

# Importance of boreal grasslands in Sweden for butterfly diversity and effects of local and landscape habitat factors

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**Abstract** A widespread decline in biodiversity in agro-ecosystems has been reported for several groups of organisms in Western Europe. The butterfly fauna was studied in 60 selected semi-natural grasslands in a coniferous-dominated boreal landscape in south-eastern Sweden. The aim was to investigate how butterfly assemblages were affected by the amount of semi-natural grasslands in the surrounding landscape. Furthermore, we wanted to determine if semi-natural grasslands in boreal landscapes harboured species otherwise declining in other parts of Europe. For each study site, the amounts of semi-natural grasslands in the landscape within radii of 500, 2,000 and 5,000 m were studied. Nine local habitat factors were also recorded. Only the amount of semi-natural grasslands within a 5,000 m radius could explain a significant part of the variation in butterfly composition, but there was no clear relationship between the amount of semi-natural grassland and butterfly diversity. Instead, this study showed that local habitat quality was very important for butterfly diversity at individual sites. Flower abundance, sward height and herb composition were the most important local factors. Patches surrounded by a small amount of semi-natural grasslands had high butterfly diversity, contrary to expectations. This may be explained by the fact that forest habitat provides a matrix with several features suitable for butterflies. The butterfly fauna was rich in species representative of low-productivity grasslands, species that are declining in other countries in Western Europe.

**Keywords** Butterflies · Boreal landscapes · Conservation · Habitat quality · Matrix

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## Introduction

A widespread decline in biodiversity in agro-ecosystems has been reported for several groups of organisms in Western Europe (Kearns et al. 1998; Krebs et al. 1999; Maes and Van Dyck 2001; Robinson and Sutherland 2002). Among invertebrates, butterflies are the most extensively studied organisms, with many reports of declining population sizes and geographic distributions (Van Swaay and Warren 1999). Butterflies seem to be sensitive to landscape changes and have experienced greater net losses than either plants or birds in Britain (Thomas et al. 2004). The most detailed studies have been conducted in grassland remnants in a matrix of arable fields in regions of intensive agriculture (e.g. Maes and Van Dyck 2001; Robinson and Sutherland 2002; Krauss et al. 2003b; Bergman et al. 2004; Wenzel et al. 2006; Öckinger et al. 2006). However, studies of grassland remnants in boreal landscapes in a matrix of coniferous forest are rare (but see Kivinen et al. 2006).

Agricultural intensification and rationalisation have led to different effects on land-use in different eco-regions. In nemoral regions, i.e. regions that are naturally dominated by deciduous broad-leaved tree species (Diekmann 1999), like oak (*Quercus* spp.), ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*), large areas of semi-natural habitats such as wetlands and grasslands have been cultivated and drained. This has resulted in larger field sizes, smaller and more isolated semi-natural grasslands, fewer woodland patches, lower landscape heterogeneity and a higher number of farms focusing on crop production only (Van Swaay and Warren 1999; Robinson and Sutherland 2002; Wenzel et al. 2006). On the other hand, in boreal regions, abandonment of grasslands is the main change of concern for maintaining biodiversity. This results in a structure of semi-natural grasslands similar to that of intensive agricultural areas (i.e. fewer and more isolated semi-natural grasslands). The agricultural statistics of Sweden clearly show these changes over time, with the number of farms decreasing between 1927 and 2004 by 79% from 307,395 to 65,801 (Swedish Board of Agriculture 2005). At the same time, the number of farms larger than 100 ha has increased by 248% and farms smaller than 20 ha have decreased by 88%. Many of these smaller farms were located in boreal landscapes and these landscapes are now changing quickly towards a more homogeneous, forested landscape, which is in sharp contrast with the more intensively farmed areas dominated by large farms and large, arable fields.

The effects of decreasing size and increasing isolation of semi-natural and natural grasslands are well documented for many butterfly species in intensive agricultural areas (Pullin 1995; Maes and Van Dyck 2001), but it is unclear what happens to butterfly diversity in semi-natural grasslands in boreal landscapes when the grasslands become isolated. Simulation studies by Fahrig (2001) suggested that the matrix quality is very important for species persistence in a landscape.

