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Maintaining plant species richness by cattle grazing: mesic semi-natural grasslands as focal habitats

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This thesis is a summary of the following papers, which are referred to by their Roman numerals.

I Pykälä, J. 2000: Mitigating human effects on European biodiversity through traditional animal husbandry. - Conservation Biology 14:705-712.

II Pykälä, J. 2003: Effects of restoration with cattle grazing on plant species composition and richness of semi-natural grasslands. - Biodiversity and Conservation 12:2211-2226.

III Pykälä, J. 2005: Plant species responses to cattle grazing in mesic semi-natural grassland. - Agriculture, Ecosystems and Environment 108:109-117.

IV Pykälä, J. 2004: Cattle grazing increases plant species richness of most species trait groups in mesic semi-natural grasslands. - Plant Ecology 175:217-226.

V Pykälä, J., Luoto, M., Heikkinen, R. K. & Kontula, T. 2005: Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. - Basic and Applied Ecology 6:25-33.

VI Pykälä, J. 2007: Why traditionally livestock grazed and mowed areas in Europe are rich in vascular plants – current paradigms and research gaps (manuscript).

Contributions

The following table shows the contributions concerning the original articles and manuscripts.

	I	II	III	IV	V	VI
Original idea	JP	JP	JP	JP	JP, ML	JP
Study design	JP	JP, MK, AA, JPö	JP, MK, AA, JPö	JP, MK, AA, JPö	JP, TK, AA	JP
Data collection	JP	JP, HS, HL	JP, HS, HL	JP, HS, HL	TK, HS	JP
Analysis	JP	JP	JP	JP	ML, JP, RH	JP
Manuscript preparation	JP	JP	JP	JP	JP, ML, RH	JP

Initials used:
AA = Aulikki Alanen, RH = Risto Heikkinen, TK = Tytti Kontula, MK = Mikko Kuussaari, ML = Miska Luoto, HL = Heidi Lyytikäinen, JP = Juha Pykälä, JPö = Juha Pöyry, HS = Henna Seppälä.

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1 Introduction

Half of the European Union's land is used for production of food (Eurostat 2006). Due to their large extent and intensity, farming practices have an immense impact on European biodiversity. As an outcome of these impacts, agricultural intensification is recognized as one of the key factors behind the decline of European biodiversity during the past 100 years (e.g. Bignal & McCracken 1996, Hindmarch & Pienkowski 1997, Sutherland 2002).

Traditional low-intensity agricultural systems tend to be rich and modern high-intensity agricultural systems poor in species (Bignal & McCracken 1996). Semi-natural grasslands managed by livestock grazing and / or mowing are the most important agricultural areas for biodiversity (Bakker 1989, WallisDeVries et al. 2002, EEA 2004). Semi-natural grasslands have originated through cutting of trees and long-term mowing and grazing. The drastic decline in the area of semi-natural grasslands in Europe during the past century (van Dijk 1991) had the result that a large number of plant and animal species are threatened. The on-going loss of habitat quantity and quality of semi-natural grasslands is among the most alarming nature conservation issues in Europe (WallisDeVries et al. 2002, Cremene et al. 2005, Reidsma et al. 2006).

Recently, there have been attempts to integrate biodiversity issues into agricultural policies in the countries of the European Union. This has clearly increased the need for applied research on how to maintain and restore biodiversity in agricultural areas (Sutherland 2002). In this introduction I will present a step-by-step overview of current understanding of selected focal issues in the effects of management on plant species richness and composition. These issues represent the thematic framework and background for this thesis.

1.1 Natural disturbances vs. livestock grazing

It is well known that species richness is dependent on historical factors (Grubb 1987, Hodgson 1987, Taylor et al. 1990, Ewald 2003). According to the species pool hypothesis, species richness should be higher in ecological conditions that have been abundantly available during evolutionary history than in historically less abundant ecological conditions (Taylor et al. 1990, Zobel 1992). Recent studies have provided support to the species pool hypothesis (Pärtel 2002, Schamp 2002).

It is generally considered that the natural landscape of Europe has historically been dominated by closed forests (e.g. Ellenberg 1988, Peterken 1996, Bradshaw & Mitchell 1999). Thus, applying the species pool hypothesis, it could be argued that richness of species adapted to shady microhabitats should be higher in Europe than richness of species of open microhabitats. However, most European plant species occur on sunny or half-shady microhabitats (Ellenberg et al. 1991). This preference for sunshine is dominating even among some arboreal organism groups (Rose 1992, Jonsell et al. 1998). Other putative explanations for higher species richness in sun-exposed sites are more rapid speciation processes in these sites receiving more energy from the sun (Rohde 1992, Wright et al. 2003), and that the devastating effects of the Ice Ages may have had a different influence on species of sun-exposed and shady habitats.

Nevertheless, the apparent mismatch between species richness patterns and the supposed structure of natural landscape has given rise to doubts about the validity of the hypothesis for the dominance of closed forests (Andersson & Appelquist 1990, Rose 1992, Wallis de Vries 1995, Nilsson & Ericson 1997, Gerken 1999, Sutherland 2000, Nilsson et al. 2001). It has been argued that large herbivores (particularly extinct megaherbivores (weight > 1000 kg)) have created grasslands or savannah-like woodlands (Andersson & Appelquist 1990, Wallis de Vries 1995). Vera (2000) even suggested that open and semi-open areas have predominated. All megaherbivores and several other large mammals disappeared from Europe ca. 10 000 – 50 000 BP probably due to hunting by humans, which increased the sensitivity of large mammals to changing climate (Martin 1984, Stuart 1991, 1999).

Recent palaeoecological studies have not challenged the view that closed forests predominated in the natural European landscape (Bradshaw et al. 2003, Birks 2005, Mitchell 2005). However, there is increasing evidence that the importance of natural disturbances may have been underestimated and that open and semi-open areas may have been more abundant in historical natural landscapes in Europe than considered hitherto (Svenning 2002, Bradshaw et al. 2003).

These results highlight the need to re-evaluate the characteristics of natural European landscape and the main driving forces behind the species richness patterns (Eriksson et al. 2002, Pärtel et al. 2005). The similarities between large (mainly extinct) herbivores and livestock grazing have attracted considerable attention among conservation biologists (Martin 1970, Janzen 1982, Andersson & Appelquist 1990, Wallis de Vries 1995, Gerken 1999). However, in general the similarities between various natural disturbances and traditional agricultural methods such as livestock grazing have not been considered.

