Grassland Plant Diversity in Relation to Historical and Current Land Use

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Abstract

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About 150 years ago agriculture was drastically reformed and around 90% of the formerly vastly distributed semi-natural grasslands, *i.e.* unfertilised and uncultivated grasslands, have since then disappeared. Accordingly, grassland plant diversity has declined due to abandonment, changed management methods and habitat loss. Grasslands are species rich as a result of a long management history; the management providing niches for a variety of organisms. Current diversity patterns are thus a result of historical and current land use in combination. This thesis explores some of the connections between historical land use and grassland vascular plants. Two studies concerns the habitat level, *i.e.* local conditions for grassland plants, two studies the landscape level, *i.e.* habitat patches in relation to neighbouring patches. In the first study, grassland plant diversity was found to be strongly correlated to 18th and 19th century land use, more so than to current land use. Furthermore, the particular sequence by which one land use changed into another from the 18th century until the mid 20th century was an important predictor of plant diversity. In the second study, detailed comparison of 18th century and current grassland management revealed that current grassland management lacks several ecological factors that the literature deems important for grassland plant reproduction. The third and the fourth study explore how plant species richness in specific grasslands is related to the surrounding landscape by studying how current, 19th and 20th century grassland connectivity and area are reflected in current species richness of grassland plants. They revealed that the response of grassland plant diversity to different fragmentation components can differ widely between two superficially similar landscapes, although historical components were important in both landscapes for explaining current diversity patterns. Moreover, the direction of livestock movement within the pre-industrial landscape appears to have been an important determinant regarding the functional connectivity between different grassland patches. Given the strong correlation between historical agricultural practices and current plant diversity patterns, this thesis discusses this diversity as a biocultural heritage. The historical aspects of grassland diversity ought to be taken into account in conservation and restoration measures.

Keywords: semi-natural grassland, land-use history, extinction debt, grassland management, fragmentation, connectivity, species-to-area relationship, biocultural heritage

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Cover photo: The maid at Naven (one of Lake Vänern's many inhabited lighthouses) tends the cows, which had to be transported by boat every day to the mainland. Early 20th century. Vänermuseet archives.

List of Appendices

Paper I-IV

The thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Eva Gustavsson, Tommy Lennartsson, Marie Emanuelsson 2007
Land-use more than 200 years ago explains current grassland plant diversity in a Swedish agricultural landscape. Biol. Conserv. 138 47-59

II. Eva Gustavsson, Anna Dahlström, Marie Emanuelsson, Tommy Lennartsson, Manuscript
Are necessary ecological factors missing in current grassland management?

III. Eva Gustavsson, Kristina Bylund, Tommy Lennartsson, Submitted Manuscript
Grassland plant diversity in relation to current and historical habitat fragmentation

IV. Eva Gustavsson, Tommy Lennartsson, Kristina Bylund, Weronika Linkowski, Manuscript
Is functional connectivity overlooked in landscape restoration? Fragmentation today and in the past in two Swedish agricultural landscapes

Paper I is reproduced by permission from Elsevier.

My contribution to the papers is that I planned all studies in cooperation with TL, performed all fieldwork and map analyses in Västergötland and all of the statistical analyses. TL, ME and AD had influence over the structure of their respective papers, but I did most of the writing except for Paper IV, to which TL contributed greatly. AD performed most of the map analyses in Paper II, KB performed the field study and most of the map analyses for Uppland and WL compiled the references on fragmentation.

Introduction

Semi-natural grasslands boast a spectacular species diversity of vascular plants, insects, birds, fungi *etc.* This diversity is under severe threat due to the drastic changes in agricultural practices following the enclosure acts in the 18th and 19th century and its subsequent industrialisation. The agricultural system preceding the modernisation processes created a wide range of grassland habitats and disturbance regimes through a variety of management practices, such as different types and dynamics of grazing, mowing, burning and irrigation. In south and central Sweden this system was introduced around 500 BC (Welinder, Pedersen & Widgren, 1998). It was based on nutrients being reallocated from pastures and hay meadows to the permanent arable fields through livestock manure (Emanuelsson, 1988). All parts of the production within a farming unit were thus interdependent. The modern system rendered semi-natural grasslands superfluous, because a new technical complex (*cf.* Myrdal, 1988; Myrdal, 1997), including *e.g.* mineral fertilisers, allowed both summer and winter fodder to be produced on arable fields. Therefore, productive grasslands were incorporated into the modern production, whereas unproductive grasslands were to a large extent abandoned (Gadd, 2000). The extent of semi-natural grasslands in Europe has decreased by around 90% and semi-natural hay meadows by 99%, of which the remaining 1% is mainly grazed, not mowed (Bernes, 1993; Stanners & Bourdeau, 1995; Piessens & Hermy, 2006). The severe habitat destruction and resulting fragmentation has led to extinctions and population decreases (Baillie, 2004; Gärdenfors, 2005; Cheffings & Farrel, 2005). Recently, concern has been expressed that the remaining fragments are not managed optimally to preserve grassland diversity (Paper II, Söderström *et al.*, 2001; Wissman, 2006; Dahlström *et al.*, 2008), thereby increasing the threat instead of the intentioned decrease.

Several early to mid 20th century authors exhibit an awareness of man's influence on semi-natural habitats (Sjöbeck, 1933; Lithberg, 1934; Selander, 1955). Managed grasslands were then still very common and, *e.g.* wooded meadows were left to succession with the intention of creating natural-like deciduous forests (Sernander, 1912). All the same, when grasslands became scarce and became subject to conservation, recommendations for many protected areas of semi-natural character were for a long time aimed at protecting grassland flora from the detrimental effects of grazing and trampling (*e.g.* Gustafsson, 1979; Ekstam & Forshed, 1996). When the "protected" (*i.e.* unmanaged) grasslands slowly turned into forest, the awareness of the need for management grew. In the wake of this awareness, the question of the naturalness of grasslands and their range of species awoke (Andersson & Appelqvist, 1990; Vera, 2000; Svenning, 2002), particularly in relation to the realisation of the impact large herbivores exert on the vegetation of the African savannas (Sinclair & Norton-Griffiths, 1979). European grassland species were obviously dependent on mankind to survive, but the few thousand years that man has had the means to effectively create grassland biotopes is too short for the evolution of all the management dependent species. Hence, the view that the European nature before the Neolithic revolution was dense forest, has been revised by *e.g.* studying paleoecological records from the Eemian (*ca.* 130,000 to 107,000 years before present) and early Holocene (which began *ca.* 10,000 years ago) interglacials (Svenning, 2002). Climate, fire and the now all but extinct megaherbivores (body weight >1000 kg, *sensu* Owen-Smith, 1987) created grassland biotopes. Due to the dry continental climate, the steppes in south-central Europe reached great proportions during the Eemian interglacial, but grasslands were patchily distributed all over Europe on nutrient poor and/or dry soils. The exact extent of these natural grasslands are not resolved as yet (*cf.* Vera, 2000; Svenning, 2002), but after the extinctions of the herbivores in late Pleistocene-early Holocene the extent of the grasslands decreased. Man was most probably a the key cause behind the megaherbivore extinction (Bulte, Horan & Shogren, 2006); also fire, which has the property of opening large clearings (Svenning, 2002) has been made scarce due to man's gradually increased control over fire. By removing these natural key components of grassland creation, man tied the fait of grassland biodiversity to himself; as long as the pre-industrial agricultural practices were upheld, grassland diversity could persevere (Pykälä, 2000). In a way, man has thus created a sort of prolonged extinction debt (Tilman *et al.*, 1994). The close bond to human-made habitats has, according to some authors, caused man to underestimate the importance of natural disturbances, such as fire, storm, flooding and, not least, the activities of wild animals, in the absence of human management (Pykälä, 2000).