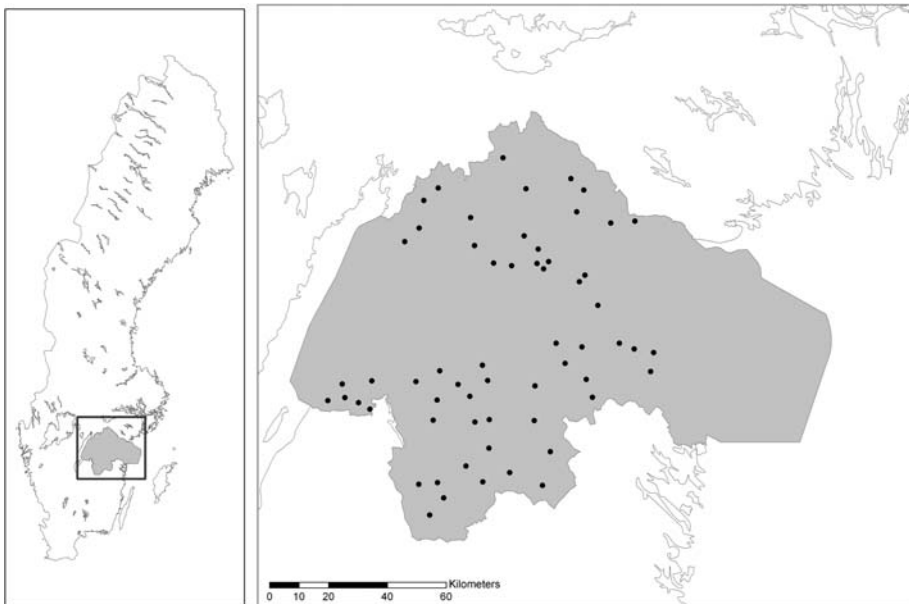
The aim of this study was to investigate how butterfly communities are affected in a gradient from small amounts of semi-natural grasslands to a large amount of semi-natural grasslands in a landscape with a matrix consisting mainly of coniferous forest. We also studied the importance of local habitat factors, such as nectar sources, sward height and openness, that are known to affect butterfly communities (Warren 1993). Further, we wanted to see if the semi-natural grasslands in boreal landscapes have a butterfly fauna that differs from the fauna of nemoral areas and if these grasslands harbour species declining or threatened in nemoral areas. This can give information that can be used in conservation planning and management.

## Material and methods

### Study area and selection of study sites

The study area is situated in the county of Östergötland (Fig. 1) in the southeast of Sweden and consists of small patches of semi-natural grassland with deciduous trees, mainly surrounded by coniferous forest and a small amount of arable fields.

The individual semi-natural grasslands that were studied were identified from regional inventory records of semi-natural grasslands supported by EU-grants at the County Administration Board in Östergötland. The sites were assessed and only sites with high species richness of vascular plants and that were grazed were selected. The selected sites could thereby be considered as high quality semi-natural grasslands with regard to vascular plant richness. The assessment was conducted in May 2004, to determine if the semi-natural grasslands were still used in a traditional way and regularly grazed. All the sites have a similar management history. All have a long history of grazing and most also as hay meadows in the 19th century. Parts of the grasslands may bear traces of light fertilisation from older times but the sites were never dominated by plants thriving in fertilised conditions. Only semi-natural grasslands with an area of 3–8 ha were included in the study. Larger areas were avoided for practical reasons and smaller areas were avoided since they were expected to be subject to strong species–area relationships (Steffan-Dewenter and Tschardt 2000). In total, 60 sites were selected for butterfly recordings. These consisted of open to half-open, semi-natural grasslands and at least 30% of the site area had to be unfertilised for the site to be included in the study. The latter was to minimise the variation between the sites so that differences due to landscape factors would be more easily detected.



**Fig. 1** Locations of the 60 studied sites in Östergötland, Sweden

## 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  $>17^{\circ}\text{C}$  and with a maximum wind speed of 3 on the Beaufort scale (only leaves and thin branches are moved by the wind).

Species names are according to Eliasson et al. (2005). The butterflies that were recorded included species from the families Papilionidae and Hesperidae, burnet moths (Zygaenidae) and two day-flying species of Sphingidae (*Hemaris tityus* and *H. fuciformis*). For convenience, all of these are referred to as “butterflies” in the following text.

