Management of semi-natural grasslands for butterfly and moth communities

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II Pöyry, J., Lindgren, S., Salminen, J. & Kuussaari, M. (2005) Responses of butterfly and moth species to restored cattle grazing in semi-natural grasslands. Biological Conservation 122: 465-478.

III Pöyry, J., Luoto, M., Paukkunen, J., Pykälä, J., Raatikainen, K. & Kuussaari, M. (2006) Different responses of plants and herbivore insects to a gradient of vegetation height: an indicator of the vertebrate grazing intensity and successional age. Oikos 115: 401-412.

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Contributions

	I	II	III	IV
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Contents

Summary

1. Introduction

Agricultural landscapes have gone through major changes in Europe during the last century, with the simultaneous but opposing forces of intensification and marginalization causing abandonment of traditional land uses such as grazing and mowing of semi-natural habitats (Bignal and McCracken 1996; Krebs et al. 1999; Benton et al. 2003; Young et al. 2005). Species diversity of semi-natural grasslands as well as other species-rich agricultural landscapes has severely declined following a widespread loss and fragmentation of these habitats with remarkably high biological diversity (Pykälä 2000; WallisDeVries et al. 2002). For example, in Finland the total area of open semi-natural habitats has declined to <1% compared with the situation in the late 1800s (Pykälä 2001). Not surprisingly, species inhabiting semi-natural habitats have also declined, with an increasing number of species now classified as threatened. Thus 22% of all threatened species in Finland inhabit primarily semi-natural habitats according to the most recent Red Data Book (Rassi et al. 2001; Pöyry et al. 2004), and 60% of butterflies inhabiting primarily semi-natural grasslands have declined during the past 50 years (Kuussaari et al. 2007).

The value of traditional agricultural habitats for biodiversity has been increasingly recognized in recent decades (Bignal and McCracken 1996; Pykälä 2000). Currently, research on the remaining species-rich low-intensity agricultural landscapes has a high priority in many European countries. The objective is to manage and restore networks of such habitats that would ensure species survival and maintain viable ecological processes and ecosystem services (Sutherland 2002; Mattison and Norris 2005; Donald and Evans 2006; Kleijn et al. 2006). National agri-environment schemes (involving e.g. organic farming, see Bengtsson et al. 2005) are the main tool for the conservation and restoration of high-diversity agricultural areas in Europe, and these schemes have been observed to have positive effects on some although not all species of agricultural landscapes (Kleijn et al. 2001; Kleijn and Sutherland 2003; Feehan et al. 2005; Kleijn et al. 2006). Therefore, it is becoming evident that new measures such as large-scale habitat restoration (WallisDeVries 1995; Sutherland 2002) or targeted zonal schemes particularly focused on biodiversity conservation (Feehan et al. 2005) may be necessary. Multinational initiatives to promote both ecologically and socially sustainable agriculture in Europe, involving e.g. the High Nature Value (HNV) areas, have been put forward to halt the loss of biodiversity in agricultural areas (European Environment Agency (EEA) 2004).

The agri-environment schemes involve support for the management of semi-natural grasslands in many European countries, including Finland (Salminen and Kekäläinen 2000). The two main methods are mechanical mowing and grazing by vertebrate animals (Bakker 1989, 1998), the latter being currently more important of the two in Finland (Pykälä 2001; Vainio et al. 2001). High grazing intensity is usually recommended in management in order to maintain and restore high species richness of vascular plants in grasslands (e.g. Bakker 1998; Olff and Ritchie 1998). The requirements of many other organisms including insects are less well known, but evidence is accumulating that many invertebrate groups tolerate the effects of grazing poorly compared to plants (Morris 2000; Bell et al. 2001; Swengel 2001). In addition, large differences in responses to grazing have been reported among individual species of grassland insects. These observations suggest that management

Box 1. The structural diversity hypothesis

The shift of maximal diversity of insects to higher vegetation in comparison to the maximal diversity of plants is commonly explained by the observation that structural diversity of tall vegetation is greater than that of low vegetation (Morris 1971, Lawton 1983). Consequently, more suitable niches (breeding and foraging resources) for grassland-inhabiting insects are available in tall, extensively managed or successional vegetation compared with short, intensively managed vegetation (Southwood et al. 1979, Morris 1990a, 2000). In addition, increasing successional age allows invertebrates with low dispersal abilities to colonize the vacant niches created by succession (Morris 1990b, Gibson et al. 1992).

In agreement with this explanation, a much greater number of species of butterflies and moths has been observed to prefer abandoned successional semi-natural grasslands with tall vegetation than actively grazed pastures with low vegetation (e.g. Balmer and Erhardt 2000, Franzén & Ranius 2004).

