardt, A. & Zettel, J. 1995. Microdistribution of butterflies in a mosaic-like habitat: The role of nectar sources. *Ecography 18*, 15-26.
Lörtscher, M., Erhardt, A. & Zettel, J. 1997. Local movement patterns of three common grassland butterflies in a traditionally managed landscape. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft **70***, 43-55.
MapInfo Corporation 1998. *MapInfo 4.5*. MapInfo Corporation. Troy. New York.
Martin-Cano, J. & Ferrin, J.M. 1998. Changes in butterfly diversity in three reforested areas in Spain. *Journal of the Lepidopterists' Society 52*, 151-165.
Marttila, O., Saarinen, K. & Jantunen, J. 1999. The national butterfly recording scheme in Finland:first seven year period 1991-1997. *Nota Lepidopterologica 22*, 17-34.
Matter, S.F. & Roland, J. 2002. An experimental examination of the effects of habitat quality on the dispersal and local abundance of the butterfly *Parnassius smintheus*. *Ecological Entomology 27*, 308-316.
Mennechez, G., Schtickzell, N. & Baguette, M. *in press*. Metapopulation dynamics of the bog fritillary butterfly: comparison of demographic parameters and dispersal between a continuous and a highly fragmented landscape. *Landscape Ecology*.
Merckx, T. & Van Dyck, H. 2002. Interrelations among habitat use, behaviour, and flight-related morphology in two cooccuring Satyrine butterflies, *Maniola jurtina* and *Pyronia tithonus*. *Journal of Insect Behaviour 15*, 541-561.
Moilanen, A. & Hanski, I. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology 79*, 2503-2515.
Mousson, L., Nève, G. & Baguette, M. 1999. Metapopulation structure and conservation of the cranberry fritillary *Boloria aquilonaris* (Lepidoptera, Nymphalidae) in Belgium. *Biological Conservation 87*, 285-293.
Munguira, M.L. & Thomas, J.A. 1992. Use of road verges by butterfly and burnet populations, and the effect of roads on adult dispersal and mortality. *Journal of Applied Ecology 29*, 316-329.
Munguira, M.L., Martín, J., Gracía-Barros, E. & Viejo, J.L. 1997. Use of space and resources in Mediterranean population of the butterfly *Euphydryas aurinia*. *Acta Oecologica 18*, 597-612.
Naturvårdsverket 1987. *Inventering av ängs- och hagmark - Handbok*. Naturvårdsverket Informerar. Naturvårdsverket. Solna. 225 pp.
Naturvårdsverket 1997. *Ängs- och hagmarker i Sverige.*. Rapport 4819. Naturvårdsverket Förlag. Stockholm. 144 pp.
Naturvårdsverket & Statistiska Centralbyrån 2000. *Naturmiljön i siffror 2000 (The Natural Environment in Figures 2000)*, 6. ed., Statistiska Centralbyrån & Naturvårdsverket. Stockholm. 296 pp.

Nève, G., Barascud, B., Hughes, R., Aubert, J., Descimon, H., Lebrun, P. & Bagurette, M. 1996. Dispersal, colonization power and metapopulation structure in the vulnerable butterfly *Proclossiana eunomia* (Lepidoptera: Nymphalidae). *Journal of Applied Ecology 33*, 14-22.

Nordström, F. 1955. De Fennoskandiska Dagfjärilarnas Utbredning. *Lunds Universitets Årsskrift 51*, 177 pp.

Oates, M.R. 1995. Butterfly conservation within the management of grassland habitats. In: *Ecology and Conservation of Butterflies* (Ed. A. S. Pullin). Chapman & Hall. London. pp. 98-112.

Oksanen, L. 2001. Logic of experiments in ecology: is pseudoreplication a pseudoissue? *Oikos 94*, 27-38.

Olsson, E.G.A. 1991. Agro-ecosystems from Neolithic time to the present. In: *The cultural landscape during 6000 years in Southern Sweden*, vol. 41 (Ed. B.E. Beglund). Munksgaard International Booksellers and Publishers. Copenhagen. pp. 293-314.

Olsson, G. 1975. Inverkan av betning och annan skötsel på hagmarkers vegetation. *Svensk Botanisk Tidskrift 69*, 393-404.

Oostermeijer, J.G.B. & van Swaay, C.A.M. 1998. The relationship between butterflies and environmental indicator values: a tool for conservation in a changing landscape. *Biological Conservation 86*, 271-280.

Opdam, P., Foppen, R. & Vos, C. 2002. Bridging the gap between ecology and spatial planning in landscape ecology. *Landscape Ecology 16*, 767-779.

Ouin, A. 2000. Hétérogénéité spatiale des payages et processus écologiques. Cas des Rhopalocères dans le bocage Breton. PhD Thesis. Department of Biology, University of Rennes 1. pp. 135.

