

# **Biological diversity values in semi-natural grasslands**

- indicators, landscape context and restoration

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Cover illustration: Stora Åsa in Södermanland, *Antennaria dioica*,  
*Gentianella campestris* and *Hygrocybe coccinea*.

Photo: Mathias Öster and Sara A. O. Cousins (Stora Åsa).

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## Biological diversity values in semi-natural grasslands: indicators, landscape context and restoration

**Abstract**—Semi-natural grasslands, which are a declining and fragmented habitat in Europe, contain a high biodiversity, and are therefore of interest to conservation. This thesis examines how plant diversity is influenced by the landscape context, and how plant and fungal diversity can be targeted by practical conservation using indicator species and congruence between species groups. Reproduction and recruitment of the dioecious herb *Antennaria dioica* was also investigated, providing a case-study on how fragmentation and habitat degradation may affect grassland plants.

Grassland size and heterogeneity were of greater importance for plant diversity in semi-natural grassland, than present or historical connectivity to other grasslands, or landscape characteristics. Larger grasslands were more heterogeneous than smaller grasslands, being the likely reason for the species-area relationship.

A detailed study on *A. dioica* discovered that sexual reproduction and recruitment may be hampered due to skewed sex-ratios. Sex-ratios were more skewed in small populations, suggesting that dioecious plants are likely to be particularly sensitive to reduced grassland size and fragmentation.

A study on indicators of plant species richness, used in a recent survey of remaining semi-natural grasslands in Sweden, revealed several problems. A high percentage of all indicator species were missed by the survey, removing an otherwise significant correlation between indicator species and plant species richness. Also, a null model showed that the chosen indicator species did not perform significantly better than species chosen at random from the available species pool, questioning the selection of the indicators in the survey. Diversity patterns of the threatened fungal genus *Hygrocybe* were not congruent with plant species richness or composition. Plants are thus a poor surrogate group for *Hygrocybe* fungi, and probably also for other grassland fungi. Implications from this thesis are that conservation of semi-natural grasslands should target several species groups, and that an appropriate scale for plant conservation may be local rather than regional.

**Keywords:** Biodiversity, connectivity, *Hygrocybe*, indicators, landscape history, plants, pollen limitation, species-area effects, surrogate species



# List of papers

The thesis is comprised of a summary and four papers, which are referred to by their Roman numerals:

- I Öster, M., Cousins, S. A. O. & Eriksson, O. Site area and heterogeneity rather than landscape context determine plant species richness in semi-natural grasslands. *Submitted manuscript*
- II Öster, M. & Eriksson, O. Sex-ratio mediated pollen limitation in the dioecious herb *Antennaria dioica*. *Submitted manuscript*
- III Öster, M., Persson, K. & Eriksson, O. Validation of biodiversity indicators used in a nationwide survey of semi-natural grasslands in Sweden. *Submitted manuscript*
- IV Öster, M. Low congruence between Waxcap (*Hygrocybe* spp.) fungi and vascular plants in semi-natural grasslands. *Submitted manuscript*

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# Introduction

Dear Reader,

This thesis examines biological values in traditionally managed grasslands, or “semi-natural grasslands”, which is a declining habitat all over Europe. Preservation and monitoring of semi-natural grasslands has a high priority in conservation in Sweden and in the European Union. Several conservation policies in Sweden concerns semi-natural grasslands, including the *Environmental and Rural Development Plan* (Anonymous, 2000) which has the aim of promoting environmentally sustainable agriculture, and the environmental quality objective *A Varied Agricultural Landscape*. The term “semi-natural” implies that the habitat is not “pristine” but rather human influenced or human made. This is correct, as semi-natural grasslands are dependent on disturbance by grazing or mowing and it may thus seem controversial and a bit paradoxical that a highly human influenced habitat can be of high conservational value. I will thus start by describing why semi-natural grasslands have a high conservational value.

## On the value of semi-natural grasslands

Several values are associated with semi-natural grasslands, i.e. cultural, aesthetical, functional, economical, and biological. Values are often controversial and a subject of intense debate that could easily fill a thesis by itself. What may be conceived as valuable for one person may not be valuable for another, and it also depends on whether something has a value only if it is useful to humans (anthropocentric) or if it can be valuable simply because it exists (biocentric). In this thesis I will focus on the values of biological diversity (or biodiversity) that are associated with semi-natural grasslands. I will not enter the debate about how, or if all biodiversity is valuable. Instead, I will use political agreements about the values of biodiversity as baseline in this thesis. Such agreements include the Swedish ratification of the UN Convention on Biological Diversity in 1992, the European Bern Convention, and the Swedish 16<sup>th</sup> environmental quality objective *A Rich Diversity of Plant and Animal Life* (Naturvårdsverket, 2003). For example, in the 16<sup>th</sup> environmental quality objective it is stated:

All species that naturally occur in Sweden shall be able to survive in long-term, have viable populations and maintain their genetic variation. Biodiversity will be preserved by safeguarding both the habitats of these species and the functions of ecosystems and processes. The natural environment, with its flora, fauna and other organisms, is an essential part of the human habitat and underpins our health and well-being.

Biodiversity has a hierarchy (e.g. genes, populations, species, communities and ecosystems), and biological values in semi-natural grasslands can be found within most levels of this hierarchy. For example, studies on plant species like *Festuca ovina* (Prentice *et al.*, 1995) and *Gentianella* spp. (Lennartsson, 1997) has demonstrated ongoing selection processes within populations, and such genetic variation has a value. However, in conservation, due to practical reasons, most emphasis is laid on the levels of populations, species and habitats and this is also the levels in the hierarchy where this thesis fits in.

Semi-natural grasslands are heterogeneous, often both in the field and the shrub layer, and contain many types of structures (old deciduous trees, ponds, ditches, stone walls, forest margins etc.). Several of the habitat types found within semi-natural grasslands are recognised on a European level to be of conservational value, i.e. habitats within the Natura 2000 network programme (Anonymous, 1979, 1992). The four most frequently occurring habitat types in Swedish semi-natural grasslands according to the Natura 2000 classification are “Fennoscandian lowland species-rich dry to mesic grasslands”, “Nordic alvar and precambrian calcareous flatrocks”, “*Molinia* meadows on calcareous, peaty or clayey-silt-laden soils” and “Fennoscandian wooded pastures” (Persson, 2005a).

Apart from several threatened habitat types, semi-natural grasslands harbour a rich diversity of species, of which several are threatened. For example, of all 3653 Red listed species in Sweden, 46% are associated with the agricultural landscape, and several of these species has semi-natural grasslands as their main habitat (Gärdenfors, 2005). Organisms associated with semi-natural grasslands include almost every species group, especially vascular plants, insects, birds, lichens and fungi (Götmark *et al.*, 1998).

When it comes to vascular plants, which is the main focus of this thesis, semi-natural grasslands are very species-rich, both in the form of a high overall richness (~600 species) and a high richness at small spatial scales (Eriksson *et al.*, 2002). It is not uncommon with over 40 plant species m<sup>-2</sup> (Pärtel *et al.*, 1996; Eriksson & Eriksson, 1997), and there are occasionally over 60 species m<sup>-2</sup> (Kull & Zobel, 1991), which is astonishingly high compared to many other habitat types in Europe. Other plant values in semi-natural grasslands include old trees, which are an important structure for both insects and lichens. Vascular plants provide the structure and character to semi-natural grasslands, and grasslands are most often described by the

floristic component they contain. Most of the conservational work has traditionally been focused around plants, although this view has recently been criticised (Pärt & Söderström, 1999; Söderström *et al.*, 2001). The core of this criticism is that a management regime that is optimal for plant diversity may not be optimal for other species groups like birds and insects.