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Morris, M.G. (1990b) The Hemiptera of two sown calcareous grasslands. I. Colonization and early succession. J. Appl. Ecol. 27: 367-378.

Morris, M.G. (2000) The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. Biol. Conserv. 95: 129-142.

Southwood, T.R.E., Brown, V.K. and Reader, P.M. (1979) The relationships of plant and insect diversities in succession. Biol. J. Linn. Soc. 12: 327-348.

recommendations should not be based on any single group of organisms (Niemelä and Baur 1998; Pärt and Söderström 1999; Söderström et al. 2001; Vessby et al. 2002; Davis et al. 2007). The transformation of this observation into actual management has only just begun, with the exception of Great Britain, where much work has already been done (Brown et al. 1990; Morris 1990a).

One option for habitat restoration in Europe is to restore former but abandoned semi-natural grassland pastures that have remained largely unforested and thus maintained at least part of their original flora and fauna. Studies of restoration have focused mainly on single insect species with a high conservation value (e.g. Thomas 1991), whereas studies covering communities

Box 2. The "dynamic equilibrium model" (DEM) of Huston

This model is based on the general observation that only a small fraction of biomass and energy is transferred to the next higher trophic level in food chains (Huston 1979, 1994). Therefore biomass, population sizes and growth rates will be lower in higher trophic levels, and according to simulations of the Lotka-Volterra competition model, recovery from mortality-inducing disturbances will consequently be slower (Huston 1979, 1994). Thus, a given frequency or intensity of disturbance is expected to eliminate more species at higher trophic levels. The model further predicts that species richness of specialist herbivores more closely follows the pattern of species richness of vascular plants, whereas species richness of generalist herbivores is more dependent on biomass production (Huston and Gilbert 1996). Therefore, the maximum species richness of specialist herbivores should occur in lower vegetation compared with generalists.

Consistently with Huston's model, Tscharntke (1997) showed that species richness of insect parasitoids (higher trophic level) was lower than that of insect herbivores (lower trophic level) in unmanaged compared with grazed reed vegetation. It has also been shown that the direct effects of grazing may disrupt multitrophic interactions in plant-herbivore-parasitoid food chains, irrespectively of the structural complexity or taxonomical diversity of the vegetation (Kruess and Tscharntke 2002).

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Huston, M. (1979) A general hypothesis of species diversity. Amer. Nat. 113: 81-101.

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of insects have hitherto been lacking (though see WallisDeVries and Raemakers 2001; Öckinger et al. 2006). Furthermore, most published examples of habitat restoration are confined to abandoned cultivated fields or species-poor improved grasslands (e.g. Morris 1990b; Gibson et al. 1992a). In the studies on the effects of grazing on single species inhabiting semi-natural habitats, both positive and negative responses have been reported, suggesting subtle species-specific responses to the onset of grazing (Thomas 1991; Oates 1995; Dolek and Geyer 2002; Saarinen et al. 2005).

Two main hypotheses have been put forward to explain the weaker tolerance of insects as compared to plants in their responses to the effects of grazing. The first explanation is based on the observation that tall grassland vegetation maintains a much greater structural diversity than does low vegetation (see **Box 1**). The second explanation suggests that maximal species richness in higher trophic levels (i.e. herbivores and their predators or parasitoids) shifts towards higher vegetation due to the weaker tolerance of disturbances caused by their smaller biomass and population sizes (see **Box 2**).

Box 3. Metapopulation theory

The metapopulation theory predicts that the probability of occurrence and population density of individual species increase with increasing habitat patch area and regional density of suitable habitat patches (Hanski 1999, 2005). Similarly, the community-level prediction is that species richness and total abundance of species increase with increasing habitat patch area and regional density of the suitable patches. Similar predictions have been made by the theory of island biogeography (MacArthur & Wilson 1967). Hanski & Gyllenberg (1997) and Hanski (2005) have shown that the basic model of the theory of island biogeography can be derived from the general metapopulation model.

The almost universal pattern of positive relationship between habitat area and species richness has also been verified in studies of insect communities inhabiting fragmented agricultural landscapes (Steffan-Dewenter & Tscharntke 2002, Tscharntke at al. 2002). In contrast, only a few studies on insects in agricultural landscapes have reported a positive effect of habitat connectivity on species richness (Wettstein & Schmid 1999, Öckinger & Smith 2006) or total abundance (Steffan-Dewenter 2003).

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Öckinger, E. and Smith, H.G. 2006. Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands Oecologia 149: 526-534.