Ouin, A. & Burel, F. 2002. Influence of herbaceous elements on butterfly diversity in hedgerow agricultural landscapes. *Agriculture, Ecosystems and Environment 93*, 45-53.

Owen, D.F. & Smith, D.A.S. 1990. Interpopulation variation and selective predation in the meadow brown butterfly, *Maniola jurtina* (L.) (Lepidoptera: Satyridae) in Canary Islands. *Biological Journal of the Linnean Society 39*, 251-267.

Pearson, S.M., Turner, M.G. & Drake, J.B. 1999. Landscape change and habitat availability in the Southern Appalachian highlands and olympic peninsula. *Ecological Applications 9*, 1288-1304.

Petit, S., Moilanene, A., Hanski, I. & Baguette, M. 2001. Metapopulation dynamics of the bog fritillary butterfly: movements between habitat patches. *Oikos 92*, 491-500.

Pollard, E. & Eversham, B.C. 1995. Butterfly monitoring 2 - interpreting the changes. In: *Ecology and conservation of butterflies* (Ed. S. A. Pullin). Chapman & Hall. London. pp. 23-36.

Pollard, E. & Yates, T.J. 1993. *Monitoring Butterflies for Ecology and Conservation*. Conservation Biology Series. Chapman and Hall. London. 274 pp.

Pryke, S.R. & Samways, M.J. 2001. Width of grassland linkages for the conservation of butterflies in South African afforested areas. *Biological Conservation 101*, 85-96.

Ray, N. 1999. *Cost Distance Matrix*. Program Script for ArcView (ESRI).

Raymakers, O.F.E. & Skage, O.R. 1996. *Ecological infrastructure in urban environments*. Swedish University of Agricultural Sciences, Department of Landscape Planning. Alnarp, Ultuna. Rapport 96:1.

Ricketts, T.H. 2001. The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist 158*, 87-99.

Roland, J., Keyghobadi, N. & Fownes, S. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. *Ecology 81*, 1642-1653.

Ruckelshaus, M., Hartway, C. & Kareiva, P. 1997. Assessing the data requirements of spatially explicit dispersal models. *Conservation Biology 11*, 1298-1306.

Saarinen, K. 2002a. Butterfly communities in relation to changes in the management of agricultural environments. PhD Thesis, *Dissertations in Biology 13*, University of Joensuu. 29 pp.

Saarinen, K. 2002b. A comparison of butterfly communities along field margins under traditional and intensive management in SE Finland. *Agriculture, Ecosystems and Environment 90*, 59-65.

Saarinen, K. & Jantunen, J. 2002. A comparison of the butterfly fauna of agricultural habitats under different management history in Finnish and Russian Karelia. *Annales Zoolgici Fennici 39*, 173-181.

Sawchik, J., Dufrêne, M., Lebrun, P., Schtickzelle, N. & Baguette, M. 2002. Metapopulation dynamics of the bog fritillary butterfly: modelling the effect of habitat fragmentation. *Acta Oecologica 23*, 287-296.

Schmiegelow, F.K.A. & Mönkkönen, M. 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. *Ecological Application 12*, 375-389.

Schultz, C.B. 1998. Dispersal behaviour and its implications for reserve design in a rare Oregon butterfly. *Conservation Biology 12*, 284-292.

Schultz, C.B. & Crone, E.E. 2001. Edge-mediated dispersal behaviour in a prairie butterfly. *Ecology 82*, 1879-1892.

Selman, P. 1993. Landscape ecology and countryside planning: vision, theory and practice. *Journal of Rural Studies 9*, 1-21.

Shreeve, T.G. 1990. The movement of butterflies. In: *Butterflies of Europe*, vol. 2 (Ed. O. Kudrna). Aula-Verlag. Wiesbaden. pp. 512-532.

Shreeve, T.G. 1992. Monitoring butterfly movements. In: *The Ecology of Butterflies in Britain* (Ed. R.L.H. Dennis). Oxford University Press. Oxford. pp. 120-138.

Shreeve, T.G. 1995. Butterfly mobility. In: *Ecology and Conservation of Butterflies* (Ed. A.S. Pullin). Chapman & Hall. London. pp. 37-45.

Shreeve, T.G., Dennis, R.L.H. & Williams, W.R. 1998. Uniformity of wing spotting of *Maniola jurtina* (L.) in relation to environmental heterogeneity (Lepidoptera: Satyrinae). *Nota Lepidopterologia 18*, 77-92.

Skage, O.R. 1984. Økologisk planlegging i kulturlandskapet - økologisk grunnsyn i praksis. In: *Kulturlandskap och samhällsplanering* (Ed. L. Emmelin). Nordisk Ministerråd. Tapir förlag. pp. 15-49.

