Final Thesis

Importance of surrounding landscape on butterfly communities in Östergötland, Sweden

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1 Abstract
In this study the butterfly fauna at 60 selected pastures was examined in a coniferous dominated landscape. The aim was to investigate how the butterfly communities were affected by the surrounding landscape. For each study site, the amount of meadows and pastures in the landscape within radii of 500, 2000 and 5000 m were calculated. Nine local habitat factors were also recorded. Only the amount of semi-natural pastures at the 5000 m scale could explain a significant part of the variation in butterfly composition but there was no clear relationship between the amount of semi-natural pastures and butterfly diversity. Instead this study showed that the local habitat quality was very important for the butterfly composition at single sites. Flower abundance, sward height and herb composition were the most important local factors. In this study, also rather isolated patches had high butterfly diversity, in contrary to the expectations. It may be explained by the fact the forest provides a diverse matrix with several features suitable for butterflies and a more recent history in decline of semi-natural pastures. In addition, the coniferous landscape generally had more butterfly species per site when compared with a similar study in agricultural landscape. The results have implications in conservation management. For the butterfly fauna in a matrix of coniferous forest, it is efficient to continue to manage even more isolated pastures. Still, it is of importance to take the whole landscape in consideration for long-term persistence of a rich butterfly fauna.

Keywords: Conservation, butterfly diversity, landscape effects, metapopulation, semi-natural pastures

2 Introduction
Habitat loss and fragmentation are major threats to global biodiversity and it is a challenging task for conservationists to determine the amount of habitat needed to preserve a species (Fahrig 2001). Habitat fragmentation reduces the habitat patch size, increases isolation of the habitat patch and contributes to loss of the original habitat which are accompanied by a decline in population size as well as species richness (Andrén 1994; Wilcox & Murphy 1985). Several studies have shown that fragmentation processes have unequal effects on different species. The most endangered are species with limited dispersal abilities, species that have special requirements, species of higher trophic levels, species with low population densities, and species with fluctuating populations (Steffan-Dewenter & Tscharntke 2000). This includes species organized according to metapopulation theories, where the distribution pattern fluctuates due to extinction and

recolonization. In a metapopulation, groups of local populations are connected through dispersal and immigration between the groups (Hanski et al. 1995), and it involves a shifting mosaic of presence and absence in the habitat patches. Patch area and isolation affects the extinction probability and alter the metapopulation dynamics (Hanski 1999). Metapopulations are vulnerable to a threshold of habitat availability below which too much habitat has been lost so that the species will decrease to extinction (Kareiva & Wennergren, 1995). This value is called the extinction threshold and below it the population's persistence is threatened (Fahrig 2001).

The process of decreasing size and increasing isolation of habitats is very evident when looking at semi-natural and natural grasslands, mostly due to intensification of agriculture and changes in land use (Eriksson et al. 1995). This decline strongly affects those species that are dependent on low-nutrient, unfertilised, semi-natural grasslands. For example, it is well documented that many butterfly species in Europe are rapidly declining (Pullin 1995; Maes & van Dyck 2001). One important factor for butterflies is the local habitat quality. Butterflies are known to be sensitive to changes in local habitat quality and they react faster to environmental changes than other organisms, for example plants (Thomas et al. 2004). Butterflies are also relatively easy to record and therefore they can be used as indicators when looking at local habitat status and environmental conditions (Naturvårdsverket 2003).

Since most butterfly species can be considered as living in metapopulations it is expected that many species in a community of butterflies respond to a decrease in area of preferred habitat in the whole landscape (Bergman et al. 2004). Several researchers have shown that patch size alone cannot predict a population's persistence, the landscape surrounding the patch is also important (Thomas et al. 1992; Bergman & Landin 2001). Generally, smaller and/or isolated patches are empty and large and/or non-isolated patches are occupied. Steffan-Dewenter & Tscharntke (2000) emphasize that at landscape level the availability of a certain habitat type as well as the size, shape, isolation and spatial arrangement of habitat fragment may be important. They also found that specialized butterfly species were much more affected by fragment area than generalist species. Moreover, simulation studies by Fahrig (2001) suggested that the best way to reduce the extinction threshold is improvement of the matrix quality, which can be accomplished through maintenance of a diverse landscape structure. All this implies that local species richness is affected by the quality of the landscape.

The aim of this study was to investigate how the butterfly communities are affected by the surrounding landscape. The butterfly fauna at 60 selected grasslands was examined in a matrix mainly consisting of coniferous forest with a gradient from small amount of pastures to a large amount of pastures in the landscape. Besides the landscape factors the importance of several local habitat factors were also analyzed. This could give information that can be used in conservation planning and management of the habitat.