1.2

Traditional vs. present grazing management

Traditional and present agricultural use of land differ fundamentally. During the era of traditional animal husbandry most of the European landscape was more or less influenced by livestock grazing and / or mowing. In northern Europe, most of the land area was used for traditional animal husbandry, and the portion of arable land of the total agricultural land was relatively small (Soininen 1974, Pykälä 2001, Luoto et al. 2003a). During the summers, arable land and meadows were fenced and livestock grazed freely elsewhere in the landscape, mainly in forests. Non-cultivated open and semi-open land was mostly used as hay meadows from where hay was collected as winter fodder for animals (Soininen 1974). After mowing and crop collection, animals were allowed to graze the meadows and arable land. A continued flow of nutrients from meadows and forests to arable land characterized traditional agricultural use and the amount of nutrients in soil was decreased in most of the landscape due to agricultural use (Emanuelsson 1988).

The present agricultural landscape and the role of livestock in it differ strongly from that of traditional animal husbandry. Modern grazing management is based on how to maximize increase of animal weight and / or milk production (Hodgson 1990). The use of fertilizers has a central role in achieving these aims. Due to the abundant use of fertilizers the amount of nutrients in soils has increased practically everywhere. Numerous studies have shown a decrease in plant species richness due to increase in the amount of nitrogen and phosphorus in soils (Grime 1979, DiTommaso & Aarssen 1989, Marrs 1993, Janssens et al. 1998), referred to as nutrient-enrichment or eutrophication. The key negative role of nutrient-enrichment on plant species richness has been demonstrated in many studies (Eriksson et al. 1995, Critchley et al. 2002, Stevens et al. 2004, Wassen et al. 2005). As few grassland species prefer nutrient-rich soils, the peak in species richness for grasslands occurs in nutrient-poor soils (Cornwell & Grubb 2003).

Livestock land use has shifted steadily from grazing to the consumption of feed crops (Naylor et al. 2005). Most fodder for livestock is grown on fertilized arable land, and grazing and mowing of non-cultivated land dramatically decreased in Europe during the past century. Even if animals still graze in semi-natural areas, some nutrient-enrichment of semi-natural areas has widely occurred for the following reasons: (1) recent or historical fertilization of semi-natural grasslands, (2) use of supplementary forages for animals (3) fencing of semi-natural grasslands together with cultivated pastures, causing the flow of nutrients and seeds of arable weeds via animal faeces from arable land to semi-natural land (Londo 1990, Pykälä 2001, Moussie et al. 2005). The use of supplementary forages may also cause decrease of plant species richness due to heavy trampling damages (Malkamäki & Hæggström 1997). Even foraging of wild animals may transfer nutrients from arable land to uncultivated land, causing significant nutrient-enrichment of the uncultivated land (Seagle 2003).

Effects of traditional animal husbandry, i.e. grazing and mowing of semi-natural areas, on plant species richness are very different from the effects of currently dominating grazing management practices. This difference is particularly caused by nutrient-enrichment typical to ”modern” grazing management, but other important factors are also involved. For example, free grazing practiced during traditional animal husbandry meant that grazing animals were important agents in dispersing plant seeds (Poschlod & Bonn 1998, Bruun & Fritzbøger 2002). These profound differences in grazing system have been insufficiently taken into account in grassland ecological studies. Consequently, the differences in grazing have hitherto been poorly described in many biodiversity studies, and the effects of grazing are not separated from the effects of feeding of animals.

Even in non-fertilized semi-natural grasslands plant species composition has changed considerably during the second half of the 20th century. Species of nutrient-rich habitats have continuously increased and species of nutrient-poor habitats decreased (Jacquemyn et al. 2003, Smart et al. 2003, 2005, Bennie et al. 2006).

1.3 Effects of traditional livestock grazing on plant species richness and composition

In northern Europe grazed and mowed semi-natural grasslands are among the most species-rich habitats, and their high value for nature conservation has been recognized (Kull & Zobel 1991, Austrheim et al. 1999, Norderhaug et al. 2000, Eriksson et al. 2002, Myklestad & Sætersdal 2004). The most valuable grasslands have been managed for centuries, and historical land use has been shown to affect present day species distribution patterns (Wells et al. 1976, Bruun et al. 2001, Lindborg & Eriksson 2004a). High plant species richness has accumulated through a long continuity of management by mowing and / or grazing (Kull & Zobel 1991, Pärtel et al. 1999, Cousins & Eriksson 2002, Myklestad & Sætersdal 2003). The species richness and nature conservation value of grasslands generally decreases after abandonment (Tamm 1956, Hansson & Fogelfors 2000, Wahlman & Milberg 2002, Luoto et al. 2003a). Livestock grazing usually has a rather strong impact on plant species composition (Steen 1958, Bakker 1989, Austrheim 2002). However, grazing may explain only a few percent of the total variation of plant species composition (Vandvik & Birks 2002, Raatikainen et al. 2007). Effects of grazing on plant species composition depend on e.g. vegetation, soil characteristics, species and race of grazing animal, grazing intensity and timing of grazing (Korte & Harris 1987, Hæggström 1990).

In Europe, traditional livestock grazing usually has a positive effect on plant species richness (Bakker 1989, 1998, Dullinger et al. 2003). A high proportion of vascular plants benefit from grazing. Positive responses to grazing also appear to dominate among rare and threatened species (Gibson et al. 1987, Jensen & Schrautzer 1999, Jutila 2001).

Not all studies have reported an increase of plant species richness due to livestock grazing. Negative effects of grazing have occasionally occurred, possibly due to nutrient-enrichment. However, some studies, that probably include rather traditionally managed sites, have also reported no change or even decline in plant species richness due to grazing (Tyler 1969, Jutila 1997).

There are two main factors which may alter species richness responses to grazing. Effects of grazing on plant species richness vary with management regime and across environmental gradients (Bakker 1998, Olff & Ritchie 1998). Livestock grazing is considered to increase plant species richness in productive environments, but to decrease it in low-productive environments (Olff & Ritchie 1998, Proulx & Mazumder 1998). When nutrients and light are the major limiting resources, grazing has a positive effect on plant species richness (Olff & Ritchie 1998). According to Olff & Ritchie (1998), livestock grazing decreases plant species richness in environments where water availability is the main limiting resource (dry environments). Furthermore, in situations where other natural factors than drought strongly limit productivity of vegetation, grazing may decrease plant species richness (Bakker 1998).

