



Land Use History and the Build-Up and Decline of Species Richness in Scandinavian Semi-Natural Grasslands

O. Eriksson
Stockholm University, Sweden

S. A. O. Cousins
Stockholm University, Sweden

R. Lindborg
Stockholm University, Sweden

Follow this and additional works at: <https://uknowledge.uky.edu/igc>



Part of the [Agricultural Science Commons](#), [Agronomy and Crop Sciences Commons](#), [Plant Biology Commons](#), [Plant Pathology Commons](#), [Soil Science Commons](#), and the [Weed Science Commons](#)

This document is available at <https://uknowledge.uky.edu/igc/20/satellitesymposium3/15>

The XX International Grassland Congress took place in Ireland and the UK in June-July 2005.

The main congress took place in Dublin from 26 June to 1 July and was followed by post congress satellite workshops in Aberystwyth, Belfast, Cork, Glasgow and Oxford. The meeting was hosted by the Irish Grassland Association and the British Grassland Society.

Proceedings Editor: D. A. McGilloway

Publisher: Wageningen Academic Publishers, The Netherlands

© Wageningen Academic Publishers, The Netherlands, 2005

The copyright holder has granted the permission for posting the proceedings here.

Land use history and the build-up and decline of species richness in Scandinavian semi-natural grasslands

O. Eriksson, S.A.O. Cousins and R. Lindborg

Department of Botany, Stockholm University, SE – 106 91 Stockholm, Sweden, Email: ove.eriksson@botan.su.se

Abstract

Scandinavian semi-natural grasslands have an exceptionally high small-scale species richness. In the past, these grasslands covered extensive areas but they have declined drastically during the last century. How species richness of semi-natural grasslands was built up during history, and how species respond to land use change, are discussed. The agricultural expansion from the late Iron Age was associated with increasing grassland extent and spatial predictability, resulting in accumulation of species at small spatial scales. Although few species directly depend on management, the specific composition of these grasslands is a product of hay-making and grazing. Grassland fragmentation initially has small effects on species richness, due to slow extinction of many species. Species loss in grasslands is, however, expected in the coming decades. Restoration efforts may fail due to slow colonization. Effects of landscape configuration may be overlooked, if land use history is not considered, since present-day species richness largely reflects landscape history.

Keywords: colonization, extinction, grassland management, landscape history, regional species dynamics, restoration, species density

Introduction

Changes in habitat conditions and in the occurrence and distribution of habitats in landscapes are among the most important drivers behind species decline and loss at present as well as in future scenarios (Sala *et al.*, 2000). Landscape changes are complex and consist of an array of different processes involving climate, chemical and physical properties of the environment, and changing networks of interactions among organisms. For habitats that are declining, the process is often described as fragmentation, which has become a core issue for research in spatial ecology (e.g. Hanski, 1999) and a primary concern for conservation biology (e.g. Meffe *et al.*, 1997). Fragmentation is manifested both as a decreasing area *per se*, thus increasing the area of surrounding landscape matrix, and an increasing isolation among remaining habitat patches. In addition, fragmentation is usually also associated with other changes, such as deterioration of local habitat conditions and edge effects (Harrison & Bruna, 1999).

Despite the recognition that ecological patterns and processes exhibit scaling relationships in both time and space (e.g. Levin, 1992), and despite extensive studies of, for example, vegetation succession (e.g. Connell & Slatyer, 1977) and effects of wildfires in forests (e.g. Zackrisson, 1977), the temporal dimension of changing landscape structure has not received as much attention as spatial phenomena such as effects of area, isolation, corridors, and edges. However, there is growing evidence that landscape history is of great importance for patterns of species distribution and abundance (e.g. Peterken & Game, 1984; Foster, 1993, 2002; Austrheim *et al.*, 1999; Motzkin *et al.*, 1999; Bruun *et al.*, 2001; Cousins & Eriksson, 2002; Bellemare *et al.*, 2002; Eriksson *et al.*, 2002; Poschlod & WallisDeVries, 2002; Lindborg & Eriksson, 2004). Much of this evidence comes from studies on habitats formed or greatly influenced by human management, such as hay-meadows, pastures and managed woodland, or habitats that have developed after abandonment of management.