3 Material and methods

3.1 Study area and selection of study sites

The study area is situated in the county of Östergötland in the southeast of Sweden and consisted of semi-natural grassland with deciduous forest, mainly surrounded by a landscape with a large amount of coniferous forest and a small amount of arable fields.

The individual study sites were identified from regional inventory records of meadows and pastures and records of semi-natural grasslands supported by EU-grants at the County Administration Board in Östergötland and selected through assessment in the field. The assessment was conducted in May 2004 to determine if the pastures still were used in a traditional way and regularly grazed. The sites consisted of open to half-open semi-natural grasslands and at least 30 % of the site area had to be unfertilized for including the site in this study. Only pastures with an area of 3-8 ha where included in the study. Larger areas were avoided for practical reasons and smaller areas were avoided since they are expected to be subject to strong species-area relationships (Steffan-Dewenter & Tscharntke 2000). In total 60 sites were selected for butterfly recordings. By using these selection criteria the selected sites could be considered as high quality pastures, which for the habitat type hold a representative flora and fauna. This was to minimize the variation between the sites so that differences due to landscape factors would be more easily detected.

3.2 Butterfly recordings

Butterfly recordings were conducted five times on each site between May and September 2004. The butterflies were recorded during daytime from 9.00 to 16.30 under predominantly sunny conditions with a temperature >17 ºC and with maximum wind of 3 on the Beaufort scale, which is when only leaves and thin branches are moved by the wind. This is because wind speed is an important factor for the amount of butterfly activity (Naturvårdsverket 2003).

Species names are according to the Entomological Society of Östergötland (2002) and the authors to the scientific names can be found in Catalogus Lepidopterorum Sueciae (Svensson et al. 1994). The butterflies that were recorded included species from the families Papilionoidea and Hesperioidea, burnet moths (Zygaenidae) and two day-flying species of Sphingidae (*Hemaris tityus* and *H. fuciformis*). All of these are referred to as “butterflies” in the following text.

The transect-line method was used to record the butterflies (Pollard 1977; Pollard & Yates 1993; Naturvårdsverket 2003). The transects were located in straight lines 25 m apart, covering the whole of each site and oriented at right angles to the narrowest side of the grassland (Figure 1). The surveyor walked along the transect line in a steady pace (50 m per min) and recorded all butterflies within 5 m on each side, up, and in front of the surveyor. Butterflies were caught in hand-net if identification could not be done immediately. If so, the transect walk was stopped and resumed again after identification. Two pairs of butterfly species were difficult to identify in the field, *Plebeius argus/P.idas* and *Leptidea reali/L.sinapis,* and were therefore treated together. For each site all the butterfly-recording occasions were merged and recalculated to number of individuals/ha before analysis.

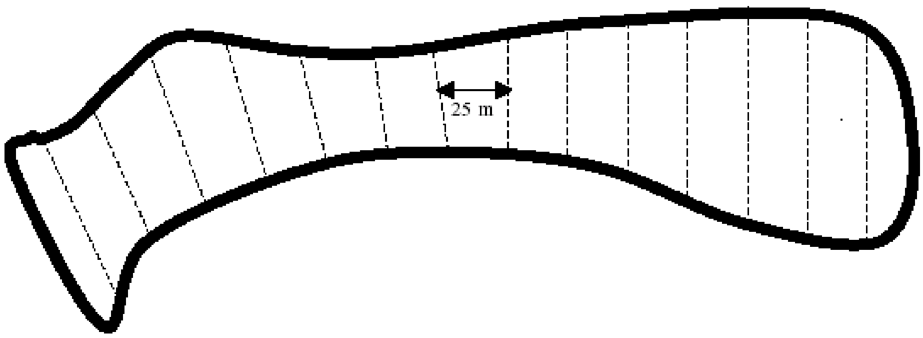

Figure 1. Example of transect-line method. No butterflies are recorded between the lines. (Naturvårdsverket 2003)

3.3 Landscape factors

The study sites were selected over a gradient from high amount of semi-natural grasslands in the landscape to more isolated grasslands. This was done to investigate if the butterfly diversity differed in a pasture-rich landscape compared to a pasture-poor landscape. For each of the 60 sites, the total area of semi-natural grasslands in the matrix surrounding the site were calculated within three circles with differing radii; 500, 2000 and 5000 m (Table 1). The calculations were made in a Geographical Information System (GIS), ArcView9, with data from the County Administration Board in Östergötland. In ArcView9 two shape-files with different inventory records of meadows and pastures were merged together and after putting three buffer zones around each butterfly site the total area of pastures in each buffer zone were calculated. The calculations were used as a measure of potential butterfly habitats in the landscape surrounding each site. The data of the three landscape variables were highly skewed and therefore log-transformed before further analysis. In the text they are referred to as Log 500, Log 2000 and Log 5000.