Grassland biotopes have the last few thousand years been created and upheld solely by man and his animals (Eriksson, Cousins & Bruun, 2002). Specific management regimes (*e.g.* Paper I & II, Maurer *et al.*, 2006) and landscape compositions (*e.g.* Paper III & IV, Lindborg & Eriksson, 2004; Helm, Hanski & Pärtel, 2006) have created specific plant diversity patterns that, due to time lags in the response of some species to ceased or changed management, are to some extent discernable still today (Alard *et al.*, 2005, Paper I). Given the fact that grassland biodiversity is dependent on human activities for its existence and that the diversity patterns have been built up by human land use, it can be seen as a biocultural heritage (Emanuelsson, 2003). Emanuelsson (2003) defines it as the living part of the historical heritage, or put in another way, biological phenomena that have been affected by anthropogenic activities. The human influence can occur on any biological organisation level – genetic, individual, population, biotope *etc*. A biocultural heritage can thus be a semi-natural hay meadow with its typical flora and fauna or a several hundred years old pollarded tree, but also a field of ley or a larch (*Larix*) plantation. Which parts of the biocultural heritage that should be considered for conservation activities should however be subject to an evaluation process, where the status of both the biological and historical values are taken into account (Emanuelsson, 2003). If mankind decides to view grassland diversity as a biocultural heritage we thereby accept the responsibility for its conservation (Pykälä, 2000).

Hypotheses and objectives

The main, underlying assumption of this thesis is that the different types of grassland management and landscape configurations that existed before the modernisation of the agricultural systems created plant diversity patterns and that traces of these types of management are discernable in current plant diversity patterns. The working hypotheses are that: 1) Not only abandonment, but also changes in grassland management may be detrimental to the grassland flora, if essential ecological factors of the historical management is missing from the current management. 2) The history of individual landscapes concerning the spatial distribution of semi-natural grasslands and functional mechanisms connecting them determines how fragmentation is correlated to plant diversity patterns.

The main objective of this thesis was to test these hypotheses by analysing how historical, relative current, land use on different spatial and temporal scales are manifested in current grassland plant diversity patterns, thereby improving our knowledge about grassland management for the conservation of biodiversity.

Study areas

The main part of the field studies have been conducted in the former jurisdictional district of Kålland (58°23'N to 58°40'N and 12°49'E to 13°12'E), now constituting the western part of the municipality of Lidköping, in the region of Västergötland, southwest Sweden. Papers I and II concern the area that constituted Källstorp manor in Örslösa parish in 1712 and the neighbouring, southern parts of Söne parish in 1787 (both in the Kålland district, around 58°50'N, 12°91'E). Papers III and IV concern grasslands all over Kålland. Papers II-IV moreover concern additional study areas, described below.

Geologically, Kålland consists of a mosaic of gneiss bedrock hills with a thin layer of till and of low-lying areas with clayey soils. Some terminal moraines cross Kålland in a roughly east-westerly direction. The hills were formerly open or semi-open pastures, but are nowadays forests dominated by *Picea abies*, *Pinus sylvestris*, *Betula pendula* and *Populus tremula*. The lower areas were historically arable fields and hay meadows, today mainly arable fields. Some currently grazed, dry-mesic open pastures occur in both higher and lower areas. A majority show signs of elevated nutrient status. In the 1960's and 1970's, most grasslands that were still in use were treated with artificial fertilisers (land owner Bengt Carlsson-Wester, pers. comm.; County administration farming adviser Lennart Hedén, pers. comm.), a common practice in the region at that time. The annual mean temperature is 6.5 °C, yearly precipitation 600 mm, and the vegetation period 195 days (Sveriges Nationalatlas, 1995).

Kålland has been populated at least since Neolithicum, which began around 6000 BC in south Sweden (Welinder, Pedersen & Widgren, 1998). During the Bronze Age (1800-500 BC) Kålland appear to have sustained a rich culture, probably due to the trading possibilities afforded by the proximity to a major trading route – Lake Vänern (Kretz, 1996). Also during the Iron Age (500 BC-AD 1050) and early Middle Ages, the area was part of a powerful region, a power manifested in an unusually high number of fortresses (Stibéus, 1996). This indicates that agriculture probably had a profound influence on the landscape already as early as 3000 years ago.