In temperate and nemo-boreal regions in Europe, the influence of land use is ubiquitous, extending back several millennia. The remnants of areas with such a long-lasting impact of “traditional” management are often associated with a high biological diversity. In this chapter we will focus on one example of such remnants of traditional management, semi-natural grasslands in Scandinavia. These grasslands contain an astonishing plant species richness at small spatial scales. It is not unusual to find 40-60 (and sometimes even more) different plant species per m² (Kull & Zobel, 1991; Eriksson & Eriksson, 1997; Austrheim *et al.*, 1999; Eriksson *et al.*, 2004). As these species-rich grasslands often lie embedded in a heterogeneous landscape, with many types of habitats, e.g. ditches, road verges, stone walls, midfield islets, ponds and forest margins, species diversity at the landscape scale is high, not only for plants, but for organisms such as insects and birds (e.g. Weibull *et al.*, 2000; Söderström *et al.*, 2001). Due to their biological value, semi-natural grasslands are an important concern for conservation programmes in Scandinavia. There are also several other reasons for these grasslands to be maintained, e.g. their aesthetic and cultural values, and their importance for attracting visitors. Moreover, traditional management of grasslands may exploit a developing market for locally produced milk and meat, thus contributing to economic sustainability of pastoral systems in parts of Scandinavia where agriculture is generally declining.

The objectives of this chapter are to (i) present a general hypothesis on how plant species richness of semi-natural grasslands was built up during the period of agricultural management from Late Iron Age up to the modernisation of agriculture, initiated during late 19th century, (ii) present an overview of how plant species richness responds to the ongoing fragmentation and deterioration of remaining semi-natural grasslands, and (iii) discuss some implications for conservation biology of considering land use history in analyses of species richness. The main arguments are based on our own studies performed in semi-natural grasslands in Scandinavia, and we thus primarily restrict the conclusions to this geographical region. However, although it was beyond the scope of this chapter to generalise across broader geographical areas, we consider the suggested hypotheses applicable also to other parts of northern Europe.

The historical build-up of species richness in semi-natural grasslands

The suggested hypothesis on the build-up of the high species richness characteristic of semi-natural grasslands are based on three premises: (a) there existed a large species pool of grassland species in the pre-agricultural landscape, (b) due to dispersal limitation, the colonisation of grassland sites is generally slow, and (c) the managed grasslands are generally open communities, i.e. provided eventual dispersal to a site, and recruitment is the likely outcome.

The first premise, which has been much discussed recently, concerns the origin of the plant species inhabiting semi-natural grasslands, i.e. what were the “natural” habitats for these species before the development of a permanent agriculture, with pastures and infield meadows. Today, no grassland habitat without a long-term history of management has a small-scale species density even close to what is found in semi-natural grasslands. For example, former fields which are presently grazed seldom contain more than 5-15 species per m², i.e. less than a third of what is common for semi-natural grasslands. Semi-open forests and woodlands developed on former grasslands that were abandoned during the last century have an even lower density of species. Moreover, approximately 50% of the plant species in semi-natural grasslands are seldom found in habitats which have not been subjected to management in the present-day landscape (Cousins & Eriksson, 2001). It might be tempting to interpret this as an indication of a close association between agricultural management and

the migration (or evolution) of species into regions where agriculture developed. However, as discussed in more detail by Eriksson *et al.* (2002), it is likely that the pool of species currently inhabiting semi-natural grasslands already occurred in the pre-agricultural landscape. The previously common notion that this landscape was covered with dense forests (i.e. excluding grassland plants) has been challenged by several authors (e.g. Vera, 2000; Svenning, 2002) who have suggested that there were open habitats harbouring grassland species. Moreover, the time span over which agriculture has existed is short (in the magnitude of some 10^3 years) compared to the average life span (in the magnitude of 10^5 - 10^6 years) of plant species (Eriksson *et al.*, 2002). Thus, we propose that the species that colonised human-made habitats such as pastures and meadows, existed in the pre-agricultural landscape in marginal habitats such as shores, river-banks, dry grasslands or temporary open sites created by wildfires, or natural grazing.