Another group of interest to this thesis is fungi. Several threatened fungi are associated with semi-natural grasslands (Rydin *et al.*, 1997; Arnolds, 2001), including species of the agaric genera *Hygrocybe*, *Camarophyllopsis*, *Dermoloma* and *Entoloma*, the aphyllophore family Clavariaceae and the ascomycete family Geoglossaceae. Some of these fungi are a conspicuous component of the total biodiversity in these grasslands, especially species of the genus *Hygrocybe* (Waxcaps). *Hygrocybe* species are often brightly coloured and they are represented by some 60 species in Europe. Grassland fungi are one of the least investigated organism groups in semi-natural grasslands. The reason is that grassland fungi are often difficult to identify in the field and that the fungal fruiting bodies (carpophores) are often ephemeral, lasting only a few days or weeks. However, fungal richness responds negatively, like plant richness, to ceased management and nutrient enrichment of semi-natural. It is therefore possible that plant richness may be used as a surrogate group for estimations of fungal richness in grasslands. This is one of the questions that I will investigate in this thesis.

With this brief introduction I hope that the reason behind the conservation concern for semi-natural grasslands is clearer. In the following, I will focus on questions regarding diversity values of vascular plants and fungi. But before I formulate my research questions around these organism groups I need to briefly describe how values can be assessed by using indicators, and also describe the history and ecology of semi-natural grasslands.

## On the use of biodiversity indicators

Comprehensive surveys of biological values are often not an option in conservation when dealing with larger, regional scales, because of budget or time constraints. Instead, it is increasingly common to use easily measurable surrogates, or “indicators” for unmeasured biological values or environmental conditions of interest (e.g. Wilhm & Dorris, 1968; Noss, 1990; Pendergast & Eversham, 1997; Margules & Pressey, 2000; Niemi & McDonald, 2004).

A suitable indicator should have several qualities, including being easy to identify and monitor, be sufficiently sensitive to changes in the “unmeasured” value it is indicating, and distributed over the whole area of interest (cf. Noss, 1990). Following McGeoch (1998) the definition of a “biological indicator” is something (species, object, process) “that readily reflects: the abiotic or biotic state of an environment; represents the impact of environmental change on a habitat, community or ecosystem; or is indicative of the

diversity of a subset of taxa, or wholesale diversity, within an area". We can thus separate indicators into three broad categories: environmental indicators, ecological indicators and biodiversity indicators depending on the type of "biological property" it is indicating (McGeoch, 1998).

The use of indicators for biodiversity has emerged only during the last decade and the idea is to use taxa that are well known and easily monitored, that will, with some degree of accuracy, represent wholesale diversity. Most studies have used either species (Lawton & Gaston, 2001; Fleishman *et al.*, 2005), or higher taxon richness (Williams & Gaston, 1994; Gaston & Blackburn, 1995; Prendergast & Eversham, 1997) as indicator of biodiversity, or a subset of it. The results from biodiversity indicator studies are so far inconclusive. Many studies have found that statistically strong correlations between taxa are rare (Prendergast *et al.*, 1993; Prendergast & Eversham, 1997; Jonsson & Jonsell, 1999; Pärt & Söderström, 1999; Ricketts *et al.*, 2002; Vessby *et al.*, 2002; Kati *et al.*, 2004; Oertli *et al.*, 2005), although there are a few exceptions (Duelli & Obrist, 1998; Negi & Gadgil, 2002; Fleishman *et al.*, 2005). Few groups of species have been found to adequately represent all diversity, especially at finer scales (national, regional). However, indicators within groups have had more success, for example in semi-natural grasslands where a subset of plant species have been shown to adequately indicate total plant richness (Vessby *et al.*, 2002; Wittig *et al.*, 2006). In this thesis I will examine the use of biodiversity indicators for plant richness, which has been used in a recent survey of semi-natural grasslands in Sweden.

## On the history of semi-natural grasslands

The history of semi-natural grasslands is tightly linked to the history of human agriculture, which started to develop in Scandinavia at least 5000 BC and in Sweden from 3900 BC (Welinder *et al.*, 1998). The first agriculture was a slash-and burn type of farming, which created a dynamic landscape with a mosaic of woodland and open areas. During late Bronze Age to early Iron Age this was developed to a more permanent farming system with animal husbandry. In this system, permanent arable fields together with meadows for winter fodder were placed in the villages (i.e. "infields") and large grazing areas (i.e. "outland") were outside the villages. This type of system remained with few changes until the modernisation of agriculture during the late 19<sup>th</sup> century. During this period open grassland areas expanded immensely, and peaked in extent during the middle of 19<sup>th</sup> century (Gadd, 2000). The full extent is not known, but we know that there were around 1.9 million ha semi-natural grasslands left in Sweden 1927, of which 25% were meadows (Ekstam & Forshed, 2000). However, by that time much of the old outland had already been transformed to forest.

The composition and structure of the natural landscape before Neolithic times is subjected to debate. On the one hand, the “high forest hypothesis” suggests that dense deciduous forests dominated Europe from mid-Holocene, with open areas only on infertile soils or in gaps created by disturbance events (Bradshaw *et al.*, 2003 and references therein). On the other hand, the “wood pasture hypothesis” suggested by Vera (2000) and Svenning (2002), proposed that large herbivores shaped the Holocene woodlands which created a mosaic of groves and meadows, suitable for more light-demanding scrubs, trees (e.g. *Quercus*, *Corylus*) and herbs. The “wood pasture hypothesis” explains the persistence of light-demanding species between the last deglaciation, when ungulate herbivores declined sharply, and the onset of human agriculture. However, according to Bradshaw *et al.* (2003), both hypothesis have their shortcomings, and a possible resolution to the debate could be a landscape in-between these hypothesis, together with a greater mosaic of disturbance types (e.g. fire, wind, grazing). Further, the time-span during which agriculture has existed is short, compared to the evolutionary age of the average plant species. It is therefore plausible that the species that colonized semi-natural grasslands during Neolithic times already were present in the landscape, but in marginal habitats such as glades, shores, dry grasslands or alpine areas (Ekstam *et al.*, 1989; Eriksson *et al.*, 2002).

## On the decline of semi-natural grasslands

During the last 100 years there has been an extensive reduction and fragmentation of semi-natural grasslands in Sweden. The pace of this landscape change has been much quicker than the build-up phase, which took thousands of years. Of 1.9 million hectare semi-natural grasslands that remained in 1927, only 0.2 million hectare remained 1990, which is a reduction of around 90% (Bernes, 1994; Ekstam & Forshed, 2000). This decline has been seen over much of Europe (van Dijk, 1991), for example an 99% reduction in Finland (Vainio *et al.*, 2001), and a 97% reduction in England (Fuller, 1987; Blackstock *et al.*, 1999). In the Swedish contemporary landscape most semi-natural grasslands that exist are pastures on former meadows. The outland has almost entirely been transferred to forest, and former meadows on productive areas are nowadays used as arable fields. However, since this change in land use has happened during a short time-span, and because many plants are perennial and may persist as remnant populations in the landscape for long time periods (Eriksson, 1996), there is a possibility that there is a cultural legacy in the current landscape (Lindborg & Eriksson, 2004a; Helm *et al.*, 2006). This may have implications for the persistence of plant species in semi-natural grasslands today, and I will elaborate on this question in the next section.