Steffan-Dewenter, I. (2003) Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. Conserv. Biol. 17: 1036-1044.

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Tscharntke, T., Steffan-Dewenter, I., Kruess, A. and Thies, C. (2002) Characteristics of insect populations on habitat fragments: A mini review. Ecol. Research 17: 229-239.

Wettstein, W. and Schmid, B. (1999) Conservation of arthropod diversity in montane wetlands: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. J. Appl. Ecol. 36: 363-373.

Three types of management actions have been proposed to accommodate the requirements of insects that suffer from intensive grazing: (1) rotational grazing with a cycle of a few years (Smith 1940; Morris 1969), (2) extensive grazing (not all plant production is consumed by the grazers, see WallisDeVries et al. 1998) in larger pastures creating variable sward structures (Brown et al. 1990), and (3) varying grazing intensity at the landscape level (Lörtscher et al. 1994; Fuhlendorf and Engle 2001; WallisDeVries et al. 2002). All three methods aim at increasing spatial heterogeneity in vegetation structure and they are thus consistent with the concept of regional patch dynamics (Levin and Paine 1974; Pickett and White 1985; Fuhlendorf and Engle 2001). These models predict that the highest species diversity of insects occurs in landscapes in which only a fraction of the total area is disturbed annually by management (cf. Connell 1978;

Pickett and White 1985). In general, habitat heterogeneity has been found to be crucial in attempts to maintain high species diversity in agricultural landscapes (Benton et al. 2003). However, more research is needed to assess the effects of these proposed management regimes on different grassland taxa. For example, empirical studies on the long-term effects of rotational grazing are still lacking, even though this concept was first presented in the literature more than 60 years ago (Smith 1940).

In addition to variation observed in local habitat quality, numerous studies have shown that high regional density of suitable habitat has a positive effect on the occurrence and abundance of insect species inhabiting open semi-natural habitats (e.g. Thomas and Hanski 2004). This observation is in accordance with the predictions of the metapopulation theory (Hanski 1999, 2005). The scope of the metapopulation theory may be further extended from the level of single species to the level of communities (Hanski and Gyllenberg 1997; Leibold et al. 2004; Hanski 2005), and predictions may be made on the effects of habitat connectivity on species richness and total abundance of species (see **Box 3**).

2. Aims of the thesis

The main aims of this thesis are:

1. To study which factors of local habitat quality have the greatest effect on insect communities living in Finnish semi-natural grasslands, with a special focus on the effects on butterflies and moths of grassland management by cattle grazing.

2. To disentangle the relative contributions of habitat patch area, habitat connectivity and various measures of local habitat quality on the observed variation in species richness and total abundance of butterflies and moths.

3. To evaluate the effectiveness of the current management practices in use in Finland for insect conservation, and if necessary to suggest improvements to the current practices.

As cattle grazing is currently the main method of management in semi-natural grasslands as well as a significant component of the Finnish agri-environment scheme, it is important to obtain better knowledge on e.g. the effects of grazing intensity on different species and groups of species inhabiting semi-natural habitats. With funding from the agri-environment scheme, cattle grazing has been restarted in a large number of previously abandoned semi-natural grasslands, and thus there is urgent need for quantitative evaluations of the success or possible limitations of this type of restoration.

I chose butterflies and moths as the focal study group of insects because their ecology is particularly well known (e.g. Boggs et al. 2003), their populations can be readily monitored using standard monitoring methods (Pollard and Yates 1993), and because comparative studies suggest that they represent relatively well other insect groups inhabiting semi-natural habitats (Thomas 2005).

3. Material and methods

Field studies

Empirical data on the occurrence and abundance of butterflies and moths were collected and several environmental variables were measured in 1999-2000 in 79 semi-natural grassland areas situated in SW Finland. Three types of observational studies were conducted at these sites.

Firstly, three types of mesic semi-natural grassland sites with differences in their management history were compared in order to study the effects of restorative grazing on butterfly and moth communities: (1) old continuously grazed pastures with a known history of grazing extending at least for several decades (n = 11 sites), (2) pastures where grazing had been resumed 3 to 8 years ago following at least ten years of abandonment (n = 10; Fig. 1c), and (3) abandoned former pastures, where grazing ceased at least ten years ago (n = 12) (**I, II**). All study sites were situated in the regions of Varsinais-Suomi and Uusimaa in SW Finland. The areas of study sites ranged from 0.29 to 1.31 ha in 1999, whereas in 2000 all sites were 0.25 ha in size. The focus of this sampling design was on species richness, total abundance, diversity, species composition (**I**) and abundances of individual species (**II**) of butterflies and moths. Sampling of butterflies and moths and measurements of the environmental variables were conducted during 1999-2000.