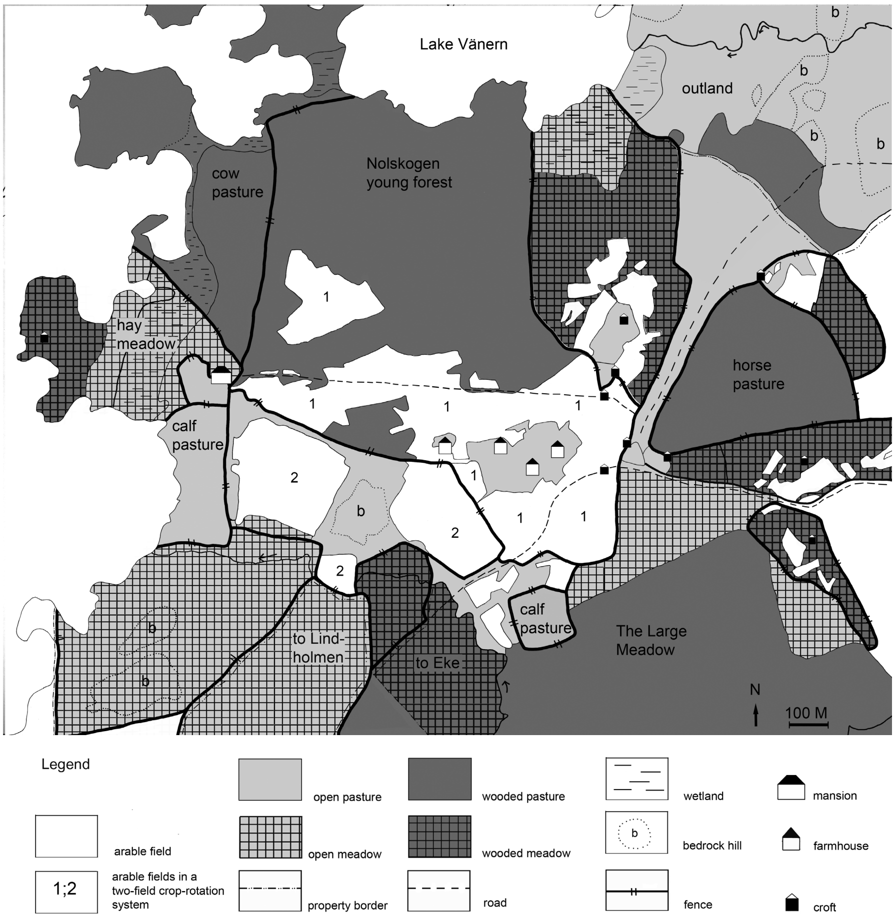

Fig. 1. The major part of Källstorp manor and its village of four cadastral farms, 1712. Drawing based on a geometrical map, scale 1:4000 (Hierpe, 1712). The outland to the north-east belonged to Söne parish (Aurell, 1787). The numbers in the arable fields show the rhythm of cultivation described under Study areas.

The predominant agricultural system from late Iron Age until the enclosure reforms (AD 800-1850) was the two-field rotational system with spring-sown crops (Jansson, 1998, Figure 1). The majority of a property's arable fields were divided into two areas, each enclosed by a fence and each comprising one year's worth of crop production. The two enclosures were used for crop production every second year; the one in fallow was instead used for grazing (Gadd, 2000). In Kålland it was common that most of the pasture area and hay meadows were enclosed with the arable fields and were thus in a two-year management rhythm: The pastures were available for full-season grazing one year and in autumn the next, whereas the hay meadows were grazed one year and mowed the next (Jansson, 1998). Cooperation with other villages saved fencing material and created fallow land that could cover several villages (Jansson, 1998), a feature Kålland had in common with *e.g.* parts of Denmark (Bruun & Fritzbøger, 2002).

After the crops had been harvested the enclosures were opened to allow the animals to graze the aftermath, hence doubling the pasture area after harvest. The production in early modern times was mainly directed towards ox trade with the iron producing areas in central Sweden (Jansson, 1998). Hence, the 17th and 18th century landscape of Kålland was dominated by extensive grasslands to supply the livestock with pasture and winter fodder. Yet, lack of pasture was probably a major reason not to cultivate autumn-sown crops, because then the fallow had to be tilled already in the autumn, thus making it inaccessible for late-season grazing (*cf.* Figure 2 in Paper II).

The local study areas of Källstorp manor and south Söne also employed a two-field system (Figure 1). Söne had some of its hay meadows enclosed with the arable fields in the two-year rotation described above, but also two large, separately enclosed hay meadows and two common outlands – one to the north and one to the south. Källstorp manor had several separately enclosed pastures and hay meadows as well as grazed forests and in addition to this, access to the southern outland of Söne parish. The 18th century map material (*cf.* Paper I) reflects a landscape almost devoid of mature forest. The outland of southern Söne was 164 hectares, of which only 5 ha was denoted "forested" (Figure 1). None of the other parts of south Söne is termed forested. In Källstorp three areas covering a total of 162 ha was termed forest, but one is named "The Large Meadow" and still today contains glades with a typical meadow flora. The other two were described as "young forest" and the last as "all fire wood, no timber" (Figure 1). This leads me to suspect that these "forests" were not forest in the modern sense, but rather grasslands strewn with trees (*cf.* Vera, 2000).

The modernisation of the region was initiated in the 1830's when severe flooding and subsequent famine highlighted the necessity of ditching (Håkansson, 1997). The landscape was transformed into a cereal-producing landscape (Jansson, 1996) and already by late 19th century the map material shows a landscape where almost all hay meadows and productive pasture had been transformed into arable fields, *e.g.* a great part of the south Söne outland (Rikets allmänna kartverk, 1986). Today, cereal production dominates Kålland, but since the possibility to acquire environmental subsidies from the European Common Agricultural Programme (http://ec.europa.eu/agriculture/capreform/index_en.htm; 11-Sep-2007) the number of managed grasslands has increased in the area (personal observation).

Paper II combines the information of 18th century and current land use in Källstorp and south Söne with that of five regions in southeast Sweden: the island of Selaön in the county of Södermanland, the parishes Fornåsa and Kristberg in the county of Östergötland and the parish Alseda in the county of Jönköping. Selaön and Fornåsa are situated in farmland plains, where the main historical, agricultural direction was grain production. Kristberg and Alseda are situated in upland regions, where livestock production was historically more important. The four areas differ geologically, the soil in Fornåsa being rich in limestone, clay and till, the other areas being dominated by poorer till and clay. Alseda parish is the only study area situated above the highest sea level after the latest glaciation. Hence, the till in Alseda contains fine soil fractions, which has been washed out by wave action from till positioned below the highest sea level. The agricultural history of these four parishes, with a focus on grassland management, is thoroughly covered in Dahlström (2006). See also Table 1, Paper II.

Papers III and IV combine the regional data from Kålland with data from the parishes Almunge, Funbo, Husby-Långhundra, Lagga and Östuna in Uppland (59°44'N to 59°56'N and 17°47'E to 18°11'E) in southeast Sweden. The annual mean temperature is 5 °C, yearly precipitation 500 mm and the vegetation period 180 days (Sveriges Nationalatlas, 1995). Uppland is a pronounced fissure valley landscape, the valleys are however filled with glacial and post-glacial clay (Sveriges Nationalatlas, 1994). The clay soils are heavily exploited for agriculture and the till-covered hills are mainly used for forestry. Funbo, Husby-Långhundra, Lagga and Östuna are located along the same fissure valley, dominated by intensive agricultural activities. Almunge is situated some distance from the other parishes to the north in a mainly forested landscape. The surveyed grasslands in Almunge are thus situated in close connection to forest, whereas in the other areas they are midfield islets or situated along the edges of the valley, between the arable fields and the forest. The till in Uppland is somewhat limey, which favours a diverse grassland flora, because of the buffering effects of *e.g.* fertilisation (Pärtel, 2002).