However, studies showing decrease of plant species richness due to grazing in low-productive habitats mainly originate from arid regions. In Europe there is evidence that grazing increases plant species richness in mesic environments, but the evidence on species richness responses in dry and water-logged environments is rather limited and controversial. Grazed dry grasslands have moderately higher plant species richness than abandoned grasslands, or there is no difference between the types (Bakker et al. 1996, Dupré & Diekmann 2001). Even on rock outcrops grazing may be beneficial to plant species richness (Tyler 1996). Austrheim & Eriksson (2001) suggested that in low-productive alpine communities (barren heath, extreme snow-beds), grazing could be negative for plant species richness. Contrasting results have been reported from water-logged areas such as seashores. Some studies have shown that grazed areas have less species than ungrazed (Tyler 1969, Jutila 1997), but others have reported the reverse (Kauppi 1967, van Wijnen et al. 1997, Vestergaard 1998), or different effects of livestock grazing on plant species richness across seashores along the elevation gradient (Bakker 1998).

The effects of different grazing animals such as cattle, horses and sheep on plant species richness are in most cases rather similar (Rook et al. 2004). However, cattle grazing is generally more beneficial to species richness than horse or sheep grazing (Pykälä 2001). This is probably because cattle is less selective in its food, and sheep and horses graze closer to the ground than cattle.

Somewhat surprisingly, only a few studies have investigated the effects of cattle grazing on plant species richness in northern Europe (Persson 1984, Hald & Vinther 2000, Wahlman & Milberg 2002, Jantunen et al. 2002, Lindborg & Eriksson 2004b, Rosén & Bakker 2005). These studies have mainly compared managed and abandoned sites or studied restoration of grasslands. All studies have been performed using rather small sample plots. Due to the scarcity of studies, the effects of cattle grazing in different environments are insufficiently known.

However, a considerable number of studies have been performed on the effects of cattle grazing on individual plant species. Some species show a consistent decrease or increase, whereas most species respond to grazing differently in different habitats, and under different grazing regimes (Vesk & Westoby 2001, Pakeman 2004). However, in Finland studies on plant species responses to cattle grazing are practically lacking in mesic semi-natural grasslands (but see Jantunen et al. 2002). Thus, more information is needed concerning plant species responses to cattle grazing for developing management recommendations of semi-natural grasslands.

1.4

Species traits and livestock grazing

Species traits have been used to make generalizations about ecosystem properties and to predict effects of changes in land use and ecosystem properties on vegetation (Lavorel et al. 1997, Smith et al. 1997). A considerable number of studies on responses of numerous different species trait groups on grazing have been conducted. Two main approaches have been used (Lavorel & Garnier 2002): 1. trait data for species is compiled from the existing literature (”soft traits”) (i.e. data on the trait is available for all or for most species), 2. traits for each species are measured in the study sites (”hard traits”).

Studies show that species with different species traits often differ in their responses to livestock grazing, but the emerging patterns tend to differ between the studies (e.g. Landsberg et al. 1999, McIntyre et al. 1999, Bullock et al. 2001, Díaz et al. 2001, Dupré & Diekmann 2001, McIntyre & Lavorel 2001, Cingolani et al. 2005, de Bello et al. 2005, Louault et al. 2005). Responses to grazing can be linked with morphological characteristics, life history or regeneration type (Lavorel et al. 1997). Grazing resistance is associated with avoidance and tolerance traits (Díaz et al. 2001). Most of the studies concerning species traits and grazing are from subtropical, mediterranean and temperate regions and from arid environments. Only a few studies have been made in northern Europe (Dupré & Diekmann 2001, Cousins & Lindborg 2004, Lindborg & Eriksson 2005).

It is known that similar species traits may show different responses to grazing in different geographical areas and vegetation types (Landsberg et al. 1999, McIntyre et al. 1999, Díaz et al. 2006). Different responses may also occur among (taxonomically) different species groups sharing similar traits (McIntyre & Lavorel 2001). This means that the relationships between species traits and grazing in northern Europe can only be revealed by studying all major types of grazed vegetation in this geographical region. Furthermore, many more species trait studies from various parts of the world are needed before reliable generalizations can be made about which traits are beneficial in grazed areas.

1.5

Persistence of grassland plants in abandoned semi-natural grasslands

Abandonment of semi-natural grasslands generally causes a decline in plant species richness (Bakker 1989, 1998). After abandonment vegetation height and the standing crop increase, a few competitive tall grass and herb species become dominant, and the amount of trees and bushes increases (Duffey et al. 1974, Bakker 1998, Poschlod et al. 1998, Kahmen & Poschlod 2004). The time scale of changes in species composition and vegetation height can vary considerably between different grasslands (Ellenberg 1988, Bakker 1998, Pöyry et al. 2006). Vegetation change after abandonment may thus be rapid (Hill et al. 1992, Stampfli 1992, Jacquemyn et al. 2003) or rather slow (Bakker et al. 1996).

The questions how long declining grassland plants persist in abandoned but treeless or semi-open semi-natural grasslands, and how much persistence varies between different grasslands, have been insufficiently examined. The answers to these questions are important because restoration can often be applied only to a limited number of abandoned grasslands and prioritizations among the candidate sites for restoration must be made.

The persistence of plant species in abandoned grasslands depends on local abiotic conditions (Vandvik & Birks 2002). For example, the occurrence of many grassland species is related to topography-related factors such as site-specific microclimatological characteristics (Grime & Lloyd 1973, Luoto 2000, Bennie et al. 2006). Microclimate is particularly important in northern Europe, where most plant species occur on their northern distribution limit.

During the evolutionary history of grassland plants, intensity of herbivore grazing has probably been lower than during the period when semi-natural grasslands have been managed by livestock grazing. This is because population sizes of natural grazing animals were limited by e.g. predators. Furthermore, many species may have been originally dependent on other disturbances such as fires, flooding and gap dynamics that occur at irregular intervals. Thus, it is possible to put forward the hypothesis that grassland plants are not strictly dependent on annual management of grasslands, and may persist in overgrowing sites for some time.

1.6

Restoration of semi-natural grasslands

Decline in the area of semi-natural grasslands in Finland between the years 1880 and 2000 exceeded 99 % (Vainio et al. 2001). The loss of traditionally mown meadows has been even more dramatic: the present area is only ca. 0.001 % of that at the end of the 1800s (Vainio et al. 2001). At present, the area of species-rich dry and mesic grasslands in Finland (excluding the Åland Islands) is only ca. 3000 ha (Vainio et al. 2001). The species composition of the remaining grasslands has also changed. Present species composition differs from that in the beginning of the 1900s and species indicating nutrient-enrichment are more abundant (Huhta & Rautio 2005).