Secondly, the relative contributions of habitat patch area, habitat connectivity and local habitat quality on species richness and total abundance of butterflies and moths were compared among 48 replicate landscapes to test the predictions of the metapopulation theory at the community level (**IV**). Here, the study sites included old continuously grazed pastures (n = 22; Fig. 1a,b) and abandoned former pastures (n = 26; Fig. 1d) with 2-50 years since the cessation of grazing. All sites were situated in the regions of Uusimaa (n = 24) and Pirkanmaa (n = 24) in SW Finland. In addition to the focal grassland patch, other semi-natural grasslands within a radius of 1.5 km were mapped in order to obtain a measure of regional habitat connectivity (**IV**). Sampling of butterflies and moths and measurement of the environmental variables were performed in 2000.

Thirdly, subsets of old continuously grazed (n = 32) and abandoned former pastures (n = 36) of semi-natural grasslands used in studies **I**, **II** and **IV** were combined to test the two main hypotheses about the differences in the responses of vascular plants and herbivorous insects to the intensity of management (**III**).

Butterfly and moth transect counts

Butterflies and moths were counted using an area-census modification (Douwes 1976) of the commonly applied transect method (Pollard 1977; Pollard and Yates 1993). A serpentine-shaped transect was placed in each study site, so that in 1999 the searching time was proportional to the area of the site (11 min/0.25 ha), whereas in 2000 a transect of 350 m in length was placed in each 0.25 ha study plot (**I**, **II**, **III**, **IV**). These sampling schemes were applied in order to obtain comparable estimates of species richness and density among the study sites.

In a subset of 48 focal grasslands, the area surrounding the 0.25 ha study plot was searched using a searching time that was related logarithmically to the area (**IV**). This was done in order to obtain an approximate estimate of species richness of butterflies and moths inhabiting the entire grassland area.

Butterflies and moths were counted four times during 1999 and seven times during 2000. The study period extended from late May to late August, thus covering the main flight season of butterflies and moths in Finland.

Environmental variables

Local scale

Several environmental variables describing variation in local habitat quality were measured/estimated for each study site. Many of these were related to the effects of grazing intensity and successional age on vegetation structure, both directly (e.g. mean vegetation height, proportion of grazed vegetation, cover of bare soil, cover of mosses) (**I**, **II**, **III**, **IV**) and indirectly (e.g. species richness and density of vascular plants, nectar plant abundance) (**I**, **II**, **III**, **IV**). Measures of vascular plant species richness and density were based on parallel studies on vascular plant communities (see Pykälä 2003; Raatikainen et al. 2007). Other local variables included solar radiation (**I**, **II**, **IV**), which was calculated using slope aspect and direction, and weather during transect counts (temperature, proportion of sunshine, cloudiness and windiness) (**I**, **II**, **IV**).

Fig. 1. Four examples of mesic semi-natural grasslands with different management history and current management intensity: (a) old pasture with intensive grazing management (Pernaja, Malmgård, July 2000; photo Juho Paukkunen), (b) old pasture with extensive grazing management (Pornainen, Jokivarsi, July 2000; photo Juho Paukkunen), (c) restored

*pasture with intensive grazing management (Somero, Häntälä, site 2b in **I**, **II**, August 1999; photo Mikko Kuussaari), and (d) former pasture abandoned 35 years prior to the study (Inkoo, Backaviken, July 2000; photo Juho Paukkunen).*

Regional scale

Geographical coordinates (latitude and longitude) of each study site were determined and included in statistical models to examine possible geographical trends in species richness and total abundance of butterflies and moths (**I**, **IV**).

Other semi-natural grasslands within a radius of 1.5 km from the focal grassland patch were mapped in each of 48 replicate landscapes using aerial photographs and topographic maps and following field evaluations digitized in GIS (ArcView 3.1; Esri Ltd., Redwoods, CA, USA). Habitat connectivity was calculated for each focal patch using Hanski's (1994) incidence function-based connectivity index S_i (**IV**):

$$S_i = \sum_{i \neq j} e^{-\alpha d_{ij}} A_j^b \qquad (1)$$

where S_i is the connectivity of patch *i*, α is a coefficient of the negative exponential function that determines how the weight given to the surrounding patches decreases with distance, d_{ij} is distance between patches *i* and *j* (precision 0.001 km), A_j is area of patch *j* (precision 0.01 ha), and *b* scales emigration to patch area. S_i gives most weight to large patches that are located close to the focal site.