The agricultural system in Uppland, before the enclosure processes, was predominantly a two-field rotational system with autumn-sown crops (Sveriges Nationalatlas, 1994). The farmhouses (hamlets or single farms) were situated on the till rich hills, the arable fields on the slopes down towards the hay meadows on the clay plains, which were often wet. In the 19th century the heavy clays were drained and turned into arable fields (Sveriges Nationalatlas, 1994). Hence, the current arable fields are to a large extent former hay meadows. The grazed outlands were situated on the ridges surrounding the valleys. Apart from the outlands, the infields were grazed in a two-year rhythm (*cf.* Paper II).

Methods

The habitat under study in this thesis was the grassland type "dry-mesic, herb-rich *Agrostis capillaris* meadow", which is typical for Scandinavian grasslands (Påhlsson, 1994). Hence, only plant species belonging to this habitat were included in the surveys. The field studies were performed in 2003-2005. The entire surface of each site was surveyed once from mid June to September, in order to make the list of grassland plant species as complete as possible. Prior to the field study a subset of 30 species in Västergötland and 32 in Uppland (of which 25 were found in each region), considered to be extra sensitive to ceased management were selected to be analysed as a separate list of "specialist species". In the Källstorp/Söne area the specialists were mapped in detail by GPS marking of every patch of the species within the sites (Paper I). Selection of specialists was based on the criteria (1) occurrence exclusively in semi-natural grassland (according to Ekstam & Forshed, 1992); (2) showing rapid population decline following fertilisation and ceased management (according to Ekstam & Forshed, 1992); (3) in the study regions confined to dry-mesic semi-natural grassland and not too common, based on earlier experience. The last criterion implies that some species were classed specialists in one region, but not the other. Three species, *Filipendula vulgaris, Helictotrichon pratensis* and (in Västergötland) *Platanthera sp*. did not meet criterion 2, but were considered grassland specialists since they, in the regions, occur only in species-rich grasslands (https://eidservice.sjv.se/tuva2/site/ index.htm; 10-Apr-2007).

In the first local study of Källstorp and south Söne (Paper I) all managed and abandoned former grasslands of the entire properties were surveyed. Areas that were too intensively exploited to sustain grassland plants were excepted, here consisting primarily of arable fields, gardens and forest plantations. Paper II concerns the spatial extent of 18th century grassland; hence the entire properties of the five study regions Källstorp/Söne, Selaön, Fornåsa, Kristberg and Alseda were included, regardless of current land use. In the regional studies (Papers III and IV) the selected grazed grasslands were all non-wooded and had been rated highest or high conservation value (Class I and II) by a Swedish, nationwide, inventory of semi-natural pastures and meadows (Naturvårdsverket, 1987; Lönn, 1988; Söderström, 1993), roughly comprising continuously managed grasslands. The abandoned grasslands (also Paper III and IV) were selected on the criteria (1) formerly being grazed grasslands of the same character and vegetation type as the currently grazed ones; (2) being abandoned around 1960-1975, *i.e.* long enough for forestation to have begun. The abandoned grasslands were all still in use in 1961, as interpreted from cadastral maps, which are based on aerial photos taken that year. No forest plantations or objects with other obvious anthropogenic influences were included.

Summary of papers

Paper I

This study investigates the relative importance of historical grassland management and current land use for grassland plant diversity. The distribution of 128 grassland plant species in an agricultural landscape in southwest Sweden was analysed in relation to current land use and land use in three historical time periods; the 18th and the 19th century and around 1960. Large-scaled, cadastral maps, which shows land use in great detail was used to analyse 18th and 19th century land use, whereas 1960's land use was analysed using the first available aerial photos of the area. Land use during the three historical periods was also combined into land-use sequences, to enable the analysis of sequential land-use continuity or change. Four diversity estimates were used: number of grassland species, number of grassland specialists, Shannon-Wiener index on the specialists and total cover/hectare of specialists. The two latter were deduced from the GPS positions on the patches of specialists. Grassland specialists were selected as a subset of the grassland species, as a group particularly sensitive to ceased management according to Ekstam & Forshed (1992).

Historical land use – especially 18th century and the land-use sequences – explained more of the variation among study sites than did current land use. This was interpreted as a response to the long continuity of a specific management type for around 1000 years prior to the 18th century (*cf.* Eriksson, Cousins & Bruun, 2002), thus creating a "base-line diversity level". The importance of continuity of a specific management type was moreover emphasised by the highest diversities being found in pastures with a land use sequence of continuous grazing since the 18th century (Figure 2). Former hay meadows, currently grazed, did not differ in any diversity estimate from abandoned hay meadows, indicating that change of management from mowing to grazing a century ago may cause diversity declines similar to abandonment some 40 years ago (*cf.* Maurer *et al.*, 2006). Limited artificial fertilisation in the managed areas may have contributed to this effect. Further decline in grassland biodiversity in the agricultural landscape is expected because a substantial proportion of grassland plant populations occur in abandoned areas (*e.g.* Pykälä *et al.*, 2005). These remnant populations constitute an extinction dept under the current conditions, but also an important resource for restoration, in which case historical management practices should be taken into account. Additionally, a number of the currently grazed grasslands are former hay meadows and although diversity already appears to have suffered losses due to the management change, there are still species present that would probably benefit from switching back to mowing.