According to the well-known species-area relationships such drastic habitat loss will have the result that most species of the habitat become extinct (Rosenzweig 1995, 2001, Hanski 2005). If 90 % of the original area of a habitat type is lost, ca. half of the species of that habitat will disappear (Ney-Nifle & Mangel 2000, but see Wilsey et al. 2005). Furthermore, small and isolated patches are prone to local extinctions of grassland plants (Fischer & Stöcklin 1997, Bruun 2000a, 2000b, Kiviniemi &

Eriksson 2002), although the effects of habitat fragmentation are small compared to the effects of habitat loss (Harrison & Bruna 1999).

Such mass extinction of grassland plants has not been reported in Finland (cf. Wilsey et al. 2005, Piessens & Hermy 2006). This is very probably because of the extinction debt (Tilman et al. 1994, Hanski & Ovaskainen 2002, but see Adriaens et al. 2006), and because most of the species of semi-natural grasslands also occur in some other habitats (e.g. in various natural habitats such as rock outcrops or shores or in various edge habitats such as arable field margins and road verges). The area of edge habitats and other open non-cultivated areas has also clearly decreased in Finland (Hietala-Koivu 2002), and their quality has weakened due to eutrophication. Furthermore, many edge habitats may be relict habitats. They are often small linear remnants of grasslands (mostly cleared to arable fields 50-150 years ago) or sites earlier managed by mowing or grazing. Mowing of edge habitats for agriculture was still very common 50 years ago (Hilli 1949).

Many perennial plants may persist as adults for some time, even several decades, in conditions where recruitment of new plant individuals does not occur (Eriksson 1996). Lindborg & Eriksson (2004a) reported time lags of 50-100 years in the response of grassland plant species richness to habitat fragmentation. In Estonian alvar grasslands the extinction debt estimated for individual alvars was around 40 % of the current species number (Helm et al. 2006). Thus, many species may represent declining relicts from an era when semi-natural grasslands were abundant in the landscape (Eriksson et al. 2002, Cousins et al. 2003). The present area of semi-natural grassland in Finland is apparently too low to maintain a large pool of grassland species (cf. Rosenzweig 2001, Cousins et al. 2003).

In Finland (excluding Åland) a moderate goal has been set to increase the amount of suitably managed traditional rural biotopes to 60 000 hectares of which ca. 13 000 ha should be dry and mesic grasslands (Salminen & Kekäläinen 2000). In order to make restoration of abandoned grasslands effective in future, there is an urgent need to study the success of present restoration efforts.

Only few managed grasslands in Finland are protected as nature conservation areas. Most grasslands are privately owned and used for agriculture by farmers or abandoned. In most cases support for grassland management is available only through the agri-environment scheme. The Finnish agri-environment scheme includes a submeasure "management of traditional rural biotopes", which has been specified as the main means of management of semi-natural grasslands, including grasslands in the Natura 2000 areas (Salminen & Kekäläinen 2000). Thus, maintaining biodiversity of the Finnish agricultural landscape heavily relies on the agri-environment scheme, the effectiveness of which is not well known. However, preliminary results suggest relatively low effectiveness (Kuussaari et al. 2004, Puurunen et al. 2004), as in other European countries (Kleijn et al. 2001, 2006, Kleijn & Sutherland 2003, Zechmeister et al. 2003).

During the past decade there has also been increasing interest in grassland restoration in Finland (Jutila b. Erkkilä 1999, Huhta 2001, Huhta et al. 2001, Tikka 2001, Jantunen 2003, Hellström et al. 2003, 2006, Hellström 2004). However, the effects of cattle – the most suitable grazing animal – on restoration of mesic semi-natural grassland has not been studied.

Several constraints prevail in the restoration of semi-natural grasslands. Major abiotic (eutrophication and acidification) and biotic (impoverished seed banks, limited dispersal range) constraints have been identified (Bakker & Berendse 1999). Effective restoration measures should be carefully designed and restoration should be focused to habitat types and geographical areas where the constraints are least severe. Restoration potential is increased by short time since abandonment (Willems 2001, Öckinger et al. 2006), low levels of soil phosphorous and nitrogen (Marrs 1993, Pywell et al. 2003, Hodgson et al. 2005) and position close to species-rich grasslands (Gibson & Brown 1992, Mortimer et al. 1998, Pärtel et al. 1998, Willems & Bik 1998, Willems 2001). Furthermore, the number of grassland species is higher in sites with high soil pH (Tyler 2000, Bruun 2001, Myklestad & Sætersdal 2004), and many rare species are confined to high pH soils (Roem & Berendse 2000, Pärtel et al. 2004).

It is most effective is to restore abandoned grasslands by cutting of trees and shrubs and restarted grazing or mowing. Attempts to change arable land to semi-natural grasslands have had only limited success (Gibson & Brown 1991, Bakker & Berendse 1999, Kleijn 2003), although increase in several common grassland species is easy to achieve (Pywell et al. 2002). If fertilization levels have been low, recovery of arable land to grassland by grazing and mowing management is more effective (Ruprecht 2006). Rather rapid vegetation changes and return of some rare species have been obtained by top-soil removal (e.g. Allison & Ausden 2004, Jansen et al. 2004). In former arable land a large pool of phosphorus has accumulated in the soil due to fertilization, and decrease of phosphorus to the level of semi-natural grasslands is extremely difficult (Gough & Marrs 1990, Bakker & Berendse 1999). Furthermore, ex-arable land is also characterized by impoverished seed banks of grassland plants and often by limited numbers of grassland species close by (Poschlod et al. 1998, Walker et al. 2004). Soil of arable land has low richness of arbuscular mycorrhizal fungi (Helgason et al. 1998). This may be an important deficiency, because a high colonization rate of arbuscular mycorrhizal fungi is considered to have a positive effect on plant species richness (Eriksson 2001). Restoration of grasslands from forests appears to be more effective than restoration from arable land (Zobel et al. 1996, Dzwonko & Loster 1998, Barbaro et al. 2001, Pykälä 2004, Bisteau & Mahy 2005).

Progress of restoration is usually studied by changes in species composition, richness and diversity. There are putative problems in using only total species richness to monitor the success of restoration. For example, total species richness includes species of other habitats than the target habitat, and increase in total species richness may be related to invasion of species of other habitats or non-native species. Furthermore, intrinsically species-poor habitats may also be important for regional species richness (e.g. by having rare specialist species) (e.g. Noss 1983). Thus, total species richness should not be used in isolation, but preferably in conjunction with other metrics such as species composition, endemism, threatened species and indicator species (Wheeler 1988, Fleishman et al. 2006).