Statistical methods

Generalized linear models (GLM, McCullagh and Nelder 1989; Nicholls 1991; Crawley 1993) were used to analyse the effects of the environmental variables on species richness and total abundance of butterflies and moths (**I**). Nonparametric Kruskall-Wallis test was used to compare species richness, total abundance, diversity and evenness of butterflies and moths between the three grassland types with dissimilar management histories (**I**). Multivariate ordination with non-metric multidimensional scaling (NMDS, Clarke 1993; McCune and Grace 2002) was applied to compare species composition between the grassland types (**I**).

Generalized linear models (GLM) and indicator species analysis (ISA, Dufrêne and Legendre 1997) were used to compare abundances of individual species of butterflies and moths between the three grassland types with different management history (**II**). Ordinations with non-metric multidimensional scaling (NMDS) were used to illustrate the centre points of abundance of individual species in the ordination space (**II**).

Generalized additive models (GAM, Hastie and Tibshirani 1990; Yee and Mitchell 1991) were fitted to predict species richness of vascular plants and butterflies and moths along the gradient of vegetation height. Randomized permutation of the data (i.e. bootstrapping, e.g Krebs 1998) was used to refit the plant as well as butterfly and moth GAMs, and Wilcoxon signed rank test was used to compare locations of maximal species richness along the vegetation height gradient (**III**).

Variation partitioning (VP, Borcard et al. 1992) based on generalized linear modelling (GLM) and hierarchical partitioning (HP, Chevan and Sutherland 1991) were used to analyse the relative independent contributions of habitat patch area, connectivity and habitat quality on species richness and total abundance of butterflies and moths (**IV**).

4. Principal results and discussion

Management history and butterfly and moth communities

Highest species richness and total abundance of butterflies and moths were observed in abandoned former pastures, whereas there were no differences between old and restarted pastures (**I**; Fig. 2a,b). By contrast, highest diversity and evenness of butterflies and moths were observed in old continuously grazed pastures, and lowest diversity and evenness were observed either in restarted or abandoned pastures (**I**; Fig. 2c).

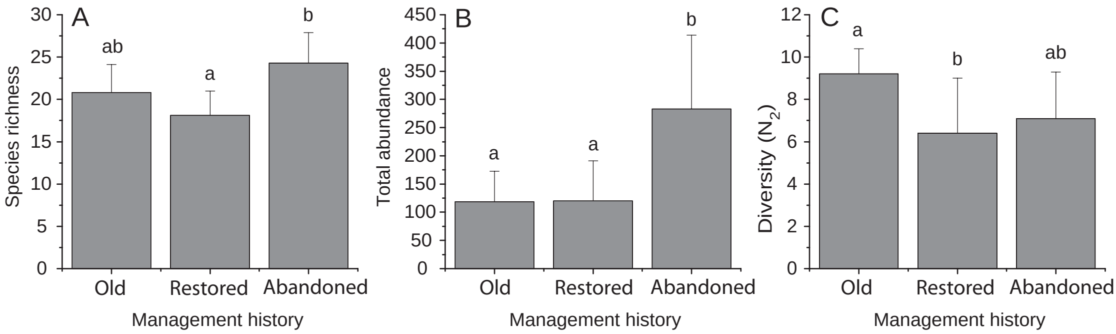

*Fig. 2. Comparison of community attributes for the grassland-preferring butterflies and moths between three pasture types differing in management history (old, restored and abandoned pastures): (a) species richness, (b) total abundance, and (c) Hill's diversity index N_2 = (Simpson's index)$^{-1}$ = $(\sum p_i^2)^{-1}$, where p_i = proportion of species i. The figure is based on results presented in Table 1 of **I**. Letters above bars indicate groups that differ significantly ($p < 0.05$) from each other according to* a posteriori *–test.*

Similar observations of increased species richness of insects and other arthropods due to relaxation of grazing intensity or abandonment of grazing have been reported in several previous studies (for reviews see Morris 2000; Bell et al. 2001; Swengel 2001) following the seminal studies conducted in Great Britain in the 1960s (e.g. Morris 1967, 1969). Increase in species richness under less intensive grazing management (Söderström et al. 2001; Kruess and Tscharntke 2002a; WallisDeVries et al. 2007) or increasing successional age since the cessation of grazing (Erhardt 1985; Balmer and Erhardt 2000; Franzén and Ranius 2004) has also been observed in studies of butterflies and moths.