Table 1. Site and landscape variables of the 60 butterfly sites with transformations before analyses indicated. The landscape variables log 500, log 2000 and log 5000 represent the amount of semi- natural grassland in the surrounding matrix within three different radii, 500, 2000 and 5000m, from each butterfly site.

Variable	Mean (min-max)	Transformation
Site variables		
Sward height (cm)	8.27 (4.6-16.5)	-
Openness (%)	59.2 (30.8-100)	-
Shrub cover (%)	13.7 (0-42.3)	-
Tree cover (%)	30.7 (0-63)	-
Vegetation structure (1-3)	2.3 (1-3)	-
Site area (ha)	4.2 (3-8.4)	Square root
Nectar supply 1, Dipsacaceae/ Cirsium (1-3)	1.7 (1-2.6)	-
Nectar supply 2, all other plants (1-3)	2.1 (1.2-2.8)	-
Herbs AX1	-	PCA-values
Herbs AX2	-	PCA-values
Landscape factors		
Log 500 (ha)	15.4 (3.6-58.7)	Log_{10}
Log 2000 (ha)	70.9 (3.6-195.6)	Log_{10}
Log 5000 (ha)	330.8 (18.5-693.5)	Log_{10}

3.4 Local habitat factors

A total of nine local habitat factors thought to affect the butterfly community were recorded in this study (Table 1).

3.4.1 Sward height

To get a measure of the grazing intensity a method by Ekstam and Forshed (1996) was used. It consists of a 30x30-cm aluminum plate (430 g) that is centered on a metal pole and allowed to move freely along the pole. The plate is placed against the grass sward and the height of the grass sward that can carry the weight of the plate is measured. At each site the sward height was recorded in the middle of July with one measure point every 20 m along transect lines 50 m apart.

3.4.2 Openness, tree- and shrub cover

The presence of ligneous vegetation was recorded at the same points as the grass sward heights. The surveyor recorded presence of any part (branch or stem) from ligneous vegetation within a radius of 2 m from the sward height point. Individuals <3 m in height were recorded as shrubs and >3 m as trees. Empty circles were used as a measure of openness and the amount of trees, shrubs and openness for each site were calculated in percent.

3.4.3 Vegetation structure

Another parameter observed was the vegetation structure, using a method by the National Environmental Protection Board of Sweden (Naturvårdsverket, 2003). The surveyor subjectively classified each site in one of three vegetation categories, (see Figure 2).

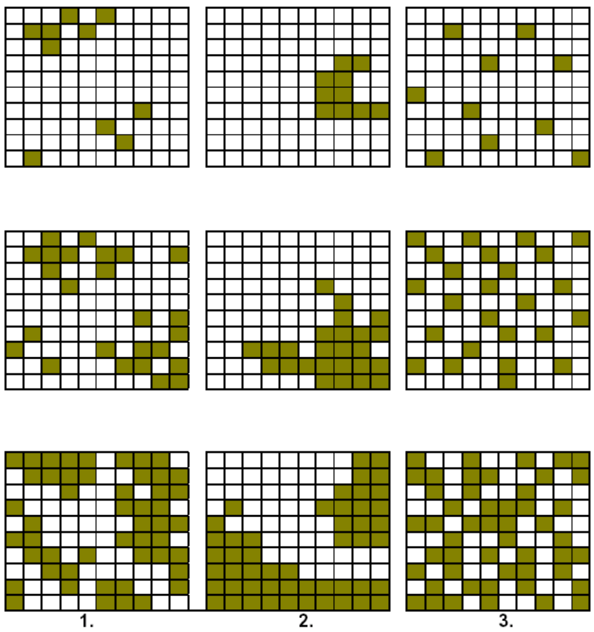

Figure 2. Different vegetation structures of trees and shrubs that can affect the amount of day-flying butterflies. 1= glades, small groves, 2= edge of wood/larger groves, 3= trees and shrubs equally spread over the area. (Naturvårdsverket 2003)

3.4.4 Herb composition

As a measure of the plant species diversity 20 plots (1x 0.2 m) were randomly selected at each site and inventoried between August and December 2004. All herbs were identified and further analysis was made on the composition of the vegetation at each site to investigate the relationship between butterfly species and herb species. The herb species were square root transformed before analysis and in further analysis named as herbs AX1 and AX2 (see section 3.5 Statistics).

3.4.5 Nectar availability

In order to characterize the availability of nectar the flower abundance was subjectively classified in one of three categories at the end of each butterfly recording. Flowering individuals of Dipsacaceae and *Cirsium*, (Nectar supply 1) were counted separately due to that they are large nectar sources for the butterflies. They were classified into: 0-25 individuals=1, 25-100individuals=2 and >100 individuals=3. All other flowering plants, (Nectar supply 2), were classified into: none/low abundance=1, intermediate=2, high amount=3. The mean of the categories at each site for both groups were calculated and used in further analysis.