The transect-line method was used to record the butterflies according to the method of the Swedish Environmental Protection Agency (2006). 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. The surveyor walked along the transect line at a steady pace ( $50\text{ m min}^{-1}$ ) and recorded all butterflies within 5 m of each side of the line, up and in front. Butterflies were caught in a 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 recording occasions were merged and the butterfly density was recalculated as the number of individuals/ha before analysis.

## Landscape and local habitat factors

The study sites were selected over a gradient from a high proportion of semi-natural grasslands in the landscape to a low proportion of grasslands. For each of the 60 sites, the total area of semi-natural grasslands in the matrix surrounding the site was calculated within three circles with differing radii: 500, 2,000 and 5,000 m (Table 1). There were some overlap between the landscapes at 2,000 and 5,000 m. The median overlap for 5,000 m was 6.9% ( $P_{25} = 0$ ,  $P_{75} = 29.4\%$ ). The calculations were made in a Geographical Information System (GIS), ArcView9, with data from the national survey of semi-natural grasslands 2002–2004 together with data from the County Administration Board of Östergötland of semi-natural grasslands receiving the largest environmental subsidies (i.e. species-rich grasslands). After putting three buffer zones around each butterfly site, the total area of semi-natural grasslands in each buffer zone was 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  $\log_{10}$ -transformed before further analysis and later are referred to as “log 500”, “log 2000” and “log 5000”.

A total of nine local habitat factors, known or suspected to affect the butterfly community, were recorded in this study (Table 1). At each site, the sward height was recorded in the middle of July with one measurement point every 20 m along transect lines that were 50 m apart. The method involved using a  $30 \times 30$  cm aluminium plate (430 g) that was centred on a metal pole and allowed to move freely along the pole. The plate was placed against the grass sward and the height of the grass sward that can carry the weight of the plate was measured. This was used as a measure of the grazing intensity (Ekstam and Forshed 1996).

The presence of ligneous vegetation was recorded at the same points as the grass sward heights were measured. The surveyor recorded the presence of any part (branch or stem) of ligneous vegetation within a radius of 2 m from the sward height measurement point.

**Table 1** Site and landscape variables of the 60 butterfly sites with data transformations conducted prior to analyses indicated

Variable	Mean	Min-max	Transformation
<i>Site variables</i>			
Sward height (cm)	8.3	4.6–16.5	–
Openness (%)	59.2	30.8–100.0	–
Shrub cover (%)	13.7	0.0–42.3	–
Tree cover (%)	30.7	0.0–63.0	–
Vegetation structure (1–3)	2.3	1–3	–
Site area (ha)	4.2	3.0–8.4	Square-root
Nectar supply 1, Dipsacaceae/ <i>Cirsium</i> (1–3)	1.7	1.0–2.6	–
Nectar supply 2, all other plants (1–3)	2.1	1.2–2.8	–
vegPC1	–0.01	–1.5 to 2.5	–
vegPC2	–0.0	–1.8 to 3.4	–
<i>Landscape variables</i>			
Log 500 (ha) (% of total area)	15.4 (19.6)	3.6–58.7 (4.6–74.7)	Log <sub>10</sub>
Log 2000 (ha) (% of total area)	70.9 (5.6)	3.6–195.6 (0.3–15.6)	Log <sub>10</sub>
Log 5000 (ha) (% of total area)	330.8 (4.2)	18.5–693.5 (0.2–8.8)	Log <sub>10</sub>

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, 2,000 and 5,000 m, from each butterfly site

Individuals <3 m in height were recorded as shrubs and >3 m as trees. The proportion of empty circles was used as a measure of the openness and the amounts of trees, shrubs and openness for each site were calculated in percent.

Another parameter recorded was the vegetation structure, where the surveyor subjectively classified each site in one of three categories (1 = glades, small groves, 2 = large blocks of open areas or trees and shrubs, 3 = trees and shrubs spread equally over the area) by a method defined by the Swedish Environmental Protection Agency (2006).

As a measure of plant species composition, 20 plots (1.0 × 0.2 m) were randomly selected at each site and surveyed once in August or September (one site in December, 2004). All herbs were identified and their frequencies (0–20) were square-root transformed before analysis.