The second premise concerns the now well-supported notion that plants are generally dispersal-limited (Turnbull *et al.*, 2000; Eriksson & Ehrlén, 2001). Dispersal limitation implies that potentially suitable sites are not necessarily inhabited by all species that may live there. If sufficiently strong, dispersal limitation may cause distribution patterns where occupied and unoccupied sites differ in age. An example is *Thymus serpyllum*, a species that in south-central Sweden has been found positively associated with Iron Age grave fields (Eriksson, 1998). These grave fields are often covered with dry grassland and, since they were generally located in the vicinity of farms or villages, which still basically occur at the same sites, they are likely to have been influenced by management for a long time, probably over a millennium. In contrast, other dry grasslands, which by experimentation were revealed to possess the same qualities for *T. serpyllum* although they often had not harboured natural populations of this species, are likely to be of a more recent origin. This example suggests that dispersal limitation may cause delays in colonisation in the magnitude of centuries. Although *T. serpyllum* is perhaps exceptional regarding the time-scale of colonization, dispersal limitation of plants is ubiquitous in the nemo-boreal landscape. Figure 1 illustrates that regional populations of many investigated plant species in our study area have a large fraction of suitable but unoccupied sites, and that this fraction is not related (linear regression; $r = 0.67$) to the general abundance of the species in the landscape, assessed as the fraction of occupied sites. Thus, dispersal limitation is not something particular for just rare species. A corollary of dispersal limitation is that landscape configuration, basically the size of grassland sites, and their connectivity in the landscape, will influence the degree of dispersal limitation (Eriksson & Ehrlén, 2001; Lindborg & Eriksson 2004). Changing landscape configuration, e.g. increasing grassland area and connectivity, will reduce limitations to dispersal.

The third premise concerns the fate of species after they have dispersed to a potentially suitable grassland site. A common assumption in ecology is that plant communities are “niche-structured” (cf. Hubbell, 2001) implying that colonising species are hindered by the presence of already established species such that increasing species richness would retard colonization. Some experiments performed in grasslands elsewhere support this idea (e.g. Naeem *et al.*, 2000). However, experiments conducted in species-rich Scandinavian grasslands (with over 40 species per m^2) suggest that these communities are basically open to colonisation, and that removal of functional groups has only slight effects on colonisation (Eriksson *et al.*, 2004). This means that the composition of these grasslands may largely reflect the propagule pressure, i.e. the inflow of seed (or generally, diaspores) arriving at the sites.

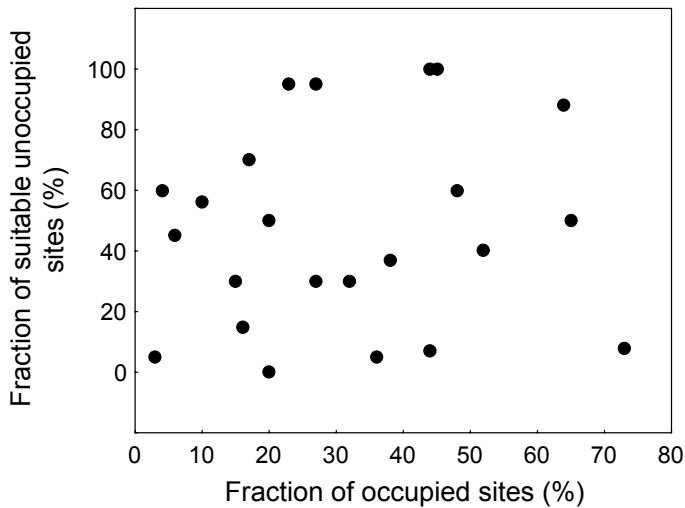


Figure 1 Dispersal limitation in 23 plant species inhabiting semi-natural grasslands or remnant habitats developed after abandonment of grasslands in the province of Södermanland, Sweden. The fraction of suitable unoccupied sites was estimated as the fraction of the unoccupied sites where suitability was detected by recruitment after experimental sowing. The fraction of occupied sites was estimated by surveys of sites subjectively determined as potentially suitable. This fraction is an approximation of abundance of species on a landscape scale. Data are from various sources: Eriksson & Kiviniemi (1999), Kiviniemi & Eriksson (1999), Ehrlén & Eriksson (2000) and O. Eriksson (unpublished data).

Combining these three premises, we suggest that the high species richness of Scandinavian semi-natural grasslands is due to an historical accumulation of species, manifested at small spatial scales. Even such small areas as a few square metres may in fact harbour the majority of species occurring at a semi-natural grassland site covering several hectares (Eriksson & Eriksson, 1997). The development of permanent farms and villages during the late Iron Age and the early Viking Age, which is still reflected in the farm structure in Scandinavia today, implied an increasing area and connectivity of grasslands, and an increase in their spatial predictability. These structural changes in the grassland configuration promoted colonization and establishment of species at existing sites. Over time, in this case a period of over a millennium, an exceptional local-scale species richness developed. Removal of biomass, due to hay-making and grazing (especially if manure was transferred to arable fields) is likely to have reduced productivity, possibly further promoting the invasibility of these grassland communities. Moreover, in the traditional agricultural landscape, seed dispersal was likely aided by moving livestock, hay and equipment (Poschlod & Bonn, 1998), acting to further reduce the effects of dispersal limitation. Thus, a characteristic feature of the semi-natural grassland plant communities in the historical landscape was the ubiquitous presence of most species at even small spatial scales. Although the specific composition and diversity of the plant communities are products of management, individual species now inhabiting semi-natural grasslands may not initially have been migrating to the landscape as a result of the development of permanent agricultural management (such as infield meadows).