Two main hypotheses have been put forward to explain the sensitivity of grassland insects to disturbances caused by grazing animals. Firstly, changes occur in species composition and perhaps more importantly in the structural diversity of vegetation due to long-term effects of vertebrate grazers, and these changes in vegetation have indirect effects on insect communities (Morris 1971; Lawton 1983; Morris 2000). A much greater number of ecological niches (for both breeding and foraging) is available in tall vegetation compared with low vegetation created by intensive grazing (**Box 1**; Southwood et al. 1979; Morris 1990a, 2000). Secondly, direct disturbance by grazing animals results in disruption of multitrophic interactions in food chains (Tscharntke 1997; Kruess and Tscharntke 2002b), an explanation that is congruent with the predictions by Huston's (**Box 2**; 1979; 1994) "dynamic equilibrium model".

Even though the greatest number of insect species may inhabit semi-natural grasslands that have been abandoned a few years earlier, in the boreal climates these habitats become gradually overgrown, colonized by bushes and trees, and the successional changes eventually result in elimination of the insect fauna typical of open habitats (**III**, Erhardt 1985; Balmer and Erhardt 2000). Therefore, in order to maintain populations of insect species inhabiting semi-natural grasslands, it is necessary to interrupt and reinitiate the natural succession leading to closed forest by introducing some kind of disturbance, typically mowing or grazing by vertebrate animals. A rotational management scheme has been proposed as a tool to meet the requirements of insects with low tolerance to intensive management (e.g. Smith 1940; Morris 1969).

The species composition of butterflies and moths did not differ between old and restarted pastures but was significantly different in abandoned pastures (**I**), suggesting that after about five years of renewed grazing the species composition of insects already resembles the targeted species composition typical of old pastures. This result is in contrast to the above observations that species richness and total abundance were lower in restored pastures than in abandoned pastures, and diversity and evenness were lower in restored pastures than in old pastures. These contradictory results make the evaluation of restoration success difficult, and apparently the responses of individual species – especially those that are declining or threatened – need to be examined before drawing final conclusions concerning butterflies and moths. Unfortunately, possible indicator values of individual species are often unknown, and hence it may be necessary to base management decisions on community-level knowledge.

Management history and individual species of butterflies and moths

Two statistical methods, GLM and ISA, were used to investigate the consequences of management history on the occurrence and abundance of particular species of butterflies and moths at the grassland sites. The two methods produced qualitatively similar results for the preference of butterfly and moth species for the three pasture types (**II**). A larger number of species (n = 12) had their highest occurrence and abundance in abandoned pastures compared with old and restored pastures, whereas only three species were most abundant in old pastures. Furthermore, three species occurred most abundantly in both abandoned and restored pastures, being thus indicative of a slow changes in species composition in the course of restoration. However, species preferring old pastures had not become more abundant in restored pastures after 5 years of resumed grazing, and therefore successful restoration of semi-natural grasslands appears to need more time (**II**).

A similar time lag in the responses of species has been observed in other studies of grassland restoration focusing on herbivorous insects (Gibson et al. 1992a; Mortimer et al. 2002). Factors that may hinder colonization of the restored pastures by the old pasture species include (1) lack of larval host plants and suitable vegetation structures (Thomas 1991; Dolek and Geyer 2002) that species need to complete their life-cycles, and (2) lack of adjacent conspecific populations from which colonizing females could immigrate (e.g. Thomas and Hanski 2004). The latter cause would suggest a sparse regional network of habitat patches in relation to the dispersal ability of the species (Hanski 2005). Both causes may have contributed to the low rate of change in species in response to environmental changes due to restoration.

The few species preferring old pastures show mostly declining distributional trends in Finland (**II**), which observation makes an important addition to the evaluation of restoration success based on community-level surrogates (**I**). Thus, it appears that a long continuous history of grazing is also important for a number of grassland-inhabiting insect species (cf. Dauber et al. 2006), as was previously firmly established for vascular plants (Bakker 1998; Eriksson et al. 2002; Pykälä 2003; Lindborg and Eriksson 2004). Due to their declining population trends, insect species associated with old continuously grazed pastures may actually be better indicators of successful restoration than the majority of species associated with abandoned pastures. However, quantitative comparisons between successional preferences and long-term population trends covering other insect groups than butterflies and diurnal moths are currently lacking, and therefore this hypothesis needs to be tested with a larger number of species.