In order to characterise the availability of nectar, flower abundance was estimated in one of three categories at the end of each butterfly recording. Flowering individuals of Dipsacaceae and *Cirsium* (nectar supply 1) were classified separately because they are important nectar sources for butterflies and the total number was counted and classified into 0–25 individuals = 1, 25–100 individuals = 2 and >100 individuals = 3. All other flowering plants (nectar supply 2) were classified as follows: none/low abundance = 1, intermediate = 2, high amount = 3. The mean amount of flowering plants at each site for both groups was calculated and used in further analyses. Site area is known to have an effect on butterfly diversity (Steffan-Dewenter and Tscharrntke 2000) and although only sites between 3 and 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 analysed in ArcView9. In further analyses, square-root transformed data were used.

## Statistical analyses

Multivariate statistical analyses were performed with the CANOCO 4.5 software package (ter Braak and Smilauer 2002) using multivariate methods based on linear assumptions, as the beta-diversity in the data was relatively low (Leps and Smilauer 2003).

Herb vegetation data were summarised by Principal Components Analysis (PCA). Principal Component 1 (vegPC1) and vegPC2 were used in subsequent analyses with the butterfly data.

The butterfly data were also summarised by PCA, and sample scores along PC1 and PC2 were correlated with local habitat factors and the landscape factors in order to show their relative importance for the main structures in the butterfly data. 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, 2,000 and 5,000 m). In the pRDAs, the local habitat factors were used as covariables, thereby eliminating differences in site quality. P-values were established for each pRDA with a Monte Carlo test with 9,999 permutations. The species data were square-root transformed, in all analyses, to minimise the influence of a small number of species which were highly abundant.

Simple linear regression was conducted between the number of butterfly species and the amount of semi-natural grassland at the 5,000 m scale.

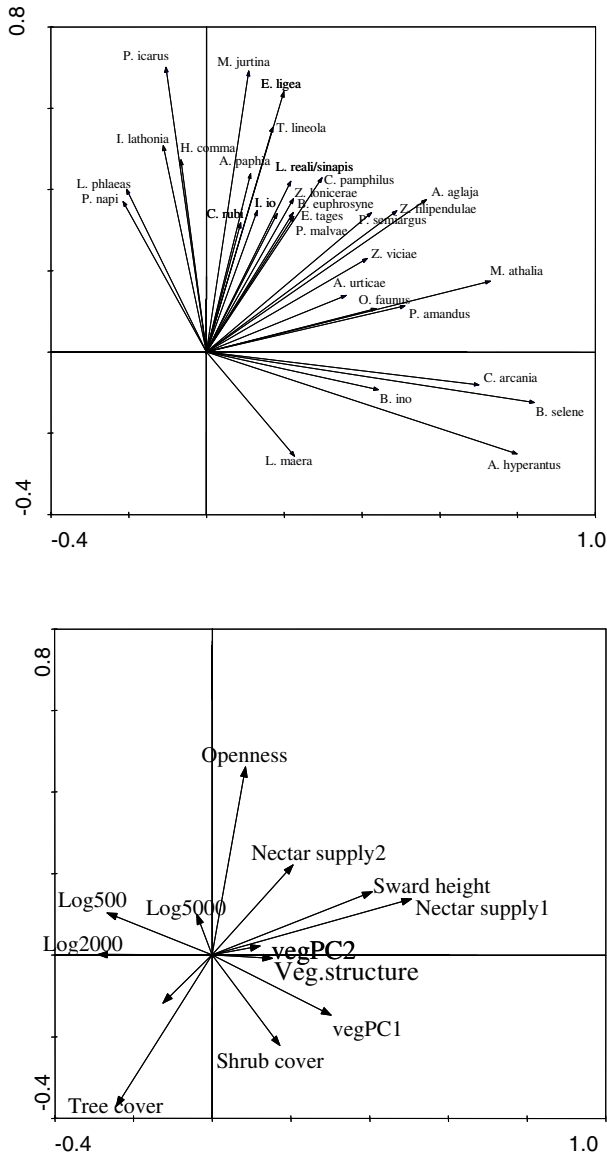
## Results

In this study, 17,153 individual observations of 64 species of butterflies were recorded. The number of species varied between 16 and 36 per site and the number of individual recordings varied between 87 and 967.