3.4.6 Site area

Site area is considered to have an effect on butterfly diversity and although only sites between 3-8 ha were included in this study the difference in area between sites was too large to be neglected. The boundaries of each site were drawn from interpretation of aerial photos and analyzed in ArcView9. In further analysis the data were square root transformed.

3.5 Statistics

The main statistical analyses were performed with the CANOCO 4.5 software using multivariate methods based on linear assumptions (ter Braak and Smilauer 2002). Principal Component analysis (PCA) was conducted to describe structures in the species data. First a PCA was carried out on the herb species. It resulted in a two-dimensional ordination diagram and the sample scores from the first two principal components (i.e. the axes which had the highest eigenvalues) were used as a measure of the herb species composition. The values from each axis were put as two new site variables, herbs AX1 and herbs AX2. These values were then included in a second PCA together with the other site variables and the landscape factors in order to show the relative importance of all the environmental variables. To further evaluate the importance of the surrounding landscape on the butterfly community, three partial Redundancy Analyses (pRDA) were conducted, one for each of the spatial scales (500, 2000 and 5000 m). In the pRDA analyses the local habitat factors were inserted as covariables whereby the difference in site quality was extracted so that only the explanatory powers of the landscape factors were shown. P-values were established for each pRDA in Monte Carlo permutation tests with 9999 permutations. In all analyses the species data were square root transformed to minimize the influence of few abundant species.

With the statistical software SPSS 11.5, a simple linear regression analysis was made on the relation between the number of butterfly species and the amount of pastures at 5000 m scale.

4 Results

In this study 17153 individual observations of 64 species of butterflies were recorded. The number of species varied between 16 and 36 per site and the number of individuals between 87 and 967.

The PCA analysis on herb species at the 60 butterfly sites described patterns in the herb composition (data not shown). A total of 153 herb species and 2393 occurrences were analyzed. The flora ranged from species representing a fertilized agricultural environment to species that are strong meadow and pasture indicators. In the first principal component (PC1) species that indicated nitrogen rich soil pointed at one direction and species indicating nitrogen poor soil pointed in the opposite direction. Species characteristic of forest flora were clustered together.

The results of the second PCA showed clear patterns in the composition of butterfly species, with the first principal component (PC1, x-axis) explaining 25.6 % of the variation in species data. The majority of the butterfly species can be located in the first quadrant of the ordination diagram (Figure 3). This variation was also correlated with several of the site and landscape variables. The PCA ordination diagram can be interpreted by noting that arrows pointing in the same direction indicate a high positive correlation, that arrows crossing at right angles indicate near zero correlation and that arrows pointing at opposite direction indicate high negative correlation (Figure 3).

By looking at the signs and relative magnitudes of the intra-set correlation it is possible to infer the relative importance of each environmental variable for prediction of species composition (Jongman et al. 1995). The environmental variables that had highest correlation with PC1 were nectar supply of Dipsacaceae/*Cirsium* (r=0.51) and sward height (r=0.41) but also herb species composition axes 1 (r=0.30). They can therefore be considered the most important environmental factors. The three landscape factors, log 500, log 2000 and log 5000 had relatively low correlation values with the butterfly communities (r=-0.27, -0.29 and -0.04 respectively). The second principal component (PC2, y-axis) explained 13 % of the variation in butterfly species data and seemed to be mostly related to openness (r=0.46).