1.7. Explanations for high plant species richness

Numerous theories have been put forward to explain plant species richness (Palmer 1994, Grace 1999, Keddy 2005). Particularly, plant species richness on a small scale, plant species coexistence, has been a favoured topic in plant ecology. Disturbance, biomass, habitat heterogeneity, environmental fluctuations, complex interactions, recruitment efficiency and species pool are among the main factors considered to affect small-scale plant species richness (Grime 1979, Huston & DeAngelis 1994, Hurtt & Pacala 1995, Grace 1999, Pärtel et al. 2000, Mouquet & Loreau 2002, Barot & Gignoux 2004, Houseman & Gross 2006).

Species richness is a scale-dependent phenomenon. Different environmental factors may have different, even contrasting, importance on different spatial scales (Whittaker et al. 2001). On large spatial scales, the length of abiotic gradients (e.g. climate, topography, soil), available energy, habitat area, historical and chance events, recruitment limitation and extinction-immigration dynamics have been considered as important factors in explaining species richness (Hurtt & Pacala 1995, Wohlgemuth 1998, Hubbell 2001, Whittaker et al. 2001, Thuillier et al. 2006). In addition, the importance of historical factors has recently been emphasized. In this respect, plant species richness is assumed to be high in habitats that have been abundantly available for plants for long periods (Taylor et al. 1990, Zobel 1992, Aarssen & Schamp 2002).

Numerous studies have reported positive effects of grazing and mowing on plant species richness in Europe (e.g. Bakker 1989, 1998). Very high small-scale species richness is typical for traditionally managed grasslands (Kull & Zobel 1991). There is less data on the importance of grazing and mowing for large scale species richness, but some studies have shown landscape-level decline in species richness after abandonment of grasslands (Dullinger et al. 2003, Luoto et al. 2003b). Furthermore, many plant species are threatened due to cessation of grazing and mowing (Rassi et al. 2001, Oostermeijer 2003). This suggests that grazing and mowing are also important for maintaining plant species richness on broader spatial scales.

Several explanations have been proposed for high plant species richness of grazed and mowed areas (e.g. Naveh & Whittaker 1979, Grime 1990, Gigon & Leutert 1996, Olff & Ritchie 1998). However, there are no reviews which have presented all the putatively important explanations for why grazing and mowing usually increase plant species richness in Europe.

1.8 Aims of the study

The present study concerns the importance of traditional livestock grazing and mowing (i.e. agricultural practices including no fertilization or other nutrient-enrichment due to management, no seeding, and no ploughing) on maintaining plant species richness. The main emphasis is on the effects of cattle grazing in mesic semi-natural grasslands, with several field studies (II-V). The two reviews (I, VI) aim to provide an assessment of the importance of grazing and mowing management in maintaining plant species richness.

This thesis concentrates on the following important and hitherto, insufficiently studied themes:

(1) natural disturbances and livestock grazing, (2) effects of cattle grazing on plant species richness, composition, species trait groups and individual species in mesic semi-natural grasslands, and (3) effects of restoration of semi-natural grasslands by cattle grazing on plant species richness and composition.

A hypothesis is presented that similarities between grazing and mowing and natural ecological processes have been crucial for maintaining plant species richness in Europe, where most of the land has been influenced by humans for several centuries or millennia (I). In mesic semi-natural grasslands the following questions were studied: How do species composition and richness of abandoned and grazed areas differ from each other and are there significant differences in species richness patterns on different spatial scales? (II, III). Is restoration of semi-natural grasslands with the agri-environmental scheme effective? (II, III). Are certain species traits linked with species responses to grazing? (IV). Are species traits in mesic grasslands differently linked to grazing than in the dry grasslands examined in previous studies? (IV). How have environmental variables and abandonment of grasslands affected richness of common and rare grassland plants in topographically variable areas (steep slopes), if grasslands have remained treeless or with only a low cover of trees and shrubs? (V). In the last part of the thesis, I present a revision of the explanations why traditional grazing and mowing increase plant species richness in Europe (VI).

2 Methods

2.1

Reviews

Material used in the reviews were collected through extensive literature surveys (I, VI). It was hypothesized that traditional animal husbandry (grazing and mowing) has partially replaced several human-suppressed and important natural processes. Extensive literature surveys were carried out in order to collect studies concerning the ecological effects of grazing and mowing and of major natural disturbances (particularly large herbivores, fires and floods) on biodiversity, and these effects were compared (I). While conducting the second review study (VI), explanations for why traditionally livestock grazed and mowed areas are rich in vascular plants were searched through extensive literature surveys.

2.2

Study areas

The field studies were performed in mesic semi-natural grasslands in south-western Finland (II-V). The main study design consisted of 31 grasslands (II-IV) which were situated on the border of the hemiboreal and southern boreal vegetation zones in inland SW Finland, 20-50 kilometres from the coast (fig. 1). Three kinds of mesic semi-natural grasslands were studied: 1. continuously seasonally cattle grazed (n=10), 2. seasonal cattle grazing restarted 3-8 years ago after over ten years of abandonment (n=10) and 3. overgrowing, over ten years ago abandoned grasslands (n=11). In the year 1999 in the river Rekijoki valley, 18 sites (six of each three types) were studied. In the year 2000, 13 additional sites (4 old, 4 new and 5 abandoned pastures) were surveyed. In 1999 the area of the studied grassland sites varied from 0.25 to 0.8 ha (mean 0.4 ha in each of the three groups). In 2000 one similar sized area (0.25 ha) was studied from each studied grassland. All studied grasslands were situated by rivers and brooks with the same soil type (clay soil) and on rather steep slopes with high incident radiation (facing S, W, or E, mainly SW or SE).

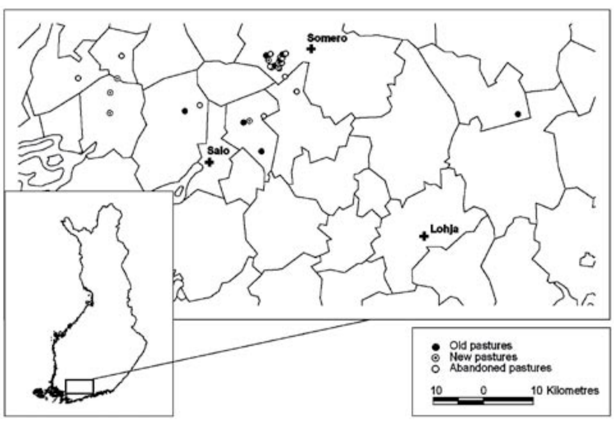

Fig. 1. The location of the study sites of articles II-IV in SW Finland.