A total of 153 herb species and 2,393 occurrences were analysed. The PCA analysis on the herb species at the 60 butterfly sites described interpretable patterns in the herb composition (data not shown). Eigenvalues for vegPC1 and vegPC2 were 0.11 and 0.092, respectively. The vegetation ranged from species thriving in fertilised grasslands to species typical for nutrient poor species-rich semi-natural grasslands. In vegPC1, species that indicated nitrogen-rich soil pointed in one direction and species indicating nitrogen-poor soil pointed in the opposite direction. Species characteristic of forest flora were also clustered together.

The PCA on the butterfly data showed clear patterns, with PC1 explaining 26% of the variation in the data (Fig. 2). The majority of the butterfly species were correlated with nectar supply and sward height and also with herb species composition (vegPC1) (Fig. 2, Table 2). The second principal component (PC2) explained 13% of the variation in the butterfly species data and seemed to be mostly related to openness ( $r = 0.46$ ; data not shown).

However, the primary aim of this study was to investigate landscape effects, and therefore pRDAs were carried out on each of the three 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 5,000 m scale significantly explained some of the variation in the butterfly communities (9,999 permutations,  $P = 0.0152$ ,  $F$ -ratio = 2.228). The eigenvalue for the  $x$ -axis was 0.0309, which indicates that 3.1% of the residual variance, after eliminating the influence of site factors, was explained by the landscape factor log 5000.



**Fig. 2** (a) PCA ordination diagram of butterfly communities at 60 sites in Östergötland, Sweden. Only the 30 species that contribute most to the model and which occur at >5 locations are shown. (b) PCA ordination diagram of environmental variables. 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, 2,000 and 5,000 m, from each butterfly site. Eigenvalues of PC1 (x-axis) and PC2 (y-axis) are 0.256 and 0.129

The results of the significant pRDA are summarised in Appendix, where the species scores of the first axis (the only constrained one), and the variance explained by the landscape factor log 5000 for each butterfly species, are shown. Species that have a positive

**Table 2** Inter-set correlation of environmental variables with axis 1 (Fig. 2) in an ordination of butterflies at 60 sites

Variables	Inter-set correlation with PC1
Nectar supply 1, Dipsacaceae/ <i>Cirsium</i> (1–3)	0.51
Sward height (cm)	0.41
vegPC1	0.30
Nectar supply 2, all other plants (1–3)	0.21
Shrub cover (%)	0.17
Vegetation structure (1–3)	0.15
vegPC2	0.12
Openness (%)	0.08
Log 5000 (ha)	−0.04
Site area (ha)	−0.12
Tree cover (%)	−0.24
Log 500 (ha)	−0.27
Log 2000 (ha)	−0.29

correlation with the landscape factor log 5000 increase in abundance with more semi-natural grasslands in the landscape at 5,000 m scale and vice versa.

The explained-variance value reveals how much of the variation for each butterfly species that is explained by the landscape factor log 5000 (Appendix). 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 have an effect. Hence, the pRDA shows that there are species positively affected by a landscape consisting of many semi-natural grasslands at the 5,000 m scale, such as *Maniola jurtina*, but also that there are species that prefer a forest matrix, such as *Gonepteryx rhamni* (Appendix).

A simple linear regression between the number of butterfly species and the amount of semi-natural grasslands at the 5,000 m scale showed a weak, non-significant, positive correlation ( $r = 0.099$ ). Hence, the number of butterfly species does not automatically increase with increasing amount of semi-natural grasslands in the boreal coniferous landscape (Fig. 3).

## Discussion

### Landscape effects

Surprisingly, there was no significant effect on the butterfly community of the amount of semi-natural grasslands within 500 and 2,000 m in the landscape and only a weak effect of the amount within 5,000 m (Fig. 2). In addition, the regression analysis between the number of butterfly species and semi-natural grassland density at the 5,000 m scale does not support the theoretical expectations of increasing diversity with semi-natural grassland density. Several studies on individual butterfly species reveal that populations are most likely to be present in habitat patches that are situated close together (Thomas et al. 1992; Thomas and Hanski 1997; Bergman and Landin 2001; Sawchik et al. 2003). The reason for the absence of effects of habitat isolation on butterfly species richness in this study is probably that the matrix contains patches of more or less suitable habitat for individual species. In a similar study by Bergman et al. (2004) 13.1% of the variance in