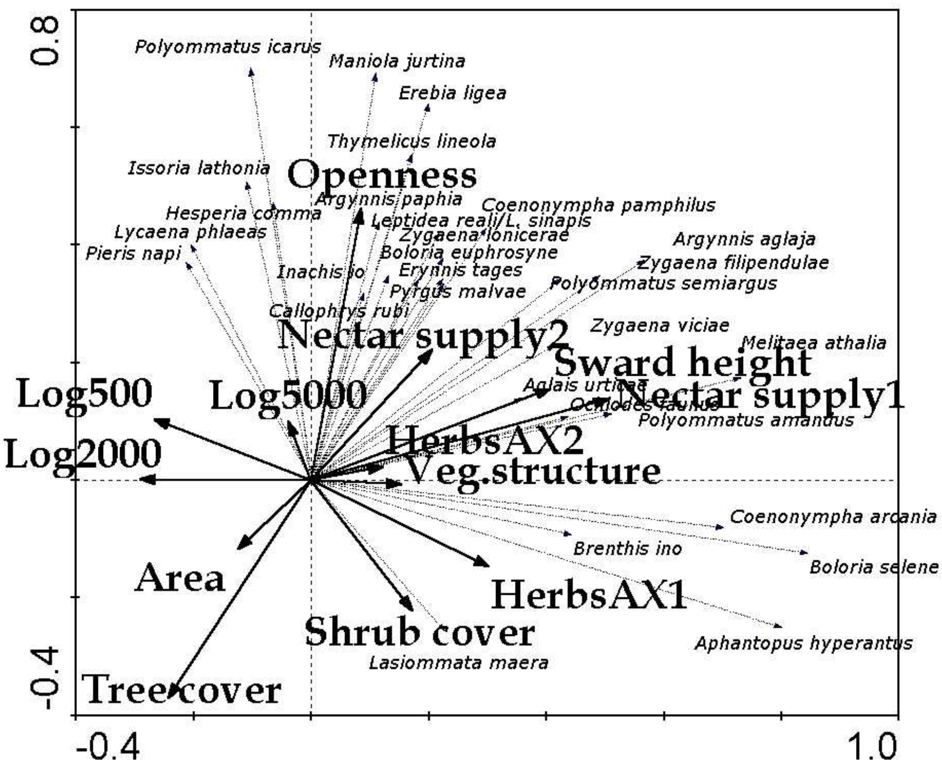

Figure 3. PCA ordination diagram of environmental variables and butterfly assemblages at 60 sites in Östergötland, Sweden. Only the 30 species that contribute most to the model and which occur at >5 sites are shown. The landscape variables log 500, log 2000 and log 5000 represent the amount of semi-natural grassland in the surrounding matrix within three different radii, 500, 2000 and 5000m, from each butterfly site. Eigenvalues of x- and y-axes are 0.256 and 0.129.

Since the aim of this study was to investigate landscape effects, pRDA was carried out on each of the landscape variables log 500, log 2000 and log 5000. Test of significance, of the canonical axes in pRDA, showed that only the amount of semi-natural grassland at the 5000 m scale significantly explained some of the variation in butterfly assemblages (p=0.0152, F-ratio=2.228). Eigenvalue for the x-axis was 0.0309, which indicates that 3.1% of the variance is explained by the landscape factor log 5000. No significance was found at 500 and 2000 m scale.

The results of pRDA are summarised in Table 2 where only the species score of the x-axis, and the variance explained by the landscape factor log 5000 for each butterfly species, are shown. Butterfly species with high species scores, both negative and positive, show high correlation with this landscape factor whereas species scores near zero indicate low correlation. Species that have a positive correlation with the landscape factor log 5000 increases in abundance with more meadows and pastures in the landscape at 5000 m scale and vice versa.

Table 2. Species scores and explained variance of pRDA on butterfly data from 60 sites in Östergötland, Sweden. Explanatory variable is the landscape factor, Log 5000, (p=0.0152). The number of occurrences and abundance of each species are shown. Species included are the 20 species that contributed most to the model and/or species that in a previous study by Bergman et al. (2004) were significantly affected at landscape scale for 50 % probability of occurrence. Species that occurred at <6 sites are not shown.

Butterfly species	Species score (x-axis)	Explained variance (%)	No. of occurrences (0-60)	Abundance
Coenonympha pamphilus	0.3578	12.81	53	438
Maniola jurtina	0.3491	12.18	27	292
Leptidea reali/L.sinapis	0.2848	8.11	57	42
Anthocharis cardamines	0.2742	7.52	28	41
Polyommatus amandus	0.2453	6.02	31	123
Erynnis tages	0.2189	4.79	32	91
Zygaena viciae	0.2147	4.61	15	54
Polyommatus semiargus	0.2002	4.01	32	123
Hesperia comma	0.1921	3.69	30	156
Aphantopus hyperantus	0.1883	3.55	60	2621
Boloria euphrosyne	0.1826	3.33	54	532
Zygaena osterodensis	0.1599	2.56	13	55
Zygaena filipendulae	0.1205	1.45	20	135
Zygaena lonicerae	0.1194	1.43	23	173
Coenonympha arcania	0.0851	0.72	60	1009
Lasiommata maera	0.0834	0.70	33	137
Adscita statices	0.0830	0.69	13	18
Aricia artaxerxes	0.0812	0.66	7	16
Boloria selene	0.0614	0.38	56	1182
Argynnis aglaja	0.0599	0.36	57	757
Brenthis ino	0.0423	0.18	25	114
Argynnis paphia	0.0306	0.09	51	312
Ochlodes faunus	-0.0192	0.04	41	97
Lycaena virgaureae	-0.0211	0.04	39	194
Pieris brassicae	-0.0617	0.38	13	18
Nymphalis antiopa	-0.0876	0.77	17	23
Pieris rapae	-0.1528	2.33	11	13
Melitaea athalia	-0.1975	3.90	60	1694
Argynnis adippe	-0.2478	6.14	39	150
Aglais urticae	-0.2852	8.13	40	110
Gonepteryx rhamni	-0.3431	11.77	58	382