Traditionally managed sites are virtually non-existent in Finland (Pykälä 2001, Vainio et al. 2001), but the study sites were selected to be as close to traditionally managed sites as possible. These sites have not recently been fertilized. However, some fertilization may have occurred in the past (peaking probably in the 1960s), and occasional nutrient-enrichment has occurred due to casual or irregular use of supplementary forages and minerals or grazing of semi-natural grasslands together with cultivated pastures.

In all the studied sites, semi-natural grasslands were used as additional pastures complementing cultivated pastures. Therefore grazing pressure in the grasslands was not constant between different years. However, according to the farmers grazing management was in most sites rather similar between different years. Animals were usually moved to other pastures when food in the semi-natural grasslands was becoming depleted.

All but two of the study sites were privately owned. None were protected for nature conservation, but 2/3 of them were included in the Natura 2000 network. The grasslands were mainly Fennoscandian lowland species-rich dry to mesic grasslands as defined in the EU Habitats Directive. All resumed pastures and most of the old pastures were included in the EU agri-environment scheme of management of traditional rural biotopes.

The study area of paper V, the river Rekijoki valley, is situated in inland SW Finland (60°36′ N, 23°20′ E) in the southern boreal vegetation zone. Most grasslands in this area have been abandoned during the past 50 years (Kontula et al. 2000, Luoto et al. 2003a). The flora of grassland patches was studied in the years 1993-1994 (Kontula et al. 2000). All landowners of the area were interviewed to record the year of the end of grazing (if grazing had ended). Grassland patches were included in the study, if (1) the time of the end of grazing was known, (2) over 80 % of the area of a patch was grassland and the cover of trees was < 20 %, (3) the area of wet grassland was less than 50 % of the patch. 162 grassland patches fulfilled these criteria.

2.3.

Measurements

Presence-absence data of vascular plants were collected from each of the studied semi-natural grasslands during July and August (II-IV). A total of 15 sample plots of one square meter were randomly selected within each site, and cover percentages of vascular plants were visually estimated. Total cover of field and ground layers, litter and the proportion of vegetation grazed <10 cm high were estimated and the mean height of vegetation was measured. At the end of September data on grazing intensity was collected from 15 randomly selected sample plots per 0.25 ha; the variables measured were mean height of vegetation, proportion of vegetation grazed <10 cm high, cover of field layer and cover of ground layer. Previous and present land use were recorded by interviewing landowners.

Species of dry and mesic grasslands of southern Finland and indicator species of biologically valuable grasslands were delimited as in Pykälä (2001). Rare species were defined as species that are rare natives or archaeophytes in either of the biogeographical provinces Ab and Ta (Hämet-Ahti et al. 1998) (II-V). Nomenclature followed Hämet-Ahti et al. (1998).

The studied grassland plant species were assigned to different groups using Ellenberg indicator values for soil nitrogen and moisture, pH, and light intensity (Ellenberg et al. 1991). Based on this, richness patterns of species of particular Ellenberg values in different pasture types were compared (III).

In the paper IV, the following species traits for which data for the whole flora was available were studied. (1) longevity: annual, biennial, perennial (Hämet-Ahti et al. 1998), (2) Raunkiaer life form (Ellenberg et al. 1991),

(3) plant height with five classes: <20 cm, 21-40 cm, 41-60 cm, 61-80 cm, >80 cm (mean height according to Hämet-Ahti et al. 1998).

In the paper V, the following explanatory variables were measured from all the 162 grassland patches and included in the analysis: area, time after abandonment (in years), cover of trees, cover of shrubs, slope angle and radiation. Mean slope angle for each grassland patch was calculated using Arc/Info Grid from a digital elevation model. An estimate of maximum theoretical solar radiation was produced using a computer model of clear sky insolation and exposure of different slopes (Griffiths 1985).

In this study, the effects of land use history, cover of trees and shrubs, topography and microclimatology on (1) total plant species richness, (2) richness of plant species of dry and mesic grasslands, (3) richness of rare plant species of dry and mesic grasslands were studied. The effects of the studied variables on the occurrence of the six most frequent rare grassland plant species were investigated separately. As the first step in the analysis, richness data was corrected for the sample area by fitting the species area equation $S=bA^z$, in which S is the species richness of plants and A the sampling area (MacArthur & Wilson 1967). The residuals were then extracted and used in the subsequent modelling.

2.4
Data analysis

Species compositions (mean cover of each species) of the three types of study areas (old, new and abandoned pastures) were compared using global non-metric multidimensional scaling (NMDS), as implemented in the program PC-ORD version 4 (McCune & Mefford 1999) (II). Species richness values per grassland and per m^2 vegetation height and cover of litter and ground layer of old, new and abandoned pastures were compared using the Kruskall-Wallis one-way ANOVA and its a posteriori test between pairs using the program Statistix 7 (II). Furthermore, the six most abundant species in abandoned pastures and differences in their cover between the three pasture types were compared (II).

Responses to grazing of species with a frequency > 5 % in the 1 m^2 squares in at least one of the three pasture types were compared with the Kruskall-Wallis one way ANOVA (III). The Mann-Whitney U-test was used to analyse whether species > 60 cm (Hämet-Ahti et al. 1998) and < 60 cm differed in terms of their cover / frequency ratio (III).

The Kruskall-Wallis one way ANOVA was used to compare numbers of species with high and low Ellenberg values and mean Ellenberg values between the three management regimes (III). Testing whether rare species and other species differed in Ellenberg values was carried out using the Mann-Whitney U-test (III).

In the paper IV, differences in species richness of studied species traits in the three different grassland types were studied with the Kruskall-Wallis test. In addition, correlations between species richness of different life forms and longevity groups and variables relating to grazing intensity were examined using the Spearman Rank correlation test.

In the analysis of the grassland patch data from the river Rekijoki valley, the plant species data was related to predictor variables using generalized additive models (V). Statistical analyses were performed using Splus (Version 6.1 for Windows, Insightful Corp.) with standard functions (gam for generalized additive models) and some custom functions. A bi-directional stepwise model selection procedure was used. A cubic smoothing spline method was chosen to smooth the studied variables, using 4 degrees of freedom by default (Venables & Ripley 2002). As the response variables were continuous values (residuals of the species area equation), a normal distribution of error with an identity link was applied (see Crawley 1993). In the analysis of individual rare grassland species occurrences, the response variable was the presence-absence of a species in each patch, and thus Binomial error and a logistic link were used (V).