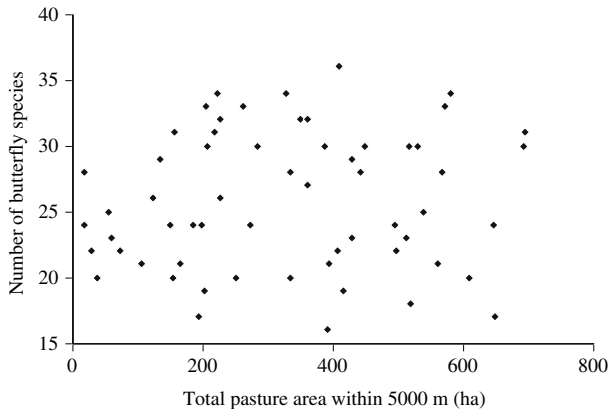


**Table 3** Comparison between frequency of butterfly species in this study and three other studies: (i) population changes in  $10 \times 10$  km breeding squares between 1979–1982 and 1995–1999 of species in the UK Biodiversity Action Plan (BAP) priority species, species of conservation concern and candidate species and extinct species in UK (Fox et al. 2001); (ii) population changes at seven German grasslands of the same UK BAP species including burnet moths between 1972 and 2001 (Wenzel et al. 2006); (iii) population changes in Flanders, Belgium in  $5 \times 5$  km<sup>2</sup> of the same UK BAP species before 1991 and after 1991 (Maes and van Dyck 2001)

Species	Proportion of occurrences Ög, Swe (60 sites) (%)	UK BAP species (%)	Western Germany (%)	Flanders Belgium (%)
<i>Melitaea athalia</i>	100	–38	–86	–100
<i>Argynnis aglaja</i>	95	–55	–86	–79
<i>Leptidea reali/L. sinapis</i>	95	(–72)	–14	(–50)
<i>Boloria selene</i>	93	–52	–100	–100
<i>Boloria euphrosyne</i>	90	–68	–100	–100
<i>Argynnis paphia</i>	85	–38	–100	–42
<i>Argynnis adippe</i>	65	–82	–	–100
<i>Polyommatus semiargus</i>	53	–100	–57	–96
<i>Erynnis tages</i>	53	–49	–43	–100
<i>Pyrgus malvae</i>	52	–48	–43	–83
<i>Hesperia comma</i>	50	–29	–100	–74
<i>Plebeius argus/P.idas</i>	42	(–47)	–	–73
<i>Zygaena lonicerae</i>	38	–	–100	–
<i>Zygaena filipendulae</i>	33	–	–14	–
<i>Zygaena viciae</i>	25	–	–57	–
<i>Adscita statices</i>	22	–	–29	–
<i>Aporia crataegi</i>	8	–100	0	–84
<i>Thecla betulae</i>	2	–39	–83	–35
<i>Melitaea cinxia</i>	2	–43	–71	–95
<i>Cupido minimus</i>	2	–41	–29	–
<i>Hamearis lucina</i>	2	–47	–83	–

The sibling species, *Leptidea sinapis/reali* and *Plebeius argus/das* were treated together in our study but apply to *L. sinapis* in UK and Flanders and *P. argus* in UK

species composition could be explained in the landscape dominated by arable fields compared to only 3.1% in this study where coniferous forest dominates. The differences between the two matrixes could explain why the amount of semi-natural grasslands in the landscape is more important in a landscape dominated by arable fields. A forest consists of several features suitable for butterflies, such as small glades, clear-cuts and bogs, which cannot be found to the same extent in an agricultural landscape. In a landscape dominated by arable fields, the matrix is often depleted of butterfly resources. Fahrig (2001) emphasise the advantages of a diverse landscape structure, especially the features that increase the survival of dispersers, provide shelters or act as food sources. Detailed behavioural studies of two butterfly species showed that more of the “empty” matrix than expected may be used (Dennis 2004). The quality of the whole landscape should therefore be included in conservation strategies and not only grasslands. There are studies that, in line with this study, have found no effects of habitat isolation on butterfly species richness (Krauss et al. 2003a). Franzén and Ranius (2004) found in their study of butterfly communities in Östergötland that only one species, *Maniola jurtina*, was significantly affected by semi-natural grassland density.