This hypothesis for the build-up of species richness during the history of the agricultural landscape in Scandinavia is concordant with the so called “species-pool hypothesis” (Zobel, 1992; Pärtel *et al.*, 1996; Franzén & Eriksson, 2001). It implies that we should expect that the maximum of local species richness was reached during the later phases of the traditional agriculture, i.e. in most of Sweden at the end of 19th century, when it is possible that the limit to local species richness was actually the size of the regional species pool. This prediction is unfortunately difficult to test due to the lack of time-series of species richness. However, the prediction can be expressed as an expected positive relationship between management continuity and local species richness. Indeed, such relationships are found in studies using historical landscape information to assess grassland continuity (Cousins & Eriksson, 2002).

From the early 20th century the area of semi-natural grasslands in Sweden has declined by at least 90%. With the introduction of ley production on fields subjected to the application of artificial fertilisers, semi-natural meadows disappeared rapidly. Remaining semi-natural grasslands were used for grazing. This was also the case for the outland, i.e. grazing outside the infields, a practice that was maintained until the 1940s. Since outland grazing is usually not included in the estimated 90% reduction, the actual loss of grasslands during the last century is probably even higher. After the 1940s a second phase of modernisation of agriculture and forestry resulted in further loss of semi-natural grasslands. During the last decades programmes for restoration of semi-natural grasslands have been initiated, usually by introducing grazing by cattle or sheep. A national goal for biodiversity in Sweden states that no further reduction in semi-natural grassland area should be accepted. However, the economic situation for many farmers, despite subsidies, implies that it is far from certain that this goal will be reached (K. I. Kumm, pers. comm.).

The response of species richness to grassland fragmentation

As a result of the changes in agricultural and forestry practices, the present-day distribution of semi-natural grasslands represents only fragments of the historical distribution (Figure 2). In order to describe the response of plant species to the fragmentation of semi-natural grasslands, we have to add a fourth premise to the three premises used for developing the hypothesis of the build-up of grassland species richness: local extinction rates of established populations are generally slow for perennial species (which constitute a majority of the grassland flora). Results from population matrix simulations and analyses of distribution patterns of selected species suggest that many species may resist extinction for up to 50-100 years after abandonment of grazing (Eriksson & Ehrlén, 2001). This means that the observed distribution of grassland species in a changing landscape may reflect historical habitat conditions rather than present-day conditions. If historical land use is overlooked in spatial analyses, there is a risk of erroneous conclusions about the importance of spatial effects (area and isolation) on species richness. Lindborg & Eriksson (2004) analysed 30 semi-natural grassland sites with respect to relationships between small-scale species richness and grassland connectivity in the present-day landscape, and in the landscapes c. 50 and 100 years ago. There were no such relationships in the present-day landscape, suggesting an apparent lack of spatial landscape effects. However, for both the 50- and 100-year old landscapes grassland connectivity was linked to species richness. The best model was actually for the oldest (100-year old) landscape, where 57% of the variation in present-day species richness of the target grasslands was explained by variation in grassland connectivity within a 2 km radius from the target site.