## On the ecology of semi-natural grasslands – the regional scale

Up until the middle of the 20<sup>th</sup> century, most research focus in community ecology was on local determinants of species richness. During the last decades there has been an increased emphasis on processes external to the local community and their influence on species richness in communities (e.g. MacArthur & Wilson, 1967; Ricklefs, 1987; Schluter & Ricklefs, 1993; Hanski, 1999; Hubbell, 2001; Leibold *et al.*, 2004). Simply put, there is an upper boundary to species richness at the local scale, and it is set by the richness of suitable species at the regional scale (Schluter & Ricklefs, 1993; Pärtel *et al.*, 1996; Zobel, 1997). Local communities are connected with each other through dispersal, and local diversity is thus dependent on the regional diversity and the rate of dispersal between communities. The dispersal rate in a landscape is influenced by the configuration and spatial arrangement of communities, populations, and patches, but also by the matrix between these (Hanski, 1999; Leibold *et al.*, 2004; Kupfer *et al.*, 2006). The landscape matrix consists of landscape features outside the study system that may either enhance or decrease dispersal between communities and patches. It is thus important to study the whole landscape context, including both the communities of interest and the matrix between these, to fully understand species richness patterns in communities (Mazerolle & Villard, 1999).

Lately there has been a rapidly growing interest in incorporating the landscape context into ecological studies (see paper I). A search on Web of Science (ISI) over the period 2000-2006 with the keywords “landscape context” and “biodiversity” revealed 155 studies (search conducted 2006-10-16). Studies on individual species and processes (e.g. dispersal, pollination) may further increase this number. What has been learnt so far is that the scale at which landscape effects are manifested and the nature of the effect vary depending on organism (Turner, 2005). For species diversity in semi-natural grasslands, the overall importance of the landscape context is still somewhat unclear, as many studies show no or weak effects of the landscape context (Eriksson *et al.*, 1995; Söderström *et al.*, 2001; Dauber *et al.*, 2003; Weibull & Östman, 2003; Lindborg & Eriksson, 2004a). For plants specifically, earlier studies in semi-natural grasslands have often shown conflicting results. For example, results regarding species-area relationships in grasslands are inconclusive (Eriksson *et al.*, 1995; Bruun, 2000; Kiviniemi & Eriksson, 2002; Lindborg & Eriksson, 2004b). Also, there are no documented relationships between diversity of vascular plants and connectivity to semi-natural grasslands in the surrounding contemporary landscape (Lindborg & Eriksson, 2004a; Helm *et al.*, 2006). Instead, some studies have found that richness of vascular plants in the present landscape is correlated to the historical landscape context, and in particular the historical extent and connectivity to other semi-natural grasslands (Bruun *et al.*, 2001; Lindborg & Eriksson, 2004a; Helm *et al.*, 2006). The suggested mechanism behind this pattern is,

as was explained above, that many plant species show a slow response to habitat fragmentation and degradation (Eriksson, 1996; Eriksson & Ehrlén, 2001). This implies that either the species richness of a site is not in equilibrium with the present-day landscape connectivity and we thus have an extinction debt in the landscape, or that we underestimate the present connectivity because many plant populations are remaining in the landscape, but not necessarily in semi-natural grasslands. It should be noted that previous studies (Bruun *et al.*, 2001; Lindborg & Eriksson, 2004a; Helm *et al.*, 2006) have only incorporated the remaining semi-natural grasslands in their studies. No effort is made to assess to what degree populations of grassland plants may be present in the landscape matrix outside the target sites. It is therefore in my opinion impossible to conclude if their results indicate an extinction debt or that they underestimate the connectivity in the landscape, although Helm *et al.* (2006) do attempt to assess the extinction debt in Estonian alvar grasslands, and finds it to be quite high. In this thesis I will attempt to elucidate whether a relationship with historical connectivity reflects an extinction debt or not (paper I).

Landscape features that could potentially increase connectivity in the landscape are road verges (Tikka *et al.*, 2000; Tikka *et al.*, 2001), railway lines, power lines (Grusell & Kyläkorpi, 2003), midfield islets and abandoned grasslands (Cousins, 2006), especially on dry soils or recently abandoned. Such sites may be potential sites for transient or remnant populations and increase dispersal of grassland species (Cousins & Eriksson, 2001), although the importance of such landscape features for persistence and dispersal of local populations is unclear (van Dorp *et al.*, 1997).

## On the ecology of semi-natural grasslands – the local scale

Given that a plant propagule has dispersed to a semi-natural community, what promotes establishment and persistence of that species and a buildup of species diversity? Let me explain some key patterns and processes.

### **Species-area relationships**

One frequently occurring pattern is that species richness increases with area. Even though species-area relationships are a well known ecological pattern (MacArthur & Wilson, 1967; Lomolino *et al.*, 2006), studies on species-area relationships in grasslands have in most cases reported no effects (Eriksson *et al.*, 1995; Pärtel & Zobel, 1999; Kiviniemi & Eriksson, 2002; Lindborg & Eriksson, 2004b; Helm *et al.*, 2006) but there are exceptions (Bruun, 2000; Adriaens *et al.*, 2006). Several mechanisms for species-area effects have been suggested. They include a higher likelihood of successful colonisation events (target effect) in larger sites, reduced extinction rates because larger sites often harbour larger populations, and also a higher degree of heterogeneity within larger areas (i.e. more niches available). An increased sampling

area also implies a higher number of sampled individuals, and thus also a greater number of species due to sampling effects (area *per se* effect) (Connor & McCoy, 1979). Furthermore, a larger area can contain a higher number of distinct patches, an effect which has been called the habitat diversity hypothesis (Williams, 1964).

### **Species richness and management continuity**

Semi-natural grasslands that have been continuously managed for long periods of time are often more species rich in plants than younger grasslands, or grasslands that have experienced interruptions in management in the past. (Pärtel & Zobel, 1999; Cousins & Eriksson, 2002). The same pattern has also been found for ants (Dauber *et al.*, 2006). The reason is that all species do not have the same dispersal potential. Some species are either common in the region, or are good dispersers, and these may quickly occupy a suitable habitat. However, for more rare species, or species that are poor dispersers, establishment may take a long time. Grasslands thus accumulate species over time, and become more species rich with age (e.g. local richness approaches the regional richness). Furthermore, because the seed bank in semi-natural grasslands generally is not long-term persistent (Kalamees & Zobel, 1998; Bakker & Berendse, 1999), a longer disruption of management may result in that plant species have to colonize the grassland again.

### **Coexistence at small scales**

Semi-natural grasslands are often species-rich at small spatial scales, where 10 species or more per dm<sup>2</sup> is not uncommon (Franzén & Eriksson, 2001). 25 species dm<sup>-2</sup> has been reported from Estonian grasslands, which is exceptionally high at a world scale (Kull & Zobel, 1991). Historically, several mechanisms have been suggested that can explain species coexistence and high species densities (see review by Grace, 1999). These mechanisms can be broadly divided into equilibrium and non-equilibrium theories and they all recognize the *competition exclusion principle* (Gause, 1934), and that species richness at all locations are limited by available niche space (Hutchinson, 1957). As mechanisms of coexistence are beyond the scope of this thesis, I will only describe the most influential theories.