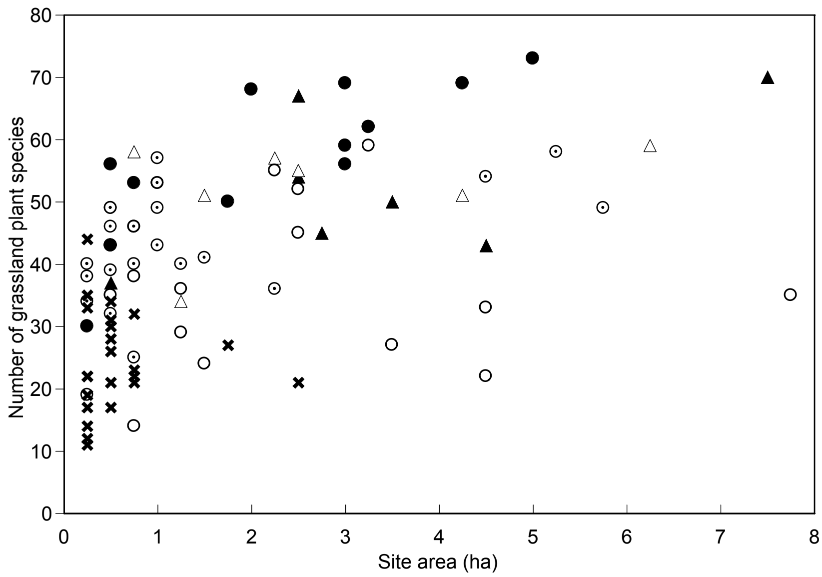

Fig. 2. Number of grassland species in relation to site area and land-use sequences: continuous pasture ●, pasture abandoned early ○, pasture abandoned late ⊙, hay meadow currently grazed ▲, hay meadow currently abandoned △ and former arable fields currently grazed ✕. Each symbol represents one site.

Paper II

Given the concerns that current semi-natural grassland management is detrimental to some parts of the grassland diversity (*e.g.* Söderström *et al.*, 2001) and the findings that plant species diversity patterns in semi-natural grasslands are highly dependent on land-use history (Paper I), this study explores historical and current grassland management quality using a combination of literature review and field data sampling.

Before the agricultural modernisation, semi-natural grasslands not only covered vast areas, they were managed in many different ways, largely depending on the regional agricultural system. Hence, it is possible that historical grassland management regimes included management components that created ecological factors necessary for grassland plant reproduction and that are missing today. Ecological factors, identified by the literature as affecting the main stages in the life cycle of grassland plant species (germination and establishment, survival and growth, seed production), were discussed in relation to pre-industrial – exemplified by the 18^{th} century – and current grassland management components. The components were grouped by how they related to timing, intensity and dynamics of management. Current and pre-industrial abundance of critical management components were then estimated for five study regions in southern Sweden by quantifying the major grassland uses hay meadow, permanent pasture and grasslands enclosed with arable fields.

The results show that pre-industrial grassland management did produce several ecological factors that are lacking in the current landscape. This is due both to the extensive loss of grassland habitat and a decrease in management variation, within and between grasslands. In particular late management, such as haymaking, and the dynamic management due to the two-field systems, that were formerly common, are missing in the current landscape. Moreover, the grazing intensity appears to have increased, due to smaller pasture areas and higher livestock densities. Additionally, dynamics in management regimes, timing and intensity between seasons are lacking in current management. The current full-season grazing, often of high intensity, is to a large extent a result of Swedish regulations for receiving environmental subsidies (http://www2.sjv.se/webdav/files/SJV/trycksaker/Jordbruksstod/JS61.pdf; 27-Jul-2007). This creates grasslands that provide good conditions for germination and seedling establishment, but less favourable conditions for plant growth and seed production. A method suggested, based on the analyses of pre-industrial management, to analyse the need for reintroducing ecological factors necessary for grassland biodiversity; the factors being present in the historical but absent from the current management. This can be done by reintroducing or imitating the management components that created the factors, thereby improving the possibilities of successful conservation of grassland species as well as expanding the managed area without increasing the number of animals needed. The potential deficit of indispensable ecological factors, caused by ”non-historical” management, highlights the necessity to restore and preserve not only grassland area, but also grassland habitat quality.

Paper III

Several recent papers have explored the effects of current and historical grassland connectivity on current grassland plant diversity (*e.g.* Lindborg & Eriksson, 2004; Helm, Hanski & Pärtel, 2006; Adriaens, Honnay & Hermy, 2006). The studies report highly diverging results regarding the importance of the past and present, as well as the significance of different fragmentation components. This study examines possible reasons for the diverging results by comparing two south Swedish regions with a similar intensity of agricultural production, Kålland and Uppland. Grazed and abandoned grasslands were surveyed for number of grassland plant species. A subset of more specialised grassland species was selected to be analysed separately. These two diversity estimates were related to current and historical (late 19^{th} and mid 20^{th} century) grassland area and connectivity (within radii of 0.5, 1 and 2 km) of each site.

In Kålland, plant diversity variation was primarily correlated to 20^{th} century connectivity, but also to 19^{th} century and current connectivity. In the 19^{th} and 20^{th} century, grassland plant diversity was best explained by connectivity within the 2 and 1 km radii, whereas in the current landscape connectivity within the 0.5 km radius explained most of the variation. This indicates that the mobility of grassland plants is impaired in the current landscape compared to the historical. Grassland plant diversity in Kålland showed limited correlation to current, but not to historical, grassland area. In Uppland the opposite pattern was found: grassland area, particularly 19^{th} and 20^{th} century, accounted for *ca.* 60% of the variation whereas connectivity provided no significant explanation. In abandoned grasslands, diversity was not correlated to the studied fragmentation components. In Kålland, number of grassland specialists was stronger correlated to current and less to 19^{th} century connectivity than number of species and not at all to area, indicating a faster reaction to fragmentation by specialists than by grassland species in general.

The different responses to fragmentation between the two study regions, between grazed and abandoned objects and between the two species groups indicate that there are a number of confounding factors that need to be taken into consideration when studying fragmentation (Ewers & Didham, 2006) and which, in the paper, are discussed in relation to a number of recent similar studies. Firstly, landscape history is likely to affect the results: The grasslands in Uppland were fragmented already in the 19^{th} century, whereas those in Kålland were not. Median grassland size in Uppland had been fairly constant through the time periods, whereas in Kålland it had decreased drastically from the 19^{th} century to today. Secondly, the lack of correlation between grassland plant diversity and the fragmentation components indicate a problem of not knowing the land use history, like longer periods of abandonment. Thirdly, the different responses of the two species groups imply that including species in the survey that are not habitat exclusive may obscure existing fragmentation effects. However, if such confounding factors are taken into account, further studies on the influence of historical and current fragmentation on grassland plant diversity may reveal important information on grassland plant reaction time to changed conditions in addition to *e.g.* fragmentation threshold levels.