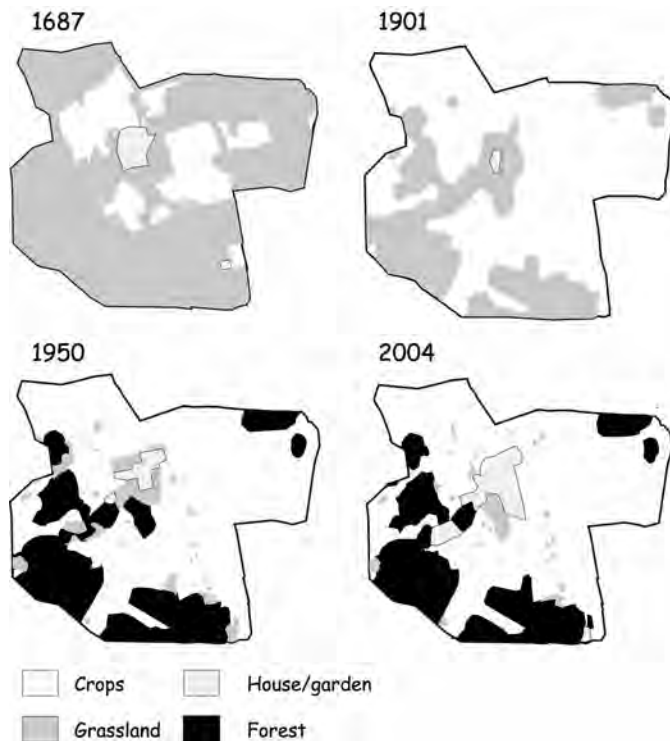


Figure 2 An example of grassland fragmentation. The distribution of semi-natural grasslands in Tösta, Sweden, from 1687 to 2004. The size of the area is c. 2 km².

The loss of species after abandonment of management occurs at a different pace for different groups of plants. Short-lived species decline relatively rapidly, and due to the existing isolation of grasslands, spontaneous colonisations balancing local extinctions are unlikely. Although good time-series are scarce, there is reasonably good evidence that typical grassland species, such as the biennial *Gentianella campestris*, decline rapidly as a result of fragmentation of the grasslands (Lennartsson & Svensson, 1996). In a study area in the province of Södermanland, 32 % of populations of *G. campestris* recorded 15 years ago had vanished (O. Eriksson, unpublished data). For long-lived species, in contrast, we still may not actually observe the decline, due to the presence of decreasing but still existing remnant populations. On a landscape scale, the “equilibrium” species richness in the modern landscape may therefore be much lower than the observed species richness. In other words, there may be an extinction debt (Tilman *et al.*, 1994; Hanski & Ovaskainen, 2002). Analyses of land-use change during the last century, combined with population monitoring, will be the best available tool to assess the time scale of these extinction processes. An additional process that is likely to influence species richness in remaining grasslands is colonisation of grassland generalists that dominate the landscape matrix surrounding semi-natural grasslands (Kiviniemi & Eriksson, 2002). This process has not yet been subject to proper study, but it may be that species with a large growth potential under conditions of increasing eutrophication slowly replace species that are less competitive under such conditions. This may cause further species loss even if management is maintained in the semi-natural grasslands.

If species, now considered specialised to semi-natural grasslands, did exist in the pre-agricultural landscape in temporary open habitats, we should ask whether the same distribution could develop if the semi-natural grasslands disappear. Will there be a “dilution process” mirroring the accumulation process that, according to the hypothesis described above, built up the exceptional species richness in semi-natural grasslands? One reason for *not* expecting this to happen is that the habitats that previously harboured grassland species no longer exist, or have been altered (e.g. by eutrophication) to such an extent that they are not any more suitable for most semi-natural grassland plants. On the other hand, sites with grassland conditions can be maintained in environments that in themselves are new, e.g. road verges provide vast areas of mown grassland, although linear in structure and often likely to be influenced by nitrogen input from the traffic. Many typical semi-natural grassland plants are indeed recorded along roads (Eriksson & Kiviniemi, 1999; Cousins & Eriksson, 2001; S. A. O. Cousins, unpublished data).

Implications for conservation biology

We can conclude that studies combining land use history and plant ecology are useful for enhancing understanding of the development of species richness in the traditional agricultural landscape, as well as for analyses of the response of species to ongoing landscape change. We believe there are four specific advantages of incorporating land use history as an aspect of research programmes aimed to promote conservation of semi-natural grasslands.

Knowledge of extinction time-lags improves interpretations of status of declining species

As illustrated by Lindborg & Eriksson (2004), evidence suggests that historical grassland connectivity has a strong effect on present-day patterns of species richness. One mechanism behind this effect is likely to be extinction time-lags, i.e. the inherent capacity of long-lived species to persist at sites despite a negative population growth rate. Also from other regions than Scandinavia, studies of plant species distributions provide indirect evidence of extinction time-lags after local habitat change (e.g. Koerner *et al.*, 1997; Motzkin *et al.*, 1999, 2002; Bellemare *et al.*, 2002; Dupouey *et al.*, 2002). The most important implication of these results is that risk assessments of endangered species associated with traditional agricultural landscapes may fail to recognize the actual status of long-lived species. Monitoring programmes are needed to evaluate the population development of putative remnant populations in order to conclude whether local hotspots of species richness, occurring isolated in a transformed modern landscape, really are sustainable. If such population studies conclude that this is not the case, the temporal dimension of the extinction time lags (assessed from population simulations, or descriptive landscape studies) may provide a time-frame for necessary conservation action.