**Fig. 3** The number of butterfly species in relation to semi-natural grasslands density at 5,000-m scale around 60 sites in Östergötland, Sweden

Apart from matrix quality, local habitat quality has also been shown to be important (Dennis and Eales 1997; Thomas et al. 2001; Binzenhöfer et al. 2005). Thomas et al. (2001) found that local habitat quality was the best predictor for determining the presence of three butterfly species in UK grasslands. In this study, the factors with highest positive correlation with the butterflies were nectar supply (i.e. flower abundance), sward height and openness. The importance of flower abundance has been identified by several authors (Mungiura and Thomas 1992; Steffan-Dewenter and Tschamtkke 1997; Schneider and Fry 2001). Herb species composition was also a factor that had a relatively high positive correlation with the butterfly communities in this study. In general plant diversity has a positive effect on butterfly diversity although grazing pressure may affect diversity negatively in unfertilised grasslands (Erhard and Thomas 1991, Vessby et al. 2002)

One other factor to consider in this study is that the results may also reflect landscape history. The decline of semi-natural grasslands in agriculturally dominated landscapes began 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 occurred later, starting around 1930 and culminated in the 1980s when new forestry legislation was established (Ekstam and Forshed 2000). The species richness may thus reflect different time scales of connectivity in different landscapes. Many plant species react slowly to changes in the environment (Vellend et al. 2006). Lindborg and Eriksson (2004) found that plant species diversity in semi-natural grasslands was related to habitat connectivity 100 years ago, not to present-day connectivity. 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 a 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 landscapes.

#### Comparison with butterfly faunas from nemoral landscapes

Northern Europe's butterfly fauna is generally more species poor than Southern Europe's, but some butterfly groups seem to have a stronghold in boreal semi-natural grasslands. In

particular, some species and groups belonging to low-productive grasslands still have strong populations. Britain has done the most comprehensive survey of butterflies in Europe (Asher et al. 2001) and list 29 species in the UK Biodiversity Action Plan (BAP) (priority species, species of conservation concern or candidate species). Of them, 22 can be found in Sweden and 15 were found in this study, including two species that are extinct in Britain. These species have all experienced serious declines in breeding populations in  $10 \times 10$  km squares in Britain (Fox et al. 2001) (Table 3). In our study, 12 of the species were common with occurrences in  $>40\%$  of our sites. In a study of calcareous grasslands in western Germany almost all of these species declined between 1972 and 2001 (Wenzel et al. 2006). This is also the case in  $5 \times 5$  km squares in Flanders in northern Belgium before and after 1991 (Maes and Van Dyck 2001). The fritillaries seem to be especially hard hit by agricultural intensification. The seven species on both the BAP list and found in this study all declined between 38 and 100%. In the current study, six of them were still common in the semi-natural grasslands in the boreal landscape: *Melitaea athalia*, *Boloria selene*, *B. euphrosyne*, *Argynnis aglaja*, *A. paphia* and *A. adippe* all occurred in  $\geq 65\%$  of the sites.

### 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 boreal coniferous-dominated landscape. The species richness and number of individuals were generally higher, compared with results from landscapes dominated by arable fields (Bergman et al. 2004). Further, the butterfly fauna was rich in species associated with low-productivity grasslands, a habitat declining in other countries in Western Europe. These small, semi-natural grasslands in the boreal landscape may therefore be important for biodiversity in Western Europe. However, the changes in agricultural practices and land use in Sweden may cause these areas to be abandoned if the process continues. The decrease in small dairy farms in Sweden is especially harmful as these often graze the small semi-natural grasslands in the boreal landscape. The result of the rationalisation may be a landscape divided into closed forest and intensive agricultural areas with low heterogeneity. Several studies have shown the importance of landscape heterogeneity and quality for species richness and persistence (Fahrig 2001; Schneider and Fry 2001; Weibull et al. 2003). A recent Swedish study comparing butterfly species richness between 1981 and 2002 in 13 grassland sites, including 8 reserves, showed a high number of local extinctions, indicating the importance of both management and the surrounding landscape (Öckinger et al. 2006).

Besides the effect of the landscape on 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 high nectar abundance, for example, 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. 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 future extinctions as well as taking historical connectivity into consideration.