Paper IV

Connectivity is an estimate of an organisms' ability to move between fragments of suitable habitat (Taylor *et al.*, 1993). In studies of connectivity influence on organism communities it is common to use measures of abundance and distance of suitable habitats to a target fragment (*e.g.* Paper III, Gu, Heikkila & Hanski, 2002;

Lindborg & Eriksson, 2004; Cousins, 2006), *i.e.* structural connectivity (*cf.* Tischendorf & Fahrig, 2000). This measure is adequate under the assumption that the probability to reach other fragments only depends on distance and neighbour fragment size, *i.e.* functional connectivity equals structural (Tischendorf & Fahrig, 2000). For plants, dispersal through the matrix often demands that the plants reproduce in the matrix. For specialised plants, such as grassland species, such reproduction is not likely in most types of matrix. Grassland plants are, on the other hand, commonly adapted to being spread across the matrix by dispersal vectors (Ozinga *et al.*, 2004), in particular animals (*e.g.* Fischer, Poschlod & Beinlich, 1996; Couvreur *et al.*, 2004), which thus generate the functional connectivity.

This study examines the relationships of number of grassland plant species in currently grazed grasslands to current and 19th century patch size and connectivity within 0.5 and 1 km in three landscape types; arable, transition and forest. Two study regions; Kålland in Västergötland and five parishes in Uppland were compared. Grassland cover was below the theoretical fragmentation threshold of 20-50% (Andrén, 1994; With & Crist 1995) in Uppland already in the 19th century, which may explain why plant diversity was not correlated to any of the connectivity measures, but instead to historical and current grassland size (*cf.* Launer & Murphy, 1994), particularly in the transition landscape.

In Västergötland historical fragmentation was around the critical threshold and grassland plant diversity was correlated to historical grassland connectivity, but only in the arable and forest landscape types. This was contrary to the expected, since matrix quality in the transition landscape, but not in the forest or arable landscapes, may have afforded possible reproduction in and thus dispersal through the matrix. However, in the agricultural landscape preceding the modernisation processes, *i.e.* before the 19th century maps used in the study, livestock were free to move over arable fields when these were in fallow. In the forest, animals moved freely at least until early 20th century. In the transition landscape, movement was also historically restricted to separately enclosed pastures; hence functional connectivity was lower than structural.

The correlations to historical rather than to current landscape conditions are due to time lags in the response of grassland plants to changed conditions. They indicate that the mobility of grassland plants is impeded in the current landscape and further diversity declines are therefore expected in response to local extinctions not being compensated for by immigration. Future restoration and management of semi-natural grasslands therefore need to take functional connectivity into consideration in order to preserve grassland plant diversity.

Implications for grassland plant conservation

The underlying assumption of this thesis, that historical grassland management types and landscape configurations still are discernable in current plant diversity patterns appears to hold true. This is both a threat and a possibility concerning the conservation of this organism group.

The threat is concerned with grassland plants as an extinction dept (Tilman *et al.*, 1994); the grassland plant populations are not in equilibrium with current conditions, which means that we can expect further diversity declines before reaching a new equilibrium. Grassland plants in successional habitats constitute an obvious extinction debt (Paper I and III). Less obvious is the probable decline in diversity also in managed grasslands. This is due to the decrease in habitat quality because of switches in management type (almost exclusively from mowing to grazing, Paper I), missing necessary ecological factors in current grassland management (Paper II) and severed metapopulation functions due to severe fragmentation (Paper III) and, additionally, loss of dispersal vectors (Paper IV).

The possibility lies in the fact that through restoration the remnant grassland populations can be restored to functioning populations. Restoration of abandoned grasslands are important to reduce fragmentation, but also restoration of habitat quality must be addressed. Historical management practices hold many keys to appropriate management regimes and how to increase functional connectivity.

Implications for the conservation of a biocultural heritage

Grassland biodiversity can be seen as an extended extinction debt, upheld by the pre-industrial agricultural practices (Pykälä, 2000). Hence, grassland biodiversity can be seen as, both on a local and on a landscape scale, a living cultural heritage. As such, I will attempt to explore more specifically the interface between grassland plants as biological organisms and their position as a biocultural heritage.

Given the specific management regime, a grassland will host a set of grassland species from the regional species pool, that are able to establish and reproduce under that management regime (Belsky, 1992; Bullock & Pakeman, 1997; Köhler *et al.*, 2005). The species content and diversity patterns of a pasture managed with full-season grazing will not be the same as a pasture managed in a two-year rhythm or a hay meadow (Paper I and II). Hence, the species content and vegetation patterns are partly an expression of the active decisions of the farmer, *i.e.* a cultural expression analogous to buildings looking differently in different geographical and social settings. The longer a specific management regime is upheld, the more the flora will reflect the specific management regime.

Like historical remains, only fragments of the biocultural heritage still exist today. With a deeper understanding of the influence of historical activities on flora and fauna, we will be able to interpret the biocultural heritage. To some extent this is already done, *e.g.* when archaeologists identify places used for charcoal production by the dense growth of *Picea abies* where the charcoal stack used to be (Emanuelsson, 2003). Like ancient remains, the biocultural heritage deteriorates when no longer managed and both may disappear completely. Most ancient remains are to be found in their original places, whereas others have been moved (by people) to new places. Analogously, some species have the ability to persevere for some time in its deteriorating habitat (*e.g.* Paper I, Pykälä *et al.*, 2005), whereas other parts of the biocultural heritage have the ability to move (spontaneously) to less unfavourable habitats as long as such are available (*e.g.*

Lennartsson & Svensson, 1996). In this way, the biocultural heritage holds many similarities to the immaterial cultural heritage, which also to some extent may persevere in new forms (Glassie, 1995), *e.g.* traditional music survives by being adopted by musicians and used in new forms (Åkesson, 2006). Both the biocultural heritage and the immaterial cultural heritage need to be actively managed to persist and correctly managed, both may even thrive.

To preserve the biocultural heritage we need to reintroduce the same ecological factors that historically created the heritage, and that are necessary for the species, vegetation characteristics *etc.* that are still present (Paper II). However, the factors need to be applied at the location where the species actually live today, even though a future goal may be to restore conditions at the original site so as to enable recolonisation of this, possibly, more optimal site. Although the ecological factors must correspond to the ecological factors provided by the historical management components, the actual management methods need not be historically "correct" (*cf.* Lennartsson, 2003). The more ecological factors the current management regime provides that corresponds to those of the historical management regime, the better the probability of a successful conservation of the target species and thereby the biocultural heritage. Hence, there is a possibility to grade a semi-natural biotope in relation to the number of ecological factors corresponding to the necessary ecological factors provided by the historical management. I would like to introduce the term management authenticity for a theoretical discussion.