Knowledge of colonization time lags may serve as basis for decisions on species introductions

In the same way as for extinction time lags, the colonisation time lags inferred from dispersal limitation (e.g. Ehrlén & Eriksson, 2000; Turnbull *et al.*, 2000) contribute to the phenomenon that present-day species richness is not able to catch up with rapid landscape change. This means that restoration programmes focussing on introducing traditional management, for example grazing or mowing on sites where management have been abandoned previously, may fail simply because dispersal limitation is sufficiently strong to hinder spontaneous re-colonisation (at least within a reasonable time-frame). Historical analyses provide an assessment of such a time-frame for dispersal limitation of species, i.e. the time we expect until spontaneous re-colonizations may occur. In turn, coupled with population studies of

remaining populations, these assessments provide a basis for evaluating the need for artificial introductions (or re-introductions) of threatened species (van Groenendael *et al.* 1998). Historical landscape analyses may also be a guide for the choice of sites useful for restoration, based on the assumption that a long history of previous management at a site promotes the likelihood of restoration success.

Knowledge of land use history improves assessments of spatial habitat configuration effects

If the distribution of species is far from equilibrium with the present habitat distribution, due to historical effects, an analysis of effects of landscape habitat configuration may yield strongly misleading results. For example, studies that fail to find present-day species-area relationships in fragmented habitats (Eriksson *et al.*, 1995; Kiviniemi & Eriksson, 2002) may underpin false conclusions that landscape structure does not influence species occurrences, and thus provide erroneous recommendations for conservation planning. If historical, but not present-day, landscape effects on species richness are documented, a corollary is that we should expect a continuing long-term decline of species, even if the present-day landscape is maintained. Moreover, landscape effects on local species richness are relevant for the question of whether conservation programmes should focus on a site-scale (i.e. single target sites of traditionally-managed grassland) or at a landscape scale, i.e. take into account also the qualities of the landscape surrounding the target sites. The results from our studies suggest that conservation programmes should be orientated towards a landscape scale.

Knowledge of land-use history improves assessment of combined biological and cultural values of landscapes, and strengthens public support for conservation plans

European conservation biologists have for long recognized that many of the most diverse (and highly valued) habitats are products of human management (e.g. hay-meadows, semi-natural pastures, coppiced woodland), and this view is gaining increased attention in North America (e.g. Foster 2002; Foster *et al.* 2002) and Australia (e.g. Yibarbuk *et al.* 2001; McIntyre 2001). Knowledge of the impact of historical land use for present-day biodiversity, in itself, does not provide guidelines for assigning values to species, habitats or landscapes. However, knowledge of land-use history is helpful in developing historical models for conservation programmes focusing on managed habitats, e.g. hay meadows and pastures. In addition, cultural heritage may add to the perceived values of habitats that are primarily given priorities due to biological reasons, thus promoting the acceptance for conservation actions. Studies in Sweden (Stenseke, 2001; 2004) suggest that cultural values, including the insight that landscapes are shaped by human activities during centuries or millennia, are important factors for the valuation of landscapes, both by stakeholders, residents and visitors. Appreciation of land-use history may also contribute to support traditional cultures and resolve possible conflicts in areas previously regarded as “wilderness”, for example land use by Australian Aborigines (Yibarbuk *et al.*, 2001), and reindeer grazing as a part of traditional management of the Sami culture in the Scandinavian mountains (e.g. Austrheim & Eriksson, 2001).

Conclusions

Land-use history of Scandinavian agricultural landscapes is an essential mechanism behind the development of the present-day plant species richness in semi-natural grasslands. Although human impact during the last millennia may not have been the intrinsic driver behind migration of grassland species to Scandinavia, due to the probable existence of grassland habitats in the pre-agricultural landscape, management, such as grazing and

mowing, have shaped the composition and small-scale diversity of the plant communities. Today, when concern of species loss is in focus, historical studies contribute important information for analyses of species response to land use change, particularly when estimating time-lags of species colonisation and extinction, and for the assessment of the influence of landscape on local-scale species richness. Moreover, knowledge of land-use history promotes necessary cross-disciplinary research on the valuation of traditional grasslands, and such knowledge enhances public support for conservation programmes.

Acknowledgements

We are grateful to M. Öster for comments on the manuscript, and to the Mistra programme “Management of semi-natural grasslands: economy and biodiversity” and the Swedish research council for environment, agricultural sciences and spatial planning (projects to OE and SC) for financial support.