The explained variance value reveal how much of the variation for each butterfly species that is explained by the landscape factor log 5000

(Table 2). Overall the variation explained by log 5000 is small, thereby indicating that other factors are also important. Still, for species with an explained variance >2 % the landscape factor can be considered to be important. Hence, the pRDA separated the butterfly species in three groups, one with species that is positively effected by a landscape consisting of many meadows and pastures at 5000 scale, for example *Maniola jurtina*, one with species that prefer more woodland and dens matrix, for example *Gonepteryx rhamni*, and a third group that can not be considered to be influenced by the landscape factor (Table 2).

A simple linear regression analysis between the number of butterfly species and the amount of pastures at 5000 m scale showed a weak positive correlation (r=0.099) but the relation is not significant. Hence, the number of butterfly species does not automatically increase with increasing amount of pastures in the landscape (Figure 4).

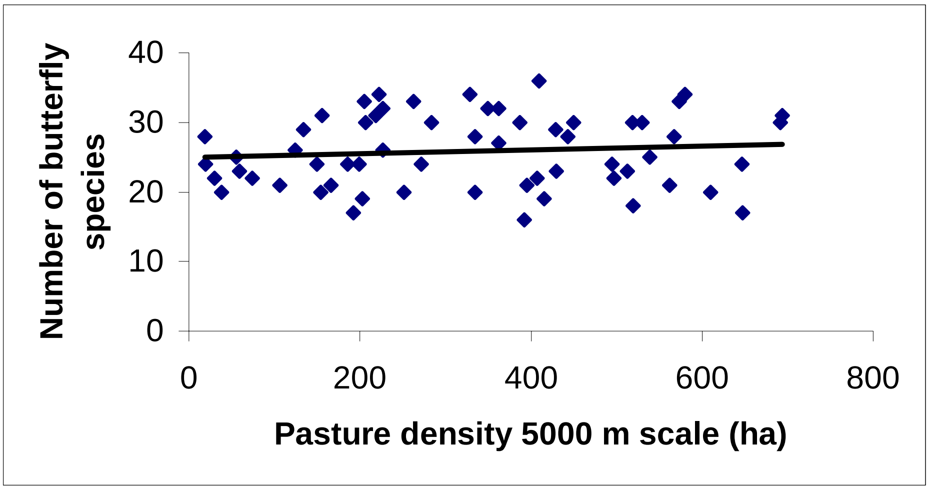

Figure 4. Number of butterfly species in relation to pasture density at 5000-m scale around 60 sites in Östergötland, Sweden.

5 Discussion

5.1 Landscape effects

In order to evaluate how the butterfly communities were affected by the surrounding landscape, three different landscape variables were studied, the amount of meadows and pastures within 500, 2000 and 5000 m. Only the amount of meadows and pastures in the landscape at the 5000 m scale could explain a significant part of the butterfly composition. However, the importance of the landscape variable, log 5000, was rather weak in contrast to what was expected. Metapopulation studies on butterflies reveal that populations are most likely to be present in habitat patches that are close together, thus the distribution of patches in a fragmented landscape is very important (Hanski & Gilpin 1997). Therefore, butterfly communities and diversity were thought to be stronger related to the amount of meadows and pastures at the 5000 m scale than what was detected in this study.

In addition, the regression analysis between number of butterfly species and pasture density at 5000 m scale does not support the theoretical expectations, although a weak positive trend was detected. Franzén & Ranius (2003) found in their study of butterfly communities in Östergötland that only one species, *Maniola jurtina*, was significantly affected by pasture density. In this study *Maniola jurtina* was the second most positively correlated species with the landscape factor, log 5000, and thereby it seems to be highly dependent of suitable habitat in the surrounding landscape.

Although 5000 m is a rather large scale for butterflies, it has been shown that if there is a high spatial correlation in the landscape structure of a scale at least a few times greater than the dispersal range of a species, it will benefit the species (Ovaskainen et. al 2002). Since many species have a dispersal range around 1000 m and some even up to 3000 m, the amount of habitat at 5000 m scale is relevant for the butterfly assemblage (Bergman et al. 2004). From empirical observations of colonisation it has been shown that migration takes place over much longer distances than that observed in mark-release-recapture studies within metapopulations (Hanski & Gilpin 1997). In addition, a minimum of 15-20 well-connected patches is required for long-term persistence of a metapopulation (Hanski & Gilpin 1997). Thus, in order to preserve the needed patches, a 5000 m scale is necessary.