Authenticity has strong cultural connotations and has evoked animated discussions *e.g.* regarding the appointment procedures of World Heritage objects being biased towards the views of the Western world as to what should be considered as authentic (Larsen, 1995). However, the choice of including authenticity in the term is intended to emphasise the aim of this type of conservation as not just being preservation of a large number of species, which may in some cases be easier achieved in *e.g.* botanical gardens than *in situ*. Instead, the aim is to emphasise the historical, anthropogenic influence on the diversity patterns, thus in combination with other historical remains augmenting the historical dimensions of the landscape. Management authenticity would then have the form of a checklist to analyse which ecological factors the current management creates in relation to the historical management that created a particular biocultural heritage (*cf.* Paper II). A biotope, where the current management provides more ecological factors in accordance with the historical management regime would thus have a higher management authenticity. The higher the level of management authenticity, the better the prognosis of maintaining the biocultural heritage.

One part of the biocultural heritage of many semi-natural grasslands is their characteristically high small-scale species diversity, *i.e.* number of species within *e.g.* one square meter (Kull & Zobel, 1991; Eriksson & Eriksson, 1997). This is seen as a result of the large amount and relatively stable spatial distribution of semi-natural grasslands in the pre-industrial landscape, thus increasing the probability of each species in the species pool to establish and spread in most suitable grasslands (Eriksson, Cousins & Bruun, 2002). The high species density is most probably higher than they would be under "natural" conditions. Hence, not only the mere presence of a certain group of species, but also the species density is a biocultural heritage. Managing this heritage demands a high management authenticity. In the case of hay meadows, continuing a mowing regime, but omitting aftermath grazing and/or spring raking without replacing them with new management components that mimics their ecological factors, will lead to a decrease in the small-scale diversity (Paper II, Svensson & Carlsson, 2005; Wallin, 2007). Hence, decreased management authenticity will lead to changes in the character of the biocultural heritage.

On a landscape level, the pre-industrial agricultural activities created conditions for functioning metapopulations, *i.e.* the spatial and functional connectivity of grasslands is a prerequisite to maintain the biocultural heritage. Hence, management authenticity must include enhanced possibilities for seed dispersal and pollen exchange. Otherwise we may reasonable expect further declines in plant diversity if current landscape contents of semi-natural grasslands are kept constant, even if management authenticity within each grassland is high (Paper III, Lindborg & Eriksson, 2004; Helm, Hanski & Pärtel, 2006). Some structural connectivity may be restored by resuming management in suitable former grasslands, but the movement of animals and hay that existed in the pre-industrial landscape has ceased in the current, hence the functional connectivity may not be restored at the same pace as the structural (Paper IV, Poschlod & Bonn, 1998; Ozinga *et al.*, 2004). Seeing as grassland plants mainly rely on seed rain for establishing new plants (Bullock *et al.*, 1994; Eriksson & Eriksson, 1997; Pywell *et al.*, 2002), restoring management authenticity may need to include boosting the inter-grassland seed rain artificially.

In the cases where the biocultural heritage exist in its "original" place, reintroducing a management that is motivated for historical reasons, like reintroducing haymaking in a former hay meadow, would in most cases increase the management authenticity (*cf.* Paper I). If the biocultural heritage however has moved, increasing the management authenticity may in fact counteract the possibility to interpret other historical remains. For example, in some cases it is possible for meadow plants to use former, low-productive arable fields as rescue sites when the "original" hay meadow has gone into succession (Dahlström, Borgegård & Rydin, 1998). The biocultural heritage in the form of meadow plants may be the only proof of former meadows in the area. The best way to manage this heritage would probably be to initiate haymaking on the former arable field and possibly in a second phase restore the former meadow. This may however confuse the historical understanding of the spatial arrangement of the historical agricultural system. I would however claim that in most cases such conflicts of interest are possible to solve if restoration is performed over a longer time period than the usual few years and of course, if managing the biocultural heritage does not damage the historical remains. In fact, I am convinced that both grassland biodiversity and the conservation of ancient remains will benefit from the cooperation between disciplines that this type of management inevitably demands. Thereby, the character of the historical agricultural landscape and the true nature of "the Swedish summer meadow", to which innumerable Swedish singers have paid their homage for its species richness, will be easier to convey to the public, thus hopefully ensuring future existence.

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Populärvetenskaplig sammanfattning på svenska

Innan moderniseringen av jordbruket på 1800-talet var ängs- och hagmarkerna näringsbasen i hela jordbrukssystemet och dominerade därför hela landskapsbilden. På ängen slog man hö till vinterfoder medan hagmarkerna betades på somrarna. Boskapen omvandlade foder till gödsel, vilket togs omhand och användes till att gödsla de permanenta åkrarna med. Framförallt mängden äng bestämde på så sätt mängden åker som kunde brukas för att få mat till människorna. Under slutet av 1700-talet, men i synnerhet under 1800-talet genomfördes en rad så kallade skiftesreformer för att modernisera jordbruket; storskifte, enskifte samt laga skifte, varav den senaste var den mest genomgripande. Växelbruk med vallgröda och så småningom handelsgödsel gjorde att man kunde börja odla vinterfoder på åkrarna och sedermera även låta boskapen beta på vallodlingar. På så sätt blev ogödslade och icke produktionsförbättrade ängs- och hagmarker överflödiga och antingen odlades de upp, planterades med skog eller övergavs. Bara ca 10% av alla dessa sk naturliga gräsmarker finns kvar idag. De allra flesta betas, oavsett om de var äng eller betesmark historiskt sett.

Eftersom naturliga gräsmarker förlorat så mycket i yta, så har en rad växt- och djurarter som hör till gräsmarksbiotoperna dött ut eller minskat kraftigt. Trots det, är de oerhört artrika. För att förhindra ytterligare utdöenden, så behöver stora ytor ny gräsmark restaureras ur igenväxta ängar och hagar och dessutom måste skötseln i dagens gräsmarker ses över. Det verkar nämligen som att dagens betesskötsel inte gynnar alla de artgrupper som lever där. Till och med växter, för vilka dagens hävd sägs vara anpassad, uppvisar negativa populationstrender. Det handlar alltså om att restaurera kvalitet lika mycket som kvantitet. Den historiska skötseln av naturliga gräsmarker är förutsättningen för deras artrikedom. Genom att undersöka mer i detalj hur den historiska hävden såg ut och hur detta skapade de ekologiska förutsättningarna, så kan vi hitta nycklar till en bättre former av gräsmarksskötsel.

I den här avhandlingen presenterar jag fyra studier som undersöker hur den historiska markanvändningen, i förhållande till dagens, påverkar artrikedomen av ängs- och hagmarksväxter i några områden i södra Sverige. Två studier behandlar hur artrikedomen i enskilda gräsmarker påverkas av hur de hävdats/hävdas, dvs lokal nivå, och två studier behandlar hur artrikedomen påverkas av hur landskapet sett/ser ut runt omkring, dvs regional nivå.