One of the first comprehensive mechanisms suggested for patterns of species density was offered by Grime (1973a; 1973b; 1979). In his “hump-backed” model competitive exclusion (dominance), which reduces density, is limited by environmental stress (e.g. drought, mineral deficiency) and disturbance. Niche differentiation and species colonization increases species density, which peaks at intermediate levels of stress and disturbance (e.g. intermediate disturbance hypothesis, Grime, 1973b; Connell, 1978).

Another theory is the resource-ratio hypothesis suggested by Tilman (1982), which stated that plants grow at different ratios of resources (e.g. N and light). If species are controlled by the same resource, the species with

the lowest requirements are expected to displace all competitors. However, competition is limited if there is local heterogeneity in the ratios of resources, or in intermediate conditions.

Some non-equilibrium models include the “mass effect theory” (Shmida & Wilson, 1985), the “dynamic equilibrium model” (Huston, 1979) and the “shifting limitations hypothesis” (Foster *et al.*, 2004). The mass effect theory states that weaker competitors are supported by influx of propagules from the surroundings. Such species would therefore disappear from the community without support from the “outside”. An important assumption here is that all species are able to be a strong competitor in some systems. In the dynamic equilibrium model diversity is low if productivity is high, because growth rates, and thus also competition, increases with productivity. If productivity is low, growth rates are reduced, and hence competition is limited. Diversity is therefore expected to be highest in habitats with low-to-moderate productivity. Disturbance reduces the influence of competition, and hence increases diversity. The dynamic equilibrium model was extended in the shifting limitation hypothesis to include regional influences on diversity (Foster *et al.*, 2004). This hypothesis combines local mechanisms with regional theories like the species-pool hypothesis previously described (see the section on regional effects). In short, diversity in high productivity habitats is limited by local processes, irrespective of the regional richness. With low productivity, or if the productive habitat is exposed to disturbance, diversity will be limited by propagule availability according to the species pool hypothesis. In this thesis I am adopting the shifting limitation hypothesis and assume that local species density is limited by regional effects rather than local. The reason is that the semi-natural grasslands that are investigated in this thesis are all nutrient poor, and subjected to a moderate disturbance by grazing or mowing.

# Aim of the thesis

The overall aim of this thesis was to investigate biodiversity values in semi-natural grasslands in terms of species richness, density and composition of vascular plants and the fungal genus *Hygrocybe*. These values and their distribution were studied at the individual species scale, at a landscape scale, and in terms of how such values can be targeted by practical conservation (biodiversity indicators and congruence between species groups). The approach to meet these aims has been broad, with descriptive field work, *in situ* experiments, and a landscape analysis. The specific aims of this thesis were:

(1) To assess whether plant species diversity patterns in fragmented Swedish semi-natural grasslands is related to the surrounding landscape context (paper **I**). Important questions were to assess whether marginal habitats for grassland species, the openness of the landscape and dispersal potential in the landscape influences local diversity in semi-natural grasslands. An answer to this question would resolve the issue regarding extinction debt vs. underestimating connectivity in the contemporary landscape as explained earlier.

(2) To study a characteristic species for semi-natural grasslands in terms of population structure and reproduction and to assess its susceptibility to the highly fragmented extent of semi-natural grasslands in the contemporary landscape (paper **II**). The approach here was a mixture of pollination and seed-sowing experiments *in situ* on the plant species *Antennaria dioica*, together with descriptive studies on its flowering dynamics both at a regional and local scale.

(3) To validate a recent survey of all remaining semi-natural grasslands in Sweden in terms of how well the survey targeted semi-natural grasslands of conservation value, and how chosen indicators for biodiversity values are performing (paper **III**). This will give insights about how biodiversity values can be targeted in practical conservation.

(4) To examine whether diversity patterns of vascular plants in semi-natural grasslands is congruent with diversity patterns of the threatened fungi genus *Hygrocybe* (Paper **IV**).

# Methods

## General overview

The field work in this thesis was conducted in semi-natural grasslands in the southern part of Sweden. In papers **I**, **III** and **IV**, studies were conducted in a total of 31 grasslands, evenly spread between the Counties Södermanland, Västra Götaland and Kronoberg (Fig. 1). These sites were selected to be imbedded in different types of landscapes, i.e. from open agricultural landscapes to more forested landscapes. The selected sites (except two sites in paper **IV**) were separated by at least 5 km, and all were dry to mesic grasslands with slightly different conservation status, based on prior knowledge in each County. All sites were managed by either grazing or mowing during the two year field study.

In paper **III**, the landscape within a 3 km radius around each site was searched for grasslands excluded from a recent survey of semi-natural grasslands but which still may harbour valuable flora. Black and white digital orthophotos were used to search for potential grasslands. A total of 25 such sites were found, evenly spread between the three different counties.

The study on *Antennaria dioica* (paper **II**) was conducted both on a local and a regional scale. The local scale study was conducted in an area covering 1.5 x 0.8 km on the island of Selaön, in the County of Södermanland, south eastern Sweden (Fig 1). This area is within one of the 31 landscapes mentioned above. The regional scale survey was conducted in the Municipality of Strängnäs, which covers 742 km<sup>2</sup>. Strängnäs is part of the County of Södermanland, and includes the island of Selaön.

## Assessing biological values in the grasslands

Data on vascular plant richness in the grassland sites (papers **I**, **III** and **IV**) were gathered during a total of three surveys conducted during 2003 and 2004. Each site was visited once in June, July and August-September, thus covering a major part of the flowering season. Species richness of vascular plants was assessed by walking over the entire site and through all vegetation types at a standardised pace. This way the census time was roughly proportional to the area of the sites. In addition to total richness, subsets of species were used in the studies. In paper **I** and **III** a list of 60 indicator plant

species were used, defined in the instructions for a recent nationwide survey of remaining semi-natural grasslands in Sweden (Persson, 2005a). In paper **IV**, I used a more broad group of grassland plants, defined according to Ekstam & Forshed (1997), which describes characteristics of species encountered in semi-natural grasslands.

In addition to the whole-site inventory, plant species density was recorded during 2003, and used in papers **I** and **III**. Ten 1 m<sup>2</sup> plots were randomly placed in each of the grassland sites, and each plot contained five 1 dm<sup>2</sup> subplots. This way I was able to describe species density at different scales (0.5-10 m<sup>2</sup>).

Data on richness of Waxcap (*Hygrocybe* spp.) fungi in the grassland sites (paper **IV**) were gathered 2003-2004 during September-November, with roughly three weeks intervals, as long as the weather was favourable for carpophore production. *Hygrocybe* species was searched for using the same method as for the vascular plants, but with more emphasis on the vegetation types that are known to harbour grassland fungi.



FIGURE 1. Map over Sweden showing the three Counties (vertical lines) where the investigated semi-natural grasslands in this thesis are situated. The magnification shows the County Södermanland, which includes the island Selaön where a detailed study on *Antennaria dioica* was conducted.

## Landscape analysis

To assess the importance of the landscape context for the diversity patterns of vascular plants in semi-natural grasslands (paper I), the landscape in a 2 km radius surrounding each grassland site was analysed. This spatial scale was chosen because it includes other grassland patches in the area, and it is a realistic dispersal distance for many plant species (Poschlod & Bonn, 1998). Digital topographical maps were used, with a resolution of 5 meters, to obtain the proportion of forest compared to other land cover types, i.e. crop-fields, grassland, urban areas, and lakes etc, in the landscape. I also investigated if there were other patches with a potential for harbouring grassland species in the landscape surrounding each study site. This was done by gathering information about grasslands that were known to nature conservation authorities, but also by analysing black and white digital orthophotos from 1998-2004. The orthophotos were used to detect grasslands as fairly open areas without any signs of being used as rotational crop-fields and without being too encroached by shrubs and trees. Connectivity of each target site was calculated as the sum of areas with suitable grassland habitat within the investigated radius, weighted by their distance from the target site (Hanski, 1999).