The fact that a large proportion of butterflies and moths is most abundant in abandoned pastures is consistent with the observation that the highest species richness of butterflies and moths occurs at less intensively managed sites compared with vascular plants (see next section). It is apparently not possible to meet the dissimilar requirements of all species and species

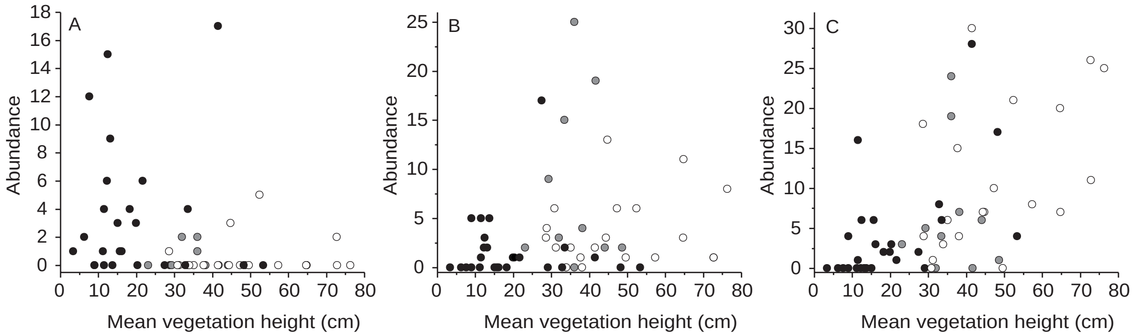

*Fig. 3. Three examples of butterfly species with different responses to vegetation height: (a) preference for low (<20 cm) vegetation (*Polyommatus icarus*), (b) preference for intermediate (30-40 cm) vegetation heights (*Polyommatus amandus*), and (c) preference for tall (>40 cm) vegetation (*Thymelicus lineola*). Black dot = old pasture, grey dot = abandoned 1-9 years ago, open circle = abandoned ≥10 years ago. Observations made in the year 2000 in old and abandoned pastures (n = 56 sites) were pooled for the scatter plots.*

groups simultaneously at a single grassland site (**I**, **II**; Fig. 3). Thus, to preserve the majority of grassland-inhabiting insects that are sensitive to intensive management (see **I**), it is imperative to preserve large areas with high structural heterogeneity of vegetation (Brown et al. 1990; Morris 1990a, 2000; WallisDeVries et al. 2007).

The preferred successional stage was different in nearly half of the butterfly and moth species between this study and previous studies conducted in Central Europe (**II**, Erhardt 1985; Balmer and Erhardt 2000). Therefore, management recommendations tailored for a particular species in one region should be applied with caution elsewhere, even in climatically similar regions.

Patterns of species richness in plants and insects in relation to vegetation height

Highest species richness of vascular plants occurred in low vegetation created by rather intensive cattle grazing, suggesting that intensive management generally favours plant species richness (**III**). This pattern of highest plant species diversity under high disturbance regime has been found in numerous previous studies, especially in those conducted in productive grasslands (Bakker 1998; Olff and Ritchie 1998; Proulx and Mazumder 1998).

By contrast, highest species richness of butterflies and moths occurred in taller vegetation associated with lower grazing intensity and more advanced successional stage (**III**), an observation that is in agreement with many previous studies (Morris 2000; Swengel 2001). It appears that the optimal conditions for species richness of butterflies and moths occur in recently abandoned former pastures, and that the decline in species richness of butterflies and moths is rather slow with increasing vegetation height, i.e. species richness remains high for a long time after the abandonment of grazing (**III**).

The differences in the highest species richness of vascular plants and their insect herbivores along a vegetation height gradient can be understood in the light of two conceptual frameworks, the structural diversity (of vegetation) hypothesis (**Box 1**; Morris 1971; Lawton 1983; Morris 2000) and the dynamic equilibrium model (DEM) of Huston (**Box 2**; Huston 1979; Huston 1994). Both hypotheses predict that butterflies and moths occur in taller vegetation than vascular plants, indicating preference for a lower intensity of grazing and longer successional age for the habitat in the former case.

In addition, species richness of butterflies and moths that are specialized in their larval host plant use peaked in lower vegetation compared with generalist species (**III**). This observation is consistent with the prediction of Huston's model (Huston and Gilbert 1996), and indicates that species richness of specialist insect herbivores is closely related to species richness of vascular plants, whereas species richness of generalist insect herbivores may be better predicted by productivity and plant biomass (**III**). These results provide further support for the application of spatially and temporally variable management regimes in semi-natural grasslands. In a network of semi-natural grasslands, some areas could be managed for specialist species and others for generalist species.

Relative contributions of local versus regional factors affecting butterflies and moths

Variables of local habitat quality showed very high independent contributions to species richness and total abundance of butterflies and moths compared with habitat patch area (**IV**). The highest independent contributions were assigned to mean vegetation height and nectar plant abundance, both of which are related to the role of current and historical management for insect communities in semi-natural grasslands (e.g. Brown et al. 1990; Morris 1990a, 2000). Mean vegetation height is related to the availability of suitable microhabitats (for both breeding and foraging) for grassland insects (e.g. Morris 1971, 2000). Abundance of nectar plants affects the distribution and movement patterns of adult butterflies (Loertscher et al. 1995) and the reproductive success of females through increased egg production (Murphy et al. 1983).