3 Results and discussion

3.1

Mitigating deleterious human effects by livestock grazing and mowing

A hypothesis was presented that traditional animal husbandry has partially compensated for the loss of natural processes suppressed by humans and can be used to mitigate deleterious human impacts (e.g. eutrophication) on biodiversity in Europe (I). A new synthesis on the importance of livestock grazing and mowing to mitigate the effects of disturbance suppression was produced. This compensation by grazing and mowing has been of utmost importance in maintaining biodiversity in Europe, where humans have long suppressed natural disturbances.

The suppression of major natural disturbances has been severe in Europe. Under the natural fire regime in Fennoscandia ca. 1 % of the forest land was burned annually (Niklasson & Granström 2000), but at present the figure is only 0.001-0.01 % (Esseen et al. 1997). The area of flood-influenced land has strongly decreased due to regulation of water levels of lakes and rivers and drainage of wetlands (for rivers see Dynesius & Nilsson 1994). Furthermore, most of the flat land naturally affected by flooding is currently under arable cultivation. In forests, trees are generally cut before they become old, and thus soil disturbances due to uprooting of trees are rare compared to natural landscapes (Schaetzl et al. 1989, Ulanova 2000). The number of large mammal species and individuals causing natural disturbances has been reduced. This is because several herbivores (particularly megaherbivores) were hunted to extinction in Europe as well as in most other continents (Stuart 1991, 1999, Johnson 2002, Brook & Bowman 2005). Beavers were hunted to extinction in most of Europe, but their numbers have partly recovered after several reintroduction programmes (MacDonald et al. 1995). Important links between these five major natural disturbances (large herbivores, fires, floods, beavers and gap dynamics) and traditional agricultural management were identified; thus the outcomes of the review (I) gave support to the hypothesis that traditional agricultural use has partially compensated for the loss of natural disturbances.

Considerable evidence exists for the key ecological role of large herbivores in ecosystems compared to other herbivores (e.g. Owen-Smith 1987, 1989, Zimov et al. 1995, Knapp et al. 1999). Most herbivore species utilize only a few plant species for their food. However, mammalian herbivores become less selective of plant material as body size increases (Demment & van Soest 1985), and large herbivores utilize a very high number of plant species. Relatively non-selective feeding behaviour of large herbivores leads to suppression of large and abundant plants. This leads to increase in plant species richness (Milchunas et al. 1988). In this study, cattle was considered to be the key animal for biodiversity, because it feeds less selectively than other livestock (I).

Several authors have suggested that livestock grazing has more or less compensated for the effects of extinct large herbivores on ecosystems (Ridley 1930, Martin 1970, Andersson & Appelquist 1990, Gerken 1999, Vera 2000, Bakker et al. 2004). Cattle, horses and sheep are descendants of native Eurasian herbivores. Cattle (*Bos taurus*) substitutes the auroch (*Bos primigenius*) and horse (*Equus caballus*) the tarpan (*Equus ferus*). Due to their substitute role, cattle and horses should be used in nature conservation in Europe (van Wieren 1995, Wallis de Vries 1995, Olff et al. 1999). However, in other continents cattle, horses and sheep are introduced species, which may have severe negative effects on biodiversity (Fleischner 1994, Parker et al. 2006).

Similarities between other natural disturbances and traditional agricultural use by grazing and mowing have generally been ignored by researchers. In this thesis, it was suggested that whereas major differences between natural disturbances and grazing and mowing can be identified, the similarities between the effects of natural disturbances and traditional animal husbandry are also prominent and ecologically very important. For example, several similarities between the ecological effects of fires and of traditional livestock grazing and mowing were identified (I).

Thomas (1993) and Thomas & Morris (1994) pointed out the detrimental effect of the Holocene climate cooling about 5000 BP for many insect species. Many species dwelling in grasslands have benefited from early successional warm habitats created by traditional agriculture and thus have been able to persist in the northern part of their distribution area (Thomas 1993). They may even have increased and dispersed further north. It seems plausible that traditional agricultural management similarly prevented the disappearance of many plant species otherwise threatened by deteriorating climate.

By and large, traditional land use by grazing and mowing has resulted in two general outcomes: (1) mitigation of the negative effects of natural climate change (Thomas 1993), and (2) compensation of the suppression of natural disturbances creating open and semi-open areas (I). These two effects have occurred during most of the Holocene period, but with spatially and temporally variable intensity. The suppression of large herbivores has occurred for millennia, but suppression of fires and flooding and beavers are more recent phenomena.

During the past century, traditional grazing and mowing management has also mitigated the effects of nutrient-enrichment on plant composition and richness (I). These two measures are currently widely used in nature conservation to ameliorate the effects of eutrophication (e.g. Anderson 1995, Weiss 1999, Power et al. 2001, Jacquemyn et al. 2003). However, grazing and mowing may only partially mitigate nutrient-enrichment. This is because they are often not effective enough in reducing the amount of nitrogen and phosphorus in soil (Härdtle et al. 2006, see also Berlin et al. 2000). Nevertheless, the importance of grazing and mowing as mitigation tools for nutrient-enrichment has continuously increased with increasing nutrient-enrichment. In northern Europe, where nitrogen deposition is lower than in Central Europe, mitigation of nutrient-enrichment by grazing or mowing would presumably be more effective.

It has been proposed that free grazing of livestock in large areas would be based on natural processes and therefore be beneficial to biodiversity (Wallis de Vries 1995). Restoring natural processes does not necessarily restore previous natural ecosystems, because humans have globally changed ecosystem properties (Foster et al. 2003). In practice, free-grazed areas in Europe would automatically include intensively cultivated former arable land. When former arable land is grazed together with semi-natural grasslands, nutrients and seeds of plants from nutrient-enriched habitats may readily transfer via animal faeces to semi-natural grasslands (Londo 1990, Moussie et al. 2005). This often causes a decline in the quality of semi-natural grasslands (Bokdam & Gleichman 2000) and even deleterious impacts on grassland species of nutrient-poor soils. Thus, large scale free grazing is apparently in most cases not suitable for nature conservation (I).

The grazing compensation hypothesis has several consequences for nature conservation (I):

(1) a large proportion of European species originally adapted to natural disturbances may at present be dependent on livestock grazing and / or mowing. (2) grazing and mowing are key management methods to mitigate the effects of nutrient-enrichment on biodiversity. The impacts of nutrient-enrichment and disturbance suppression have increased during recent decades. Because of this, many plant species of various habitats may become extinct in the long run if active management of their habitats is not commenced. Traditional grazing and mowing are the most effective management methods to prevent extinction of many species sensitive to nutrient-enrichment or disturbance suppression. (3) The cessation of grazing and mowing does not necessarily lead to a species composition more similar to natural conditions (in which ecosystem properties are not changed by human activities).