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## Appendix

**Appendix 1** Butterfly species and their frequency and abundance at 60 sites in Östergötland, Sweden (Ög, Swe)

Species	No. of occurrences	No. of ind	Association with density of semi-natural grasslands	Explained variance (%)
<i>Melitaea athalia</i>	60	1,694	–	3.9
<i>Aphantopus hyperantus</i>	60	2,621	+	3.5
<i>Coenonympha arcania</i>	60	1,009	+	0.7
<i>Gonepteryx rhamni</i>	58	382	–	11.8
<i>Argynnis aglaja</i>	57	757	+	0.4
<i>Leptidea reali/L. sinapis</i>	57	442	+	8.1
<i>Pieris napi</i>	56	577	+	2.1
<i>Boloria selene</i>	56	1,182	+	0.4
<i>Boloria euphrosyne</i>	54	532	+	3.3
<i>Lycaena phlaeas</i>	53	208	+	1.2
<i>Coenonympha pamphilus</i>	53	438	+	12.8
<i>Polyommatus icarus</i>	52	611	+	0.01
<i>Argynnis paphia</i>	51	312	+	0.09
<i>Inachis io</i>	46	182	–	0.9
<i>Ocholdes faunus</i>	41	97	–	0.04
<i>Aglais urticae</i>	40	110	–	8.1
<i>Argynnis adippe</i>	39	150	–	6.1
<i>Erebia ligea</i>	39	176	–	0.4
<i>Lycaena virgaureae</i>	39	194	–	0.04
<i>Thymelicus lineola</i>	34	118	+	0.4
<i>Lasiommata maera</i>	33	137	+	0.7
<i>Polyommatus semiargus</i>	32	123	+	4.0
<i>Erynnis tages</i>	32	91	+	4.8
<i>Polyommatus amandus</i>	31	123	+	6.0
<i>Pyrgus malvae</i>	31	63	+	0.3
<i>Hesperia comma</i>	30	156	+	3.7
<i>Anthocharis cardamines</i>	28	41	+	7.5
<i>Callophrys rubi</i>	27	43	+	0
<i>Maniola jurtina</i>	27	292	+	12.2
<i>Plebeius argus/P.idas</i>	25	64	+	1.4
<i>Brenthis ino</i>	25	114	+	0.2
<i>Zygaena lonicerae</i>	23	173	+	1.4
<i>Polygonia c-album</i>	20	27	+	0.5
<i>Zygaena filipendulae</i>	20	135	+	1.4
<i>Nymphalis antiopa</i>	17	23	–	0.8
<i>Zygaena viciae</i>	15	54	+	4.6
<i>Pieris brassicae</i>	13	18	–	0.4
<i>Zygaena osterodensis</i>	13	55	+	2.6
<i>Adscita statices</i>	13	18	+	0.7

## Appendix 1 continued

Species	No. of occurrences	No. of ind	Association with density of semi-natural grasslands	Explained variance (%)
<i>Pieris rapae</i>	11	13	–	2.3
<i>Lycaena hippothoe</i>	10	18	+	1.4
<i>Issoria lathonia</i>	7	15		
<i>Pararge aegeria</i>	7	10		
<i>Aricia artaxerxes</i>	7	16		
<i>Celastrina argiolus</i>	7	33		
<i>Glaucopsyche alexis</i>	6	7		
<i>Aporia crataegi</i>	5	6		
<i>Colias palaeno</i>	4	12		
<i>Vanessa cardui</i>	3	3		
<i>Lasiommata petropolitana</i>	3	4		
<i>Hipparchia semele</i>	3	6		
<i>Neozephyrus quercus</i>	3	4		
<i>Plebeius optilete</i>	3	3		
<i>Argynnis niobe</i>	2	2		
<i>Carterocephalus silvicola</i>	2	4		
<i>Thecla betulae</i>	1	1		
<i>Melitaea cinxia</i>	1	4		
<i>Boloria aquilonaris</i>	1	1		
<i>Vanessa atalanta</i>	1	1		
<i>Limenitis populi</i>	1	1		
<i>Lasiommata megera</i>	1	4		
<i>Cupido minimus</i>	1	1		
<i>Hamearis lucina</i>	1	2		
<i>Hemaris tityus</i>	1	1		

Positive or negative association with density of semi-natural grasslands and explained variance in the pRDA are shown for species with  $\geq 10$  occurrences. The landscape factor, log 5000, was used as an explanatory variable ( $P = 0.0152$ ) and nine site variables were used as covariables, thereby eliminating most of the differences in site quality

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