Unlike in many previous studies on insects in agricultural landscapes (Wettstein and Schmid 1999; Steffan-Dewenter and Tscharntke 2000; Krauss et al. 2003; Franzén and Ranius 2004; Öckinger and Smith 2006), only a weak effect of habitat area was detected on species richness and total abundance of non-declining butterflies and moths (**IV**). It is possible that the generally high variation of habitat quality at the study sites masked the effect of habitat patch area on species richness and total abundance of declining butterflies and moths. Furthermore, vascular plant species richness and diversity of grassland vegetation types decreased with increasing habitat area, suggesting that management history in large semi-natural grasslands had a negative effect on habitat heterogeneity possibly through nutrient enrichment (Pykälä and Heikkinen 2005; Raatikainen et al. 2007).

Regional connectivity of the habitat patch network had a positive effect on total abundance of declining butterflies and moths, suggesting that the currently most viable populations of declining butterflies and moths occur in well-connected networks of semi-natural grasslands (**IV**). Therefore, populations of declining butterflies and moths are best buffered against extinction in the densest patch networks (e.g. Hanski 2005). However, no effect of connectivity was observed on species richness of declining butterflies and moths. This was unexpected because (1) the replicate landscapes showed much variation in the degree of fragmentation (e.g. Hanski and Pöyry 2007), (2) an effective landscape-level measure of habitat connectivity was used (cf. Moilanen and Nieminen 2002) and (3) partitioning methods that can distinguish between independent and joint effects between multicollinear predictor variables were applied in the statistical analyses (e.g. Heikkinen et al. 2005). Some studies on insect communities have reported a positive relationship between connectivity and species richness (Wettstein and Schmid 1999; Summerville and Crist 2004; Öckinger and Smith 2006), but very few studies have previously found a positive effect of connectivity on total abundance (Steffan-Dewenter 2003).

The results of this study (**IV**) add further support to the view that management of semi-natural grasslands should be implemented at the landscape level. Restoring networks of differently managed grasslands is therefore crucial in order to maintain viable populations of grassland insects. With limited resources it would be reasonable to direct conservation and management efforts to those networks that can be expected to have the lowest extinction rates of declining insect species (cf. Hanski 2005).

5. Conclusions

Although the butterfly and moth species compositions of restored semi-natural pastures generally resembled the compositions observed in old pastures after about five years of resumed cattle grazing, diversity of butterflies and moths remained at a lower level compared with old pastures. Furthermore, none of the butterfly and moth species typical of old pastures had become more abundant in restored pastures compared with abandoned former pastures. Therefore, it appears that successful restoration of butterfly and moth communities inhabiting semi-natural grasslands requires a longer time than was available for monitoring in this study.

Highest species richness and peak abundance of most individual species of butterflies and moths were observed in taller grassland vegetation compared with vascular plants, suggesting a preference towards less intensive management and a more advanced successional stage of the habitat in insects. These differences between plants and their insect herbivores may be understood in the light of both the higher structural diversity of vegetation in tall vegetation (**Box 1**; Morris 1971; Lawton 1983) and weaker tolerance of disturbances by herbivorous insects than by plants (**Box 2**; Huston 1979; Huston 1994).

The ecological requirements of all species and species groups inhabiting semi-natural grasslands are probably never met at single sites with restricted areas. Therefore, it is imperative to have dissimilarly managed areas at the regional scale, but at the same time to maintain historical management regimes at the local scale. Those insect species that are sensitive to intensive grazing may be accommodated into conservation strategies by applying management regimes that enhance structural diversity of vegetation through increasing spatial and temporal variability in grazing intensity. Such regions may be created by applying extensive (i.e. not all plant growth consumed by grazing animals, see Brown et al. 1990; WallisDeVries et al. 1998), spatially variable (Lörtscher et al. 1994; Fuhlendorf and Engle 2001; Dolek and Geyer 2002) or temporally rotated (Smith 1940; Morris 1969) grazing regimes.

Regional planning and implementation of management in semi-natural grasslands is critical for meeting the requirements of different species and species groups and minimising the risk of extinction of the declining species by maintaining and restoring dense networks of semi-natural grasslands. With the limited resources often available for conservation, it would be reasonable to focus much of the management efforts in the densest networks of suitable habitat.

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