Road verges, railway tracks and power lines over non-crop areas may have a potential for inhabiting grassland species and promoting dispersal of those species in the landscape. I therefore recorded and digitised such linear elements by analysing digital topographical maps.

The landscape from 50 years ago for each study site was analysed according to Lindborg and Eriksson (2004a). Cadastral maps from the period 1946-1954 were used for the analysis. These maps are based on orthophotos, thus being equivalent to the digital orthophotos from today although they are not digital. First, each map was scanned and georeferenced before we analysed the historical distribution of semi-natural grasslands within a 1 km radius around the investigated sites. This was the scale at which an earlier study had detected a relationship between diversity and historical connectivity 50 years ago (Lindborg & Eriksson, 2004a). All open areas that were not classified as urban areas, arable fields, or pastures on former arable fields were classified as potential semi-natural grasslands and digitised into a GIS-layer. Up to a 50 % tree and shrub cover was allowed for in the "open areas". As a ban on forest grazing was effectively put into practice in the 1950s, areas with a sparse tree and shrub cover located close to farms were presumed to have a potential to harbour grassland species. Historical connectivity was calculated in the same way as for the contemporary landscape.

## Studies on *Antennaria dioica*

*Antennaria dioica*, which is a dioecious herb, is a typical species for species-rich, nutrient poor semi-natural grasslands with a long history of management (Ekstam & Forshed, 1997). The species is declining in Sweden, although it still has a widespread distribution. Populations of the species are often made up of isolated patches, sometimes composed of only one sex (probably a single genet), that are found particularly on dry or nutrient poor parts of the grasslands. *A. dioica* are thought to be a pollination generalist with a diverse and potentially effective pollen transfer system.

Flowering and sex-ratio in *A. dioica* were studied during each summer 2002-2005 at a local (1.2 km<sup>2</sup>) scale, and during 2004 at a regional (742 km<sup>2</sup>) scale. Recorded variables included area covered with *A. dioica*, number of flowering ramets, number of putative genets, the shortest distance between the sexes and sex ratio.

In May-June 2003 and 2004, a hand-pollination experiment was conducted in semi-natural grasslands in the local scale system. Up to 40 female flowering ramets from one or two genets were marked at each of 16 different locations (10 locations in 2004) that differed in population structure, and half of these were given supplemental pollen. The locations were at least 20 m apart, but could have *A. dioica* ramets between them. Response to treatment was assessed by calculating seed set, defined as total number of mature seeds divided by total number of ovules on a flowering ramet (including all heads on the ramet).

In the autumn 2003, a seed sowing experiment was carried out in the local scale system. A total of 45 0.5 × 0.5 m squares were placed in areas that differed in *A. dioica* cover, from very high (10 m<sup>2</sup> cover within a 5 m radius) to no *A. dioica* present within a 25 m radius. This enabled us to examine both how the natural seedling establishment varies with surrounding seed pressure, and if there is seed limitation in the system. Seeds were sown using three different treatments: disturbed, moderately disturbed (only litter removed) and undisturbed grass sward. All surviving seedlings were recorded in spring 2005.

## A nationwide survey of semi-natural grasslands

In paper **III**, the assessed biological diversity values in the investigated grassland sites were compared to the result of a recent survey of semi-natural pastures and meadows in Sweden, called “Ängs- och Betesmarksinventeringen” (hereafter ÄoB), that was conducted 2002-2004. The survey targeted all semi-natural grasslands in Sweden larger than 0.1 hectares that were known or suspected to contain significant biological or cultural values. The aims of the survey were, apart from assessing the extent of Swedish semi-natural grasslands, to provide a basis for conservation decisions and for

evaluations of different conservation policies regarding semi-natural grasslands in Sweden. The survey will also be a basis for conservation decisions regarding the Natura 2000 network, based on the habitat- and bird directives from the European Union (Anonymous, 1979, 1992). The data recorded by the survey will be used in the evaluation process to meet these aims.

A full description of the methodology used in the ÄoB survey can be found in Persson (2005b). Of most interest to this thesis is the 68 indicator species that was searched for in the ÄoB survey. The indicator species were chosen from the previous survey (e.g. Naturvårdsverket, 1987) where the selection was based on expert opinions, and not on empirical testing. 60 of these species are indicators of long and continuous management, and implicitly also species richness and density. Species richness at semi-natural grassland sites, as well as small-scale (often 1 m<sup>2</sup>) species density, are well known qualities related to long continuous management of these grasslands (Ekstam & Forshed, 1996; Cousins & Eriksson, 2002; Eriksson *et al.*, 2002). The other eight species are indicators of poor management (nutrient enrichment and overgrowth). All these indicators have to my knowledge never been validated.

# Results and discussion

## Importance of the landscape context

The landscape part of this thesis revealed several interesting results (paper **I**). First of all there was a strong positive relationship between area of study sites and plant diversity at several scales. This is in contrast to earlier studies on plant species richness in Swedish semi-natural grasslands (Eriksson *et al.*, 1995; Kiviniemi & Eriksson, 2002; Lindborg & Eriksson, 2004b) where no such relationship was found. There are several possible reasons for these conflicting results (see paper **I**) but the most likely main reason behind this pattern is that larger sites contain more vegetation types, which the study also showed. Since the adopted vegetation type classification, although described in terms of occurrences of characteristic species, basically reflects soil conditions, this implies that heterogeneity of soil conditions (i.e. more niches available) is the most likely underlying mechanism.

Another interesting result was that there was a scaling relationship between the measured diversity variables, such that diversity at broad scales was correlated with diversity at finer scales. This suggests that a large local species pool at the site level may enhance species colonisation also at a plot scale level of 1 m<sup>2</sup>, which confirms previous results that local and regional species richness is usually correlated in semi-natural grasslands with a long history of uninterrupted management (Pärtel *et al.*, 1996; Franzén & Eriksson, 2001).

The main result was that connectivity to other grassland habitats in the landscape, both in the historical and contemporary analysis, did not affect plant species diversity in the investigated semi-natural grasslands. Instead local characteristics (area and heterogeneity) had a dominating influence on species diversity. However, plant species richness increased with amount of forest in the landscape, although diversity at a plot scale decreased. This result was interpreted as a result of higher propagule pressure from generalist species in forested landscapes (e.g. Söderström *et al.*, 2001; Kiviniemi & Eriksson, 2002). The reduced plot scale species density in forested landscapes is most likely a result of deteriorating habitat conditions that reduces abundance of species and species density.

The lack of a relationship between present-day diversity and the historical connectivity challenges the generality of previous results that have docu-

mented such effects (Lindborg & Eriksson, 2004a; Helm *et al.*, 2006). Local plant species richness is therefore not determined by regional processes, and there is no equilibrium between local and regional richness. It implies that there are no immediate extinction debts in Swedish semi-natural grasslands due to isolation *per se*. Rather, as plant diversity is related to grassland size and management, we may expect future extinctions to occur in grasslands that are reduced in size or that experience ceased management.