Den första studien visade att mängden ängs- och hagmarksväxter i ett studieobjekt berodde mer på hur de olika objekten sköttes på 1700- och 1800-talet än på om de betas idag eller har växt igen. Även skötselutvecklingen från 1700-talet till 1960-talet betydde mer än dagens skötsel, t ex så hade betesmarker som varit betade sedan 1700-talet högre artantal än de betesmarker som en gång varit ängar. Att 1700-talet var så betydelsefullt beror förmodligen på att den skötsel som var på 1700-talet hade varit ungefär densamma i nästan tusen år. Det var mot slutet av järnåldern (*ca.* 800 e Kr i södra Sverige) som man slog ihop ensamgårdar till byar och skapade de jordbrukssystem som överlevde fram till skiftesreformerna. Växterna hade alltså haft mycket lång tid på sig att hitta alla lämpliga växtplatser. Lång kontinuitet av en viss hävdregim är alltså viktigt för antalet arter.

I den andra studien gjordes en detaljerad jämförelse mellan 1700-talets och dagens skötsel av naturliga gräsmarker. Från litteraturen identifierades ett antal ekologiska faktorer som påverkar ängs- och hagmarksväxters reproduktion. Det visade sig att den historiska skötseln innehöll en mängd olika hävdkomponenter – olika områden sköttes vid olika tidpunkter under sommaren, vissa områden betades hela sommaren ena året och bara på hösten året därpå, betet varierade i intensitet från år till år osv – vilket skapade alla de viktiga ekologiska faktorerna. Dagens skötsel skapar vissa ekologiska faktorer, men långt ifrån alla, vilket innebär att på lång sikt kommer ett antal hagmarksarter troligtvis att försvinna från hagmarkerna.

I den tredje och fjärde studien undersöktes hur mängden hagmarker i landskapet påverkar artantalet i studieobjekten. Tanken är att ju mer hagmarker som finns i ett landskap, desto större antal arter kan finnas där och desto fler arter kan finnas i studieobjektet. En region i Västergötland jämfördes en region i Uppland. Båda är idag fullåkerslandskap och hagmarkerna är ungefär lika fragmenterade. Trots det så var artantal i de två regionerna beroende av helt olika fragmenteringskomponenter. I Västergötland var artantal kopplat till mängden hagmarker i landskapet på 1800-talet och på 1960-talet, samt till en viss del idag. I Uppland var artantal inte alls kopplat till landskapet, utan till storleken på studieobjektet, framförallt 1800-talets storlek. I Uppland var hagmarkerna mycket fragmenterade redan på 1800-talet och eftersom arterna därför inte kunde röra sig mellan objekten, så kunde inte landskapet påverka artantalet. Arters rörelse inom ett landskap beror inte bara på avståndet mellan lämpliga biotoper, utan också möjligheten att transportera sig. Ängs- och hagmarksväxter är till stor del beroende av att lifta med djur och det visade sig att i landskapstyper där djur på 1700- och 1800-talet hade kunnat röra sig fritt mellan olika hagmarker, där hade mängden hagmarker i landskapet större betydelse än där djuren bara rörde sig inom en hagmark.

Kopplingen är alltså stark mellan artantal och historisk markanvändning och landskap. Det innebär att artantalet inte ”ställt in sig” till de nya förhållandena. Om vi upprätthåller samma hävd som nu, så kommer alltså arter förmodligen att dö ut ändå. Det kallas för en utdöendeskuld. En utdöendeskuld kan också ses som någonting positivt, eftersom vi fortfarande har en möjlighet att förbättra förhållandena och på så sätt förhindra utdöenden. Historisk kunskap om hur man skötte olika marker och om hur djur och människor rörde sig i landskapet, kan ge oss viktiga nycklar för att bevara den biologiska mångfalden i ängar och hagar.

Tack!

Nog för att det är mitt namn som står på framsidan, men det är många människors insatser som gjort att den här avhandlingen blev klar. Först och främst Tommy Lennartsson, tack för att du tog dig an det här projektet! Jag har känt mig fullständigt trygg med din expertis i ryggen och ditt totala lugn. Marie Emanuelsson, för att du delat med dig av dina tvärvetenskapliga insikter samt ditt organisatoriska geni. Med både Marie och Tommy har jag kunna stöta och blöta agrarhistoria och ekologi ofta, länge och väl. Och tack för all hjälp, framförallt de senaste månaderna. Det har varit en intressant resa! Clas Tollin, som var den som planterade hela idén och som har hjälpt mig att tolka historiska kartor och därigenom hur det historiska jordbruket fungerade. Nordiska museets forskarskolas ledning, som trodde på projektet och gav mig chansen att doktorera. Tack också för de intressanta kurserna, vilka gett mig nya inblickar i museisverige och humanvetenskapernas värld. Ulrich Lange, för att du styrt och ställt och fixat för alla oss doktorander. Doktoranderna på forskarskolan för kul diskussioner och samkväm. Jag saknar er redan, men vi ses nog snart igen! Alla ni på Naturicum som jag tyvärr inte lärt känna så väl som jag velat, eftersom jag suttit på distans. Jag har alltid känt mig välkommen och ni har alltid funnits på andra sidan luren. CBM och Natuvårdskedjan för bra kurser. Sture och Carina, Lars och Liselotte Eliasson med familjer som kommit med glada tillrop när krupit omkring på Källstorp och räknat växter. I'll be back… Min chef Lars Johansson, för att du helhjärtat stöttat mig och för att du utvecklar Vänermuseet till ett forskande museum (och för att du blundat för att jag fuskat med att jobba för museet de senaste månaderna). Mina kollegor på museet, för att ni gett mig en länk tillbaka till arbetet. Inte minst vill jag tacka Lisbeth Alm som oförtrutet kämpat med alla dessa kartbilder – de blev gôrsketabra! Marcus Drotz, helt plötsligt fanns det en annan biolog att diskutera allt från statistik till dispuations-bra-saker-att-veta med. Catharina Holmstrand för att allt det administrativa bara funkat. Tack också släkt och vänner som hejat på och alltid erbjudit en fristad från datorn när jag behövt. Mamma och pappa, ni har alltid trott på mig och stöttat mig. Sist men inte minst; Janne! Tack för att du finns och för att du alltid ställer upp på mina galna idéer (som nu senast när jag gick och köpte en häst)… Nu kommer jag hem och hjälper dig att bygga hus!