References

- Austrheim, G. & O. Eriksson (2001). Plant species diversity and grazing in the Scandinavian mountains – patterns and processes at different spatial scales. *Ecography*, 24, 683-695.
- Austrheim, G., E. G. A. Olsson & E. Grøntvedt (1999). Land-use impact on plant communities in semi-natural sub-alpine grasslands of Budalen, central Norway. *Biological Conservation*, 87, 369-379.
- Bellemare, J., G. Motzkin, & D. Foster (2002). Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. *Journal of Biogeography*, 29, 1401-1420.
- Bruun, H. H., B. Fritzboøger, P. O. Rindel & U. L. Hansen (2001). Plant species richness in grasslands: the relative importance of contemporary environment and land-use history since the Iron Age. *Ecography*, 24, 569-578.
- Connell, J. H. & R. O. Slatyer (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, 111, 1119-1144.
- Cousins, S. A. O. & O. Eriksson (2001). Plant species occurrences in a rural hemiboreal landscape: effects of remnant habitats, site history, topography and soil. *Ecography*, 24, 461-469.
- Cousins, S. A. O. & O. Eriksson (2002). The influence of management history and habitat on plant species richness in a rural hemiboreal landscape, Sweden. *Landscape Ecology*, 17, 517-529.
- Dupouey, J. L., E. Dambrine, J. D. Laffite & C. Moares (2002). Irreversible impact of past land use on forest soils and biodiversity. *Ecology*, 83, 2978-2984.
- Ehrlén, J. & O. Eriksson (2000). Dispersal limitation and patch occupancy in forest herbs. *Ecology*, 81, 1667-1674.
- Eriksson, Å. (1998). Regional distribution of *Thymus serpyllum*: management history and dispersal limitation. *Ecography*, 21, 35-43.
- Eriksson, Å. & O. Eriksson (1997). Seedling recruitment in semi-natural pastures: the effects of disturbance, seed size, phenology and seed bank. *Nordic Journal of Botany*, 17, 469-482.
- Eriksson, Å., O. Eriksson & H. Berglund (1995). Species abundance patterns of plants in Swedish semi-natural pastures. *Ecography*, 18, 310-317.
- Eriksson, O. & J. Ehrlén (2001). Landscape fragmentation and the viability of plant populations. In: J. Silvertown & J. Antonovics (eds) Integrating ecology and evolution in a spatial context. Blackwell, Oxford, 157-175.
- Eriksson, O. & K. Kiviniemi (1999). Site occupancy, recruitment and extinction thresholds in grassland plants: an experimental study. *Biological Conservation*, 87, 319-325.
- Eriksson, O., S. A. O. Cousins & H. H. Bruun (2002). Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. *Journal of Vegetation Science*, 13, 743-748.
- Eriksson, O., S. Wikström, Å. Eriksson & R. Lindborg (2004). Species-rich Scandinavian grasslands are inherently open to invasion. *Biological Invasions* (in press).
- Foster, D. R. (1993). Land-use history (1730-1990) and vegetation dynamics in central New England, USA. *Journal of Ecology*, 80, 753-772.
- Foster, D. R. (2002). Thoreau's country: a historical-ecological perspective on conservation in the New England landscape. *Journal of Biogeography*, 29, 1537-1555.
- Foster, D. R., B. Hall, S. Barry, S. Clayden & T. Parshall (2002). Cultural, environmental and historical controls of vegetation patterns and the modern conservation setting on the island of Martha's Vineyard, USA. *Journal of Biogeography*, 29, 1381-1400.
- Franzén, D. & O. Eriksson (2001). Small-scale patterns of species richness in Swedish semi-natural grasslands: the effects of community species pools. *Ecography*, 24, 505-510.
- Hanski, I. (1999). Metapopulation ecology. Oxford University Press, Oxford, 313pp.