### Pollen limitation in a dioecious herb

The species study on *Antennaria dioica* documented a considerable spatio-temporal variation in both flowering and sex-ratio at the local scale. The regional part of this study showed that populations were in most cases structured into several patches of different size, and that populations with few patches also had patches of smaller average size. This was interpreted as an effect of differences in habitat quality between populations due to the recent fragmentation and degradation of semi-natural grasslands. The regional scale survey also showed that small patches of *A. dioica* tended to have skewed sex-ratio.

Experimental hand-pollinations showed, in agreement with results from many other studies of pollen limitation (e.g. Burd, 1994; Ghazoul, 2005), that *A. dioica* was pollen limited. The degree of pollen limitation increased with increasingly female-skewed sex-ratio in the vicinity of the experimental plants. Thus, even though *A. dioica* is pollinated by many different insects, a fragmented population structure has a large influence on reproductive performance of *A. dioica*. The results of the sowing experiments indicate that a reduced seed production due to pollen limitation, translates into recruitment, at least under conditions where there is disturbance in the grass sward. It is therefore plausible that reduced seed production due to pollen limitation translates into reduced recruitment.

The results from the local and the regional scale indicate that a large fraction of local patches and populations of *A. dioica* have hampered sexual reproduction. *A. dioica* is a perennial species with clonal growth, which may promote persistence of this species even with limited reproduction, as long as habitat conditions are suitable. Because a fragmented population structure hampers sexual reproduction and therefore regional dynamics, it is possible that there may be an extinction debt in the regional *A. dioica* populations in our study area, and potentially in the rest of south-central Sweden where conditions are similar. If the habitat for *A. dioica* continues to be more and more impoverished in Sweden by fertilization and less intensive grazing, extinction rate is likely to increase during the coming decades.

It has been debated whether or not dioecious species are more threatened than other plants and thus warrant more attention from a conservation viewpoint (Aizen *et al.*, 2002; Ghazoul, 2005; Vamosi & Vamosi, 2005). The

present study of *A. dioica* suggests that the sensitivity to fragmentation of habitats increases as a result of spatial separation of the sexes. Habitat fragmentation reduces population size, and for a dioecious plant such as *A. dioica* the effect on pollen limitation becomes even more pronounced due to spatial and temporal sex-ratio skewness. Irrespective of whether or not habitat fragmentation simultaneously reduces pollinator diversity and abundance, a conclusion is that the dioecious life form is likely to be particularly vulnerable to habitat fragmentation.

## Validation of plant biodiversity indicators

The analysis of the recent survey (ÄoB) of remaining semi-natural grasslands in Sweden (paper III) suggests that it was successful in targeting sites that harbour species-rich grassland communities. Included grasslands contained significantly higher biodiversity than sites excluded from the survey, although some indicator species, including indicators for poor management, were abundant in both types of sites. Further, results showed that survey and control sites could not be separated by using the indicator species for poor management (and thus low diversity), even though abundance data was included in the analysis. One of the indicator species of poor management (*Filipendula ulmaria*) actually showed a highly significant positive relationship to plant species richness at the sites, opposite to expectation.

There was no correlation between number of indicator occurrences and species richness when we used the recorded occurrences from the survey. The reason behind this was the poor precision of the survey, as 42% of the indicator species occurrences were missed on average. This poor precision could be a result of too high pace of the survey (3 hectare per hour) or that species were overlooked due to their phenology. However, the biodiversity indicators did accurately indicate a high species density at the sites, when the recorded occurrences from the ÄoB survey were used. In comparison, results from the in-depth study showed that the indicator species did successfully indicate biodiversity values in these grasslands, thus confirming earlier work by Vessby *et al.* (2002) in Swedish grasslands, and by Wittig *et al.* (2006) in German grasslands. Plant species richness and species density at two scales were all strongly positively correlated to the number of indicator species, when “true” indicator occurrences were used.

Moreover, the null model showed that the indicator species used by the survey did not perform better than randomly chosen indicator species. The indicator species represent a large subset of the total species found at each site (about a sixth of the species), which probably is one reason why random species perform as well as the chosen subset.

All in all, the results suggests that there are potential problems associated with the use of biodiversity indicators in practical conservation work, mainly because they might fail as indicators due to poor precision of the actual

monitoring work. This may happen even though real correlations exist between taxa or between a subset of species and total diversity. To minimise these problems it is important to be very careful in the initial selection of the indicators, to follow the published guidelines that exists, and to empirically test the indicators. Indicators have to be chosen based on the time of the year the monitoring work will be done, how thorough the monitoring work will be, and how experienced the personnel are. Also, if the effort needed to search for the indicator species is high, it may be more efficient to go directly into assessing the biological values they are supposed to indicate. For researchers it might be worthwhile to provide some sort of ‘confidence intervals’ for suggested biodiversity indicators, so that managers know how much precision a survey has to have for them to work.

### Congruence between grassland fungi and plants

The study on diversity patterns of plants and *Hygrocybe* spp. revealed low congruence between the groups (paper **IV**). Although there is a positive relationship between *Hygrocybe* richness and species richness in plants in grasslands, so that grasslands with high plant richness tend to have a high richness of *Hygrocybe* species as well, the relationship was rather weak ( $r = 0.38$ ). The relationship was higher between *Hygrocybe* richness and richness of grassland specialist plants ( $r = 0.46$ ), but again not very strong. The richest *Hygrocybe* sites were not the sites with the highest plant richness.

Neither of the investigated groups showed a significant pattern of nestedness in relation to site area. These results indicate that although smaller sites harbour a lower richness than larger sites, it does not necessarily suggest that smaller sites have a depauperate subset of species, or more common species, compared to larger sites. Smaller sites may thus harbour species that are rare in the dataset.

All three groups were strongly nested in relation to species richness, showing that species poor sites contain a subset of species from the species-rich sites. This implies that plants and *Hygrocybe* do not occur randomly in communities, and suggests that there are some processes or gradients that cause rare species to be over-represented in species-rich sites.

The composition of the *Hygrocybe* communities did not show a significant pattern of nestedness in relation to richness in vascular plants, which shows that plant and *Hygrocybe* communities do not accumulate species along the same gradient. This is an important result for conservation of semi-natural grasslands, as it indicates that a site selection based on vascular plants may not include all species of grassland fungi. Further, fungi and plants (both total plants and specialists) did not show similar between-site similarities in species composition. Thus, two grassland sites that were very dissimilar in plant species composition could be similar in respect to *Hygrocybe* composition and vice versa. This also shows that conservation of semi-

natural grasslands based on complementarity and optimal site selection may not be applicable.

The conclusion is that there is a low congruence between plant and *Hygrocybe* species diversity. The low overlap in species composition patterns between sites make plants a poor surrogate group for *Hygrocybe* fungi, and probably also for other grassland fungi.

# Synthesis

## General implications

What are the general conclusions from this thesis, which adds to our understanding of biological values in semi-natural grasslands? I suggest the following:

First, an appropriate scale for the conservation of plant diversity in semi-natural grasslands may not be a landscape scale. No study has demonstrated that increased connectivity in the landscape increases local plant diversity in grasslands. Instead, the strong relationship between local species density and overall species richness, together with strong species-area relationships, implies that an appropriate scale for conservation of plant diversity in semi-natural grasslands may be set by the size of the grassland. Still, even though local characteristics may be of highest importance, regional effects are of importance in the long term, although possibly at larger scales than those studied thus far, and with more emphasis on rare long-distance dispersal events. Dispersal of grassland plants by human activities is limited in the contemporary landscape compared to the historical landscape (Poschlod & Bonn, 1998). Movement of animal, machines, tools and people are much more local today than historically when for example animals were herded over large “outland” areas. It is therefore possible that the relevant regional area for dispersal has decreased to include only the area of the grassland or the individual farm (compare with results in Weibull *et al.*, 2003). In addition, long-distance dispersal events are expected to decrease when target areas become smaller, and as plants become rarer in the landscape. Even so, it has been shown that semi-natural grasslands are inherently open to invasions, and it thus seem unlikely that species richness is constrained by local mechanisms (Eriksson *et al.*, 2006). Conservation should therefore, apart from ensuring appropriate management of remaining grassland sites, also consider restoring human influenced dispersal processes in the landscape and thus maintain the regional richness and increase the relevant regional scale. Suggestions of ways to enhance dispersal could be to increase movement of dispersal vectors between sites in the landscape (e.g. moving animals more), or to artificially disperse seeds. I will elaborate on this question below.