Bergman et al. (2004) showed that the majority of the investigated butterfly species were significantly affected by the amount of suitable habitat at 5000-m scale in an agricultural dominated matrix. Although the results in the present study agree with this, the effect in a coniferous landscape was smaller, only 3.1 % of the variance in species composition could be explained, compared to 13.1% in the agricultural landscape. It should be noted, when comparing the results from this study with the study by Bergman et al. (2004), that their landscape factor included both deciduous forest and semi-natural pastures, taking more of the suitable matrix in consideration. When looking at the abundance and occurrences of butterflies, the study by Bergman et al. (2004) had overall lower values, the number of species in this study varied between 16 and 36 per site, in the agricultural landscape it varied between 6 and 34 species. The abundance of individual species also differed between the two landscapes, for example the fritillary *Melitaea athalia* had a total of 73 individuals at 62 sites in agricultural landscape and 1694 individuals at 60 sites in coniferous landscape (see Appendix 1). Fritillaries as a group may be used as an indicator of a landscape rich in butterflies (Bergman et al. 2004). The frequency of the whole group of fritillaries is much higher in this study than in the previous one by Bergman et al. (2004). The total frequency was 920 individuals at 62 sites in agricultural landscape compared to 3065 individuals at 60 sites in coniferous landscape (see Appendix 1). This suggests that the butterfly composition differ between an agricultural landscape and a more coniferous landscape, probably due to the more hostile environment that exists in the intensively managed arable fields. A similar pattern was found by Schneider & Fry (2001) where species composition differed markedly between a fine-grained landscape with high cover grasslands and forest and a coarser-grained study area with grasslands spread in a matrix of arable fields. They suggested that it was the fine grain mosaic of grasslands adjacent to forest areas that explained the higher butterfly diversity in the fine-grained landscape.

The differences between the two matrixes could explain why the amount of meadows and pastures in the landscape are more important in an agricultural landscape. The forest consists of several features suitable for butterflies, such as glades, clear-cuts, bogs and small roads, which cannot be found in the agricultural landscape. Fahrig (2001) emphasis the advantages of a diverse landscape structure, especially the features that increase the survival of dispersers, provide shelters or act as food sources. If the conditions in the matrix are right it also serves as an area of reproduction for many butterfly species. In a coniferous landscape the butterflies might be able to move from patch to patch more easily through the many glades and clear-cut areas. In a landscape dominated by arable field the dispersal ability is more important since the butterflies often have to travel long distances in more windy conditions to get to another patch. Weibull et al. (2003) found that the species richness of butterflies on conventional farms was correlated to large- and small-scale landscape heterogeneity. The quality of the whole landscape should therefore be included in conservation strategies (Fahrig 2000).

One factor to consider in this study is that the results to a large extent can reflect the landscape history. The semi-natural pastures of today are only small remnants of much larger areas consisting of old-managed meadows used for haymaking and grazing. In Sweden, habitats of this type have declined with 82% since 1880 (Angelstam et al. 1993). However, the time aspect is different between pastures in agricultural landscape and pastures in coniferous landscape. The decline of semi-natural pastures in agricultural dominated landscape begun in the 19th century with the agricultural revolution and became more severe in the early 20th century due to the intensification and mechanisation of agriculture. The change in land-use in coniferous landscape took turn later, starting around 1930 and culminated in the 1980-ties when a new forestry legalisation was established (Ekstam & Forshed 2000). The species richness thus reflects different time scales of connectivity in different landscapes. Many plant species react slowly to changes in the environment and Lindborg & Eriksson (2004) found that plant species diversity is not related to present-day connectivity; instead the habitat connectivity 100 years ago had a strong positive effect. Butterflies are thought to react in a similar way. Hanski et al. (1996) concluded that there is a delay in metapopulation dynamics in a declining patch network and that it takes decades for most metapopulations to reach the new equilibrium (i.e. extinction). This time lag in the response to a changing habitat may therefore be misleading when analysing species diversity in present-day landscape. Many rare and endangered species may already be committed to extinction unless the loss and fragmentation of their habitat is reversed (Hanski et al. 1996).

5.2 Local habitat quality

The outcome of the PCA showed that the landscape factors had relatively low correlation values with the butterfly communities. Further it showed that the local factors had equal and even more importance for the variation in butterfly abundance. From the rather low explained variance value for many of the butterfly species in the pRDA it was also evident that factors other than the landscape factor were important for the butterfly community.

The factors with highest positive correlation with the butterflies were nectar supply (i.e. flower abundance), sward height and openness. This is not surprising since the importance of local habitat quality for butterfly diversity is well known. For example, several authors have identified the importance of flower abundance (Schnieder & Fry 2001; Steffan-Dewenter & Tscharntke 1997; Munguira & Thomas 1992). Herb species composition was also a factor that had relatively high positive correlation with the butterfly communities in this study. Eriksson et al. (1995) showed that habitat heterogeneity had a positive effect on plant species richness and occurrences and that pastures influenced by fertilisation had negative effect. Thomas et al. (2001) also found that local habitat quality was the best predictor to determine the presence of three butterfly species in UK grasslands.