Skånes, H. 1996. Landscape Change and Grassland Dynamics. PhD Thesis. *Avhandlingsserie Nr. 8*. The Department of Physical Geography. Stockholm University.

Slotte, H. 2000. Lövtäkt i Sverige och på Åland. PhD Thesis. *Acta Universitatis Agriculturae Sueciae 236*, Department of Landscape Planning, Ultuna. Uppsala.

Smallidge, P.J. & Leopold, D.J. 1997. Vegetation management for the maintenance and conservation of butterfly habitats in temperate human-dominated landscapes. *Landscape and Urban Planning 38*, 259-280.

Söderström, B., Svensson, B., Vessby, K. & Glimskär, A. 2001. Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodiversity and Conservation 10*, 1839-1863.

Sparks, T.H. & Parish, T. 1995. Factors affecting the abundance of butterflies in field boundaries in Swavesey fens, Cambridgeshire, UK. *Biological Conservation 73*, 221-227.

Statistiska Centralbyrån 2002. Jordbruksstatistisk årsbok 2002. Statistiska Centralbyrån. Stockholm.

Statens Offentliga Utredningar (SOU) 1971. Hushållning med mark och vatten. Statens Offentliga Utredningar. Lund.

StatSoft. 1997. *Statistica 5.0.* Tulsa, USA.

Steen, E. 1991. Långvariga landskapsvårdsförsök med olika skötselmetoder. Naturvårdsverket. Rapport 3884. Statens Naturvårdsverk. Solna.

Steffan-Dewenter, I. & Tscharntke, T. 1997. Early succession of butterfly and plant communities on set-aside fields. *Oecologica 109*, 294-302.

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

Sutcliffe, O.L. & Thomas, C.D. 1996. Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings. *Conservation Biology 10*, 1359-1365.

Sutcliffe, O.L., Bakkestuen, V., Fry, G. & Stabbetorp, O.E. 2003. Modelling the benefits of farmland restoration: methodology and application to butterfly movement. *Landscape and Urban Planning 63*, 15-31.

Sutcliffe, O.L., Thomas, C.D. & Peggie, D. 1997. Area-dependent migration by ringlet butterflies generates a mixture of patchy population and metapopulation attributes. *Oecologia 109*, 229-234.

Svensson, I. 1993. *Fjärilkalender*. Lepidoptera-calendar. Kristianstad. 124 pp.

Svensson, R. 1988. Floravård i jordbrukslandskapet. *Svensk Botanisk Tidskrift 82*, 458-465.

Svensson, R. & Ingelög, T. 1990. Floran i dagens och morgondagens jordbrukslandskap. *Svensk Botanisk Tidskrift 84*, 9-19.

Swengel, A.B. 1998. Effects of management on butterfly abundance in tallgrass prairie and pine barrens. *Biological Conservation 83*, 77-89.

Swetnam, R.D., Ragou, P., Firbank, L.G., Hinsley, S.A. & Bellamy, P.E. 1998. Applying ecological models to altered landscapes - Scenario-testing with GIS. *Landscape and Urban Planning 41*, 3-18.

ter Braak, C.J.F. & Smilauer, P. 1998 *CANOCO reference manual and user's guide to Canoco for Windows; software for canonical community ordination (version 4)*. Microcomputer Power. Ithaka, USA

Thomas, C.D. & Jones, T.M. 1993. Partial recovery of a skipper butterfly (*Hesperia comma*) from population refuges: lessons for conservation in a fragmented landscape. *Journal of Animal Ecology 62*, 472-481.

Thomas, C.D., Hill, J.K. & Lewis, O.T. 1998. Evolutionary consequences of habitat fragmentation in a localized butterfly. *Journal of Animal Ecology 67*, 485-497.

Thomas, C.D., Thomas, J.A. & Warren, M.S. 1992. Distribution of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia 92*, 563-567.

Tolman, T. & Lewington, R. 1997. *Butterflies of Britain and Europe*. Collins Field Guide. Harper Collins Publishers. London. 320 pp.

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

Väisänen, R., Kuussaari, M., Nieminen, M. & Somerma, P. 1994. Biology and conservation of *Pseudophilotes baton* in Finland (Lepidoptera, Lycaenidae). *Annales Zoologici Fennici 31*, 145-156

Van Dyck, H. & Matthysen, E. 1999. Habitat fragmentation and insect flight: a changing 'design' in a changing landscape? *Trends in Ecology and Evolution 14*, 172-174.

Van Swaay, C.A.M., Maes, D. & Plate, C. 1997. Monitoring butterflies in the Netherlands and Flanders: The first results. *Journal of Insect Conservation 1*, 81-87.