What about previously reported effects of historical landscape connectivity not supported by this thesis? I suggest two potential explanations for

the difference between my results and previous studies (Lindborg & Eriksson, 2004a; Helm *et al.*, 2006). First, the presence of a historical legacy may be related to the nature and pace of land use changes in different landscapes. The studies have investigated different landscapes, and land-use changes may have occurred at different times in different landscapes. Land use changes happened early in some of the landscapes that were included in my study, and the historical legacy could therefore have been lost. In addition, it may be that the connectivity models used in the studies, which uses the same dispersal kernel in both temporal scales, are insufficient to describe a landscape where both the spatial pattern (grassland extent) and process (dispersal rate) may have changed.

Second, it is also possible that differences in results are due to differences in sampling intensity and site history. For example, my study and Adriaens *et al.* (2006) sampled species richness in the whole area, whereas studies that have documented a historical legacy all have sampled in a subset of the area. Another intriguing difference is that the studies who have reported a historical legacy also report a lack of species-area effects, whereas the studies that do not find a historical legacy do find strong species-area relationships. This is truly puzzling, and a likely explanation is that sites may have had different histories in terms of interruptions in management, and area loss. Indeed, Lindborg & Eriksson (2004a) did investigate sites that had a history of ceased management, and recently had been restored. A lack of species-area effects implies a higher amount of unexplained variation in species-richness, which can be related to connectivity. However, this is pure speculation, and may not explain why a historical legacy was found. Either way, if a solution can be found to why some landscapes show a historical legacy and others do not, it may provide important insights to how, and how quickly plant diversity responds to land use changes.

Even though an extinction debt is unlikely in all semi-natural grasslands due to a historical legacy or isolation *per se*, fragmentation could have other negative effects as illustrated by the study on *Antennaria dioica*. Fragmentation reduces population sizes, and small population sizes are known to have several negative effects on species. One example is reduced pollination in the *A. dioica*, but also altered habitat quality through edge effects, or in some cases inbreeding. In addition, smaller semi-natural grasslands only sustain a few grazing animals, and they are thus not as economically interesting for farmers as larger grasslands, except in agro-environmental schemes. Smaller grassland may therefore in a higher degree be exposed to periods of interrupted management, which are a threat to both grassland plants and fungi.

Another conclusion is that it is important to base conservational decisions on multiple species groups, and not on plants only. This thesis showed that there are poor congruence between plant and fungal diversity. Other groups that are also not correlated with plant diversity include the insect groups butterflies, bumblebees and beetles (Vessby *et al.*, 2002). For birds, results

thus far have shown conflicting results, although there seem to be poor congruence also between diversity of birds and plants (Pärt & Söderström, 1999; Söderström *et al.*, 2001; Vessby *et al.*, 2002). All in all, this suggests that conservation should not use a single-taxon approach when setting up conservation actions and management programs for semi-natural grasslands if the aim is to preserve all biodiversity values associated with this habitat. In addition, results in this thesis suggest that there are no easy shortcuts when it comes to conservation of semi-natural grasslands, at least in terms of correlations between species groups or suitable indicators.

## Implications for restoration

One major issue in the conservation of semi-natural grasslands in Sweden and Europe is to restore or recreate grasslands. For example, in Finland the aim is to increase the amount of semi-natural meadows from around 20.000 hectares to 60.000 (Salminen & Kekäläinen, 2000). In Sweden the aim is to double the amount of meadow from 5.000 to 10.000 hectares and also increase the amount of valuable semi-natural pastures with 13.000 hectares (Anonymous, 2006). Based on the results from this thesis, I suggest two recommendations for restorations of semi-natural grasslands.

First, the lack of a relationship between connectivity to other semi-natural grasslands and plant diversity values in my study suggests that restoration should favor areas that still contain biological values. The cause for the apparent lack of connectivity effects is probably that the contemporary extent of semi-natural grasslands is highly fragmented and that most of the grasslands are isolated. Due to this, dispersal processes that was common in the old “traditional” landscape has virtually disappeared, together with its dispersal vectors (Poschod & Bonn, 1998). In addition, the seed bank in semi-natural grasslands may only persist for a short while, after grassland abandonment, and the species present in the seed bank are often not the species targeted by restoration (Bakker *et al.*, 1996; Kalamees & Zobel, 1998; Bakker & Berendse, 1999). Such seed limitation has reduced the success of several restoration efforts conducted in semi-natural grasslands in the past (Kotiluoto, 1998; Stampfli & Zeiter, 1999; Pywell *et al.*, 2002; Hellström, 2004). With limited dispersal both in time (seed bank) and space, restoration should target sites that either contains remnants of biological values, or that have species-rich semi-natural grasslands in the immediate vicinity. Further, local diversity could potentially be increased by artificial dispersal of seeds, which has been tested in some studies with encouraging results (Stampfli & Zeiter, 1999; Zobel *et al.*, 2000; Pywell *et al.*, 2002; Edwards *et al.*, 2006; Lindborg, 2006). However, any artificial dispersal has to be carefully conducted so that any deleterious genetic effects are avoided. It is preferred if any artificial dispersal mimic those dispersal processes that has historically built the plant diversity.

Second, there should be less emphasis on the spatial configuration of potential grasslands for restoration and more emphasis on their size, remaining biodiversity, and heterogeneity. Still, the spatial configuration of grasslands may be important for more mobile species groups like birds and insects. However, this will probably not benefit plant diversity.

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# Svensk sammanfattning

Förändrad markanvändning och modernisering av jordbruket har drastiskt förändrat Sveriges och övriga Europas landskap under de senaste 100 åren. Ett tidigare öppet, och ofta småskaligt landskap, har förändrats till att bli mer beskogat och bestå av större jordbruksenheter. En av de största förändringarna har skett i utbredningen av naturbetesmarker och slätterängar, eller gemensamt kallat naturliga fodermarker. Sådana fodermarker var fram till slutet av 1800-talet på flera håll den dominerande naturtypen. De har minskat i utbredning på grund av modernisering av jordbruket och förändringar i samhället exempelvis förbud mot skogsbete. Minskningen i areal naturlig fodermark har skett snabbt och i stor omfattning. Av omkring 2 miljoner hektar naturlig fodermark i Sverige år 1927 fanns det bara drygt 200 000 hektar kvar år 1990. 1927 hade dessutom en betydande andel av utmarksbetena redan övergått i skog. De naturliga fodermarker som finns kvar idag har en fragmenterad utbredning och är små till storleken jämfört med tidigare. En fråga man kan ställa sig är hur en så drastisk förändring av landskapet påverkar de växter och djur som är knutna till naturliga fodermarker? Ett av syftena med min avhandling är att försöka komma närmare ett svar på den frågan genom att undersöka hur växter påverkas av landskapsförändringen.