- Hanski, I. & O. Ovaskainen (2002). Extinction debt at extinction threshold. *Conservation Biology*, 16, 666-673.
- Harrison, S. & E. Bruna (1999). Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography*, 22, 225-232.
- Hubbell, S. P. (2001). The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, 375pp.
- Kiviniemi, K. & O. Eriksson (1999). Dispersal, recruitment and site occupancy of grassland plants in fragmented habitats. *Oikos*, 86, 241-253.
- Kiviniemi, K. & O. Eriksson (2002). Size-related deterioration of semi-natural grassland fragments in Sweden. *Diversity and Distributions*, 8, 21-29.
- Koerner, W., J. L. Dupouey, E. Dambrine & M. Benoit (1997). Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. *Journal of Ecology*, 85, 351-358.
- Kull, K. & M. Zobel (1991). High species richness in an Estonian wooded meadow. *Journal of Vegetation Science*, 2, 711-714.
- Lennartsson, T. & R. Svensson (1996). Patterns in the decline of three species of *Gentianella* (Gentianaceae) in Sweden, illustrating the deterioration of semi-natural grasslands. *Symbolae Botanicae Upsaliensis*, 31, 169-184.
- Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology*, 73, 1943-1967.
- Lindborg, R. & O. Eriksson (2004). Historical landscape connectivity affects present plant species diversity. *Ecology*, 85, 1840-1845.
- McIntyre, S. (2001). Biophysical and human influences on plant species richness in grasslands: comparing variegated landscapes in subtropical and temperate regions. *Austral Ecology*, 26, 233-245.
- Meffe, G. K., C. R. Carroll and contributors (1997). Principles of conservation biology, 2nd edition Sinauer, Sunderland, 729pp.
- Motzkin, G., P. Wilson, D. R. Foster & A. Allen (1999). Vegetation patterns in heterogeneous landscapes: the importance of history and environment. *Journal of Vegetation Science*, 10, 903-920.
- Motzkin, G., R. Eberhardt, B. Hall, D. R. Foster, J. Harrod & D. MacDonald (2002). Vegetation variation across Cape Cod, Massachusetts: environmental and historical determinants. *Journal of Biogeography*, 29, 1439-1454.
- Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy & S. Gale (2000). Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos*, 91, 97-108.
- Pärtel, M. M. Moora & M. Zobel (1996). Variation in species richness within and between calcareous (alvar) grassland stands: the role of core and satellite species. *Plant Ecology*, 157, 205-213.
- Peterken, G. F. & M. Game (1984). Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *Journal of Ecology*, 72, 155-182.
- Poschlod, P. & S. Bonn (1998). Changing dispersal processes in the central European landscape since the last ice age: an explanation for the actual decrease of plant species richness in different habitats? *Acta Botanica Neerlandica*, 47, 27-44.
- Poschlod, P. & M. F. WallisDeVries (2002). The historical and socioeconomic perspectives of calcareous grasslands – lessons from the distant and recent past. *Biological Conservation*, 104, 361-376.
- Sala, O. E. & 18 Coauthors (2000). Global biodiversity scenarios for the year 2100. *Science*, 287, 1770-1774.
- Söderström, B., B. Svensson, K. Vessby & A. Glimskär (2001). Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodiversity and Conservation*, 10, 1839-1863.
- Stenseke, M. (2001). Landskapets värden: lokala perspektiv och centrala utgångspunkter. *Choros*, 2001:1, 3-106. (In Swedish)
- Stenseke, M. (2004). Bönder och naturbetesmarker. Del 1: Bygdeperspektiv. *Choros*, 2004:1, 1-88. (In Swedish)
- Svenning, J.-C. (2002). A review of natural vegetation openness in Northwestern Europe. *Biological Conservation*, 104, 133-148.
- Tilman, D., R. M. May, C. L. Lehman & M. A. Nowak (1994). Habitat destruction and the extinction debt. *Nature*, 371, 65-66.
- Turnbull, L. A., M. J. Crawley & M. Rees (2000). Are plant populations seed-limited? A review of seed sowing experiments. *Oikos*, 88, 225-238.
- van Groenendael J., N. J. Ouborg & R. J. J. Hendriks (1998). Criteria for the introduction of plant species. *Acta Botanica Neerlandica*, 47, 3-13.
- Vera, F. W. M. (2000). Grazing ecology and forest history. CAB International, Wallingford, 506pp.
- Weibull, A.-C., J. Bengtsson & E. Nohlgren (2000). Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. *Ecography*, 23, 743-750.
- Yibarbuk, D., P. J. Whitehead, J. Russell-Smith, D. Jackson, C. Godjuwa, A. Fisher, P. Cooke, D. Choquenot & D. M. J. S. Bowman (2001). Fire ecology and Aboriginal land management in central Arnhem Land, northern Australia: a tradition of ecosystem management. *Journal of Biogeography*, 28, 325-343.
- Zackrisson, O. (1977). Influence of forest fires on the north Swedish boreal forest. *Oikos*, 29, 22-32.
- Zobel, M. (1992). Plant species coexistence – the role of historical, evolutionary and ecological factors. *Oikos*, 65, 314-320.