Wahlberg, N., Klemetti, T., Selonen, V. & Hanski, I. 2002. Metapopulation structure and movements in five species of checkerspot butterflies. *Oecologia 130*, 33-43.

Weibull, A.-C. 2002. Diversity in the agricultural landscape. PhD Thesis. *Acta Universitatis Agriculturae Sueciae 326*. Department of Ecology and Crop Production Science. Uppsala.

Weibull, A.-C., Bengtsson, J. & Nohlgren, E. 2000. Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. *Ecography 23*, 743-750.

Wickman, P.-O., Wiklund, C. & Karlsson, B. 1990. Comparative phenology of four satyrine butterflies inhabiting dry grasslands in Sweden. *Holarctic Ecology 13*, 238-346.

Wilson, R.J. & Thomas, C.D. 2002. Dispersal and the spatial dynamics of butterfly populations. In: *Dispersal Ecology* (Eds. J. Bullock, R. Kenward & R. Hails). Blackwell Science. Oxford. pp. 257-278.

Wood, B.C. & Pullin, A.S. 2002. Persistence of species in a fragmented urban landscape: the importance of dispersal ability and habitat availability for grassland butterflies. *Biodiversity and Conservation 11*, 1451-1468.

Wu, J. & Hobbs, R. 2002. Key issues and research priorities in landscape ecology: An idiosyncratic synthesis. *Landscape Ecology 17*, 355-365.

Acknowledgements

I want to thank my supervisor Olav Skage for the opportunity to do my PhD at the Department of Landscape Planning at Alnarp. I am very thankful for the encouragement and support he has given me during the years. I am very grateful to Gary Fry, my co-supervisor, who has spent a lot of time discussing and commenting on this thesis at all stages. Gary has always been very encouraging, enthusiastic and inspiring. His help and support have been crucial for the completion of this thesis. I also want to thank Roland Gustavsson who gave me the possibility to participate in the Faculty Programme “The Pastoral Landscapes”, which together with the Department of Landscape Planning financed this thesis.

I am grateful to John Dover, who showed me how to mark butterflies and helped both with the setting up of the first mark-release-recapture study and the field work. I thank John also for the good co-operation concerning the second paper of the thesis. I also want to thank the fieldwork assistants Louise Hansare, Carl Dahlberg, Eric Jergil and Jenny Hedh for their help with the mark-release-recapture study. I thank Jan-Erik Englund and Vegar Bakkestuen for all the help with the statistical analysis. Mary McAfee corrected and improved the English of the framework of the thesis and several manuscripts, for which I am very thankful.

I want to thank my friends and colleagues at the department not only for their help and the discussions, but also for creating a very nice working atmosphere. Especially I thank Anna Peterson for the many discussions concerning our work (and beyond…), for working together in Bråbygden, and the many other things she helped me with. Ingrid Sarlöv-Herlin has been of great support, especially at the beginning of the thesis, when I was new in Sweden. I also want to thank Jan Lannér, Anders Larsson, Swantje Oostra and Ann-Margreth Berggren-Bärring for their encouragement, discussions or participation in the progress of my work. I am very thankful to Lars Andersson, who helped me a lot with almost everything that has to do with the computers at the department. He digitized one of the study areas, helped me with all the questions I had about GIS and always took the time to explain programs and all other computer equipment – especially if things did not work as expected. I also want to thank Nina Lindberg for the work she did in digitizing the other study area. Pål Skage has been of great help with the least-cost analysis and I want to thank him for the time he spent both on the analysis and on teaching it to me.

Jan Bengtsson was a great opponent at my final seminar and I want to thank him for the thorough reading of the manuscripts and the many valuable comments he gave. I am also glad to have been in contact with Ann-Christin Weibull and for the possibility to exchange experiences and results while we were both working with PhD theses of a similar topic.

I am pleased that I – due to the participation in the Faculty Programme – got to know the area of Bråbygden. I want to thank Mårten Aronsson for the meetings we had there, where he answered my questions concerning the study area, but also for all other discussions concerning more general issues about landscape preservation. Kajsa and Per-Erik Kennestig have been wonderful landlords of the accommodation provided in Bråbygden. I also want to thank the farmers of the two study areas, who were without exception positive to my work on their land.

My friends Dietlind und Ulrike have been of great support during my work with the PhD and I am grateful for their encouragement and for the nice afternoons we have spent together with our children.

I am thankful to my mother Rosemarie for her encouragement and support, not only by spending parts of her summer holiday looking after my son and allowing me to work in the field, but also for always encouraging me in my work. Christopher, my son, you are the most wonderful excuse that this thesis took its time to complete. You made it possible that some of the papers are actually in print at the time of my disputation! Finally I want to thank you, Svein, not only for the help with the more sophisticated parts of IT-technology, but mostly for making it possible for me to combine research with having a family.