Naturliga fodermarker hyser en hög artrikedom av både flora och fauna, vilket inkluderar en stor andel av Sveriges hotade arter. Några förekommande organismgrupper som kan nämnas är växter, lavar, svampar, fåglar och insekter. När det gäller växter så hyser naturliga fodermarker en anmärkningsvärd artrikedom, både totalt och på små ytor. Det är inte ovanligt att finna över 30 arter per kvadratmeter och i litteraturen finns uppgifter på över 60 arter per kvadratmeter.

För att upprätthålla den höga artrikedomen av växter behövs en återkommande störning i form av bete eller slätter. Genom störningen hålls konkurrenskraftiga arter nere och därmed kan konkurrenssvagare arter klara sig. Bete kan också gynna etablering av arter genom att boskapens tramp gör luckor i grässvålen vilket främjar groning av frön. Om störningen upphör växer fodermarkerna igen med buskar och sly. Igenväxning tillsammans med konstgödsling och skogsplantering är vanligt förekommande hot mot artrikedomen i naturliga fodermarker.

Traditionellt sett har växter varit den mest undersökta organismgruppen i naturliga fodermarker. Svampfloran är däremot föga undersökt trots att den är rik i naturliga fodermarker. En anledning till det är att svamp, på grund av

svårigheter med artbestämning, är mödosammare att inventera än till exempel växter. Dessutom kan bildningen av fruktkroppar hos svamp vara relativt nyckfull på grund av en stark koppling till väderlek. Ängssvamp förekommer i störst mängd i marker som har hävdats kontinuerligt under lång tid. De är liksom flertalet växter känsliga för konstgödsling och igenväxning. Det finns ett stort behov av att identifiera de lokaler som är rika på ängssvamp i Sverige, men kunskap och resurser finns inte för detta. Därför är det av intresse för praktisk naturvård att undersöka om värdefull växt och svampflora har samma förekomstmönster i landskapet. Om det finns ett samband mellan hög diversitet av svampar och växter skulle det betyda att ett bevarandeprogram baserat på växter också inkluderar svampar.

I min avhandling undersöker jag fyra frågor i relation till biodiversitet i naturliga fodermarker: (1) är diversitet av växter i naturliga fodermarker relaterat till hur det omgivande landskapet ser ut idag eller har sett ut historiskt?; (2) hur påverkas reproduktionen och rekryteringen hos örten kattfot (*Antennaria dioica*) av fragmentering och försämring av naturliga fodermarker?; (3) fungerar de signal- eller ”indikatorarter” som traditionellt används för att indikera hög diversitet av växter i naturliga fodermarker?; och (4) kan hög artrikedom av växter användas som en indikator på hög artrikedom av det hotade svampsläktet *Hygrocybe*? För att besvara frågorna har jag undersökt diversiteten av växter och svamp i 31 naturliga fodermarker i södra Sverige, med lokaler i Södermanlands, Västra Götalands och Kronobergs län.

Resultaten i avhandlingen visar att storleken av och heterogeniteten i naturliga fodermarker har stor betydelse för artrikedom av växter. Däremot finns det inget samband mellan artrikedom och mängden av, samt närheten till annan naturlig fodermark i landskapet, varken i dagens landskap eller historiskt. Detta är i motsats till tidigare forskning som har visat på en koppling mellan dagens artrikedom och landskapets utformning 50-100 år sedan. Mina resultat visade däremot att den totala artrikedomen ökade något i skogrika landskap, troligtvis på grund av ökad spridning av arter som är generalister men som har sin populationstygdpunkt i skog. Detta gällde dock endast artrikedom i hela hagen i skogrika landskap, medan tendensen på små ytor var den omvända. Slutsatsen av studien är att det kan vara viktigare för bevarandet av växter att bevara stora och heterogena marker, snarare än att bevara eller återskapa en historisk landskapsstruktur.

Vidare visade resultaten i avhandlingen att växtarter som är tvåbyggare (han- och honblommor på olika individer) kan vara extra känsliga för fragmentering och minskning av naturliga fodermarker. Populationer av kattfot (*Antennaria dioica*) visade sig ha skeva könskvoter när populationerna var små. En skev könskvot visade sig ha negativa effekter på pollinationen av denna art, vilket reducerade frösättning och reproduktion. Experiment med utsådda frön visade att rekrytering av kattfot begränsas av både tillgänglighet av frön och störning av grässvålen. Det är därför troligt att en minskad frö-

produktion på grund av pollenbrist i sin tur påverkar rekryteringen hos denna art. Eftersom fragmentering ofta leder till en reduktion i populationsstorlek är det troligt att tvåbyggare, som kattfot, kan vara en grupp arter som är särskilt hotade av denna förändring.

Studien av indikatorarter visade på både möjligheter och problem med användandet av indikatorarter i praktisk naturvård. Sveriges länsstyrelser avslutade nyligen en inventering av kvarvarande naturliga fodermarker i Sverige. Inventeringen använde 60 indikatorarter som genom sin närvaro ska indikera hög artrikedom av växter. Mina studier visade att dessa indikatorarter fungerar tillfredställande när det finns tid att utföra noggranna undersökningar av naturliga fodermarker och deras flora. Däremot missade länsstyrelsernas inventeringar, som inte kunde vara så pass noggranna, 42 % av indikatorarternas förekomster. Detta gjorde att indikatorerna inte längre fungerade och kunde användas för att hitta fodermarker med hög artrikedom. Dessutom var de utvalda indikatorerna inte bättre på att indikera hög artrikedom av växter, än ett slumpvis urval av arter (från de totalt 340 funna arterna). Det betyder att andra arter kan fungera lika bra som indikatorarter och det finns möjligheter till förbättring i urvalet. Förslagsvis bör ett urval av indikatorarter inkludera arter som är lätta att hitta under en stor del av säsongen. Vidare visade det sig att 9 andra indikatorarter som skulle indikera otillfredsställande hävd inte fungerade. Till exempel visade förekomsten av älgört (*Filipendula ulmaria*), en av indikatorerna för otillfredsställande hävd, ett positivt samband med god hävd.

Det fanns ett svagt samband mellan artrikedom av svampsläktet *Hygrocybe* och artrikedom av växter. Sambandet var dock inte tillräckligt starkt för att kunna användas effektivt inom naturvård. Dessutom visade *Hygrocybe* och växter klara skillnader i förekomstmönster på artnivå. Till exempel kunde två naturliga fodermarker ha väldigt lika svampfloror men samtidigt mycket olika växtfloror. Innebörden av dessa resultat är att bevarandebeslut till gagn för diversitet av växter inte automatiskt är gynnsamt för bevarandet av svamp.

Sammanfattningsvis visar min forskning att man nödvändigtvis inte behöver ett landskapsperspektiv i bevarandet av växter i naturliga fodermarker. Desto viktigare är det att säkerställa att kvarvarande naturliga fodermarker sköts på ett gynnsamt sätt. Sådana marker bör vara stora och gärna heterogena för att gynna många arter. Det finns ett behov i Sverige och Europa av att restaurera igenväxta naturliga fodermarker. Eftersom artrikedomen inte verkar ha något samband med landskapets struktur är det istället viktigt att restaurera marker som fortfarande innehåller många arter. Om sådana inte finns att tillgå, kan en metod kan vara att artificiellt så ut arter för att öka artrikedomen och bevara florán.

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