5.3 Conservation implications

In conclusion this study has shown that the effects of the surrounding landscape on butterfly communities are rather complex and that there is no clear relationship between the amount of semi-natural grasslands and butterfly diversity in a coniferous dominated landscape. The results showed that butterfly communities were affected by the amount of meadows and pastures in the landscape at 5000 m scale. The species richness and number of individuals were generally higher, compared with results from agricultural dominated landscapes (Bergman et al 2004). The reason is probable the larger heterogeneity with small-scale farms in the studied landscape. Several studies have shown the importance of landscape heterogeneity and quality for species richness and persistence (Fahrig 2001; Schneider & Fry 2001; Weibull et al. 2003).

Besides the effect of the landscape on the butterfly composition this study also showed that the local habitat quality is very important for the occurrences of a species at a site. Sites with for example high nectar abundance were often species rich, even if they were rather isolated. Thus, appropriate local management of a site in the studied landscape seems to ensure a rich butterfly fauna.

However, another aspect is that a metapopulation of butterflies may occur in a fragmented area simply because there is a delay of decline to extinction (Hanski et al. 1996). Preservation of the existing patches in the landscape might not be enough in the long term and future species loss may be expected. If this is the case, the need for restoration in the fragmented parts of the study area is urgent to prevent this process, as well as taking historical connectivity into consideration.

In summary, the butterfly communities in a coniferous landscape seem to be affected both by habitat quality and to some extent also the landscape quality. The coniferous landscape is a more butterfly rich landscape than the agricultural landscape probably due to the combination of a more diverse matrix and a recent history in the decline of suitable habitat. This has implications for conservation management. It is very important to support a traditional land-use and to keep a continuous grazing regime. In a matrix of coniferous forest it is efficient also to continue to manage more isolated pastures since they still show high butterfly diversity. Nevertheless it is important to consider the whole landscape in conservation strategies and especially the different features of the landscape that the species operate in.

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Appendix

Appendix 1. Butterfly species and their frequency and abundance at 60 sites in Östergötland, Sweden.

Species	No. of occurrences	Abundance
Fritillaries	60	3065
Melitaea athalia	60	1694
Aphantopus hyperantus	60	2621
Coenonympha arcania	60	1009
Gonepteryx rhamni	58	382
Argynnis aglaja	57	757
Leptidea reali/ L. sinapis	57	442
Pieris napi	56	577
Boloria selene	56	1182
Boloria euphrosyne	54	532
Lycaena phlaeas	53	208
Coenonympha pamphilus	53	438
Polyommatus icarus	52	611
Argynnis paphia	51	312
Inachis io	46	182
Ocholdes faunus	41	97
Aglais urticae	40	110
Lycaena virgaureae	39	194
Erebia ligea	39	176
Argynnis adippe	39	150
Lasiommata maera	33	137
Thymelicus lineola	34	118
Polyommatus semiargus	32	123
Erynnis tages	32	91
Polyommatus amandus	31	123
Pyrgus malvae	31	63
Hesperia comma	30	156

Appendix 1. (continued)

Species	No. of occurrences	Abundance
Anthocharis cardamines	28	41
Callophrys rubi	27	43
Maniola jurtina	27	292
Plebeius argus/P.idas	25	64
Brenthis ino	25	114
Zyganeidae	25	435
Zygaena lonicerae	23	173
Polygonia c-album	20	27
Zygaena filipendulae	20	135
Nymphalis antiopa	17	23
Zygaena viciae	15	54
Pieris brassicae	13	18
Zygaena osterodensis	13	55
Adscita statices	13	18
Pieris rapae	11	13
Lycaena hippothoe	10	18
Issoria lathonia	7	15
Pararge aegeria	7	10
Aricia artaxerxes	7	16
Celastrina argiolus	7	33
Glaucopsyche alexis	6	7
Aporia crataegi	5	6
Colias palaeno	4	12
Vanessa cardui	3	3
Lasiommata petropolitana	3	4
Hipparchia semele	3	6
Neozephyrus quercus	3	4
Plebeius optilete	3	3
Argynnis niobe	2	2
Carterocephalus silvicola	2	4
Thecla betulae	1	1
Melitaea cinixa	1	4
Boloria aquilonaris	1	1
Vanessa atalanta	1	1
Limenitis populi	1	1
Lasiommata megera	1	4
Cupido minimus	1	1
Hamearis lucina	1	2
Hemaris tityus	1	1