3.2

Effects of cattle grazing on plant species richness and composition in mesic semi-natural grasslands

In northern Europe the flora and vegetation of grazed and mowed mesic grasslands have been described in many studies (e.g. Norrlin 1870, Teräsvuori 1920), but the effects of livestock grazing in these habitats have been poorly studied. Only two published small-scale studies exist (Persson 1984, Hellström et al. 2003). Some studies have included mesic grasslands as well as other grassland types (e.g. Kotiluoto 1998, Lindborg & Eriksson 2004b).

Due to the scarcity of studies, the management recommendations for maintaining plant species richness of mesic grasslands rely more on information obtained from practical management work carried out than on scientific studies (see Ekstam & Forshed 1996). These recommendations have been criticized as too simplistic and monotonous for providing the most beneficial means to maintain biodiversity in grasslands (Pärt & Söderström 1999).

Effects of grazing on flora are also scale-dependent (Chaneton & Facelli 1991). Most studies have been carried out in small scale (< 100 m^2). Species density of traditionally grazed and mowed areas (most often measured as number of species per m^2) is known to be exceptionally high (Kull & Zobel 1991), but the differences in species richness patterns on different spatial scales have been insufficiently examined.

A comparison based on multivariate analyses (non-metric multidimensional scaling) showed that three different types of mesic semi-natural grasslands differ significantly in their species composition (II). Moreover, plant species richness was highest in continuously grazed grasslands, lowest in abandoned grasslands and intermediate in grasslands where grazing had restarted 3-8 years ago (II). This difference occurred in total species richness, richness of species of dry and mesic grasslands, richness of indicator species of biologically valuable grasslands and richness of rare plants in all three studied scales (0.01 m^2, 1 m^2 and 0.25-0.8 ha, mean 0.4 ha). This congruence between different scales and species list definitions suggests that cattle grazing has a clear positive effect on plant species richness over a range of scales. Differences in species richness between pasture types were in agreement with other studies (Bakker 1998, Dupré & Diekmann 2001), especially on the small spatial scales.

The number of species indicating nitrogen-poor soils, high light intensity and low soil moisture was highest in old and lowest in abandoned pastures (III). By contrast, the number of species indicating nitrogen-rich soils was highest in abandoned pastures. Grazing appeared to have a positive effect on indicator species of both high and low pH. The mean Ellenberg light value (calculated across all grassland species in each study site) increased and the corresponding nitrogen, pH and moisture values decreased as a response to increasing grazing. These results mainly agree with other studies (Ewald 2000, Pakeman 2004, Spiegelberger et al. 2006). However, Ewald (2000) found a positive correlation between grazing and Ellenberg pH value. Mean Ellenberg N values were higher than those obtained from Scandinavian traditionally managed grasslands (Myklestad & Sætersdal 2004), which suggests that some nutrient-enrichment of the study sites has taken place.

Positive effects of cattle grazing were observed for most grassland plants; 34 species were significantly more frequent in grazed than in abandoned grasslands and only four in abandoned grasslands (III). Furthermore, most grassland plants were more frequent in old than in new pastures. Several species had intermediate frequencies in new pastures compared to old and abandoned pastures, thus suggesting that the recovery of the plant populations is due to resumed grazing.

The results of studies in mesic semi-natural grasslands (II, III) show that (1) most plant species benefit from grazing, and the number of grazing intolerant species is low, (2) almost no new species invade abandoned grasslands if they remain without trees and shrubs, (3) a few tall species such as Alopecurus pratensis, Anthriscus sylvestris, Calamagrostis epigejos, Cirsium arvense, Elymus repens increase their cover and frequency after abandonment. This strong increase evidently causes decline of most other species, (4) indicator species of biologically valuable grasslands and rare species are more abundant in grazed than in abandoned grasslands, (5) a significant change in species composition and richness after resumed grazing can occur already during a period of 5 years, (6) grazing management is apparently not suitable for enhancing the populations of all grassland species, and other management methods such as mowing may be required to complement grazing.

3.3

Species traits and cattle grazing in mesic semi-natural grasslands

Species richness in mesic semi-natural grasslands was higher among most species trait groups in old than in abandoned pastures and showed some recovery in new pastures (IV). More pronounced differences were found on the fine-scale (1 x 1 m study plots) level than in the grassland site plots. Richness of perennial and biennial plants, as well as of hemicryptophytes and chamaephytes, was highest in old and lowest in abandoned pastures on both spatial scales. In addition, richness of annual plants was significantly higher in the grazed sites on the 0.25 ha scale. The number of geophyte species was lower in grazed than in abandoned pastures both per m^2 and per grassland patch. Richness of small and medium-sized plants was higher in grazed than in abandoned grasslands.

The proportion of species trait groups in which species richness was higher in grazed than in abandoned grasslands, was high compared to previous studies (Dupré & Diekmann 2001, de Bello et al. 2005, Peco et al. 2005). This may be largely due to differences in the grassland type (mesic vs. dry or wet). It may thus be argued that species trait responses to grazing are related to how effectively natural factors (e.g. drought, flooding) limit plant growth (IV). In mesic grasslands, natural factors limit plant growth less than in dry or wet grasslands. Because of this the number of groups of species with different species traits benefiting from grazing is higher in mesic than in dry or wet areas (IV). Furthermore, cattle is less selective than other livestock. Because of this cattle grazed areas often have higher plant species richness than areas grazed by other livestock.

It has been suggested that species traits can be used as indicators for monitoring land use change (Smith et al. 1997, McIntyre et al. 1999). There has been some success in using species traits in analyzing land-use change (see Diaz et al. 2001, McIntyre & Lavorel 2001) or restoration progress (Hellström et al. 2003, Pywell et al. 2003).

However, it should be noted that a considerable amount of information is lost by categorizing species into a few species trait groups. Moreover, responses of individual plant species sharing similar traits to grazing often differ. Several plants show a consistent response to grazing through habitat and grazing intensity gradients, but responses of other species may depend on habitat type, grazing intensity, site productivity and identity of neighbour plants (Vesk & Westoby 2001, Pakeman 2004). Cousins & Lindborg (2004) found no association between successional change and plant functional traits in a grassland-forest gradient. Furthermore, Lindborg & Eriksson (2005) found only weak association between land use change and species response traits. Some species may also show high phenotypic variability. Such species may belong to different trait groups under different ecological conditions (Dyer 2001). Furthermore, numerous traits can be generated, but it is difficult to evaluate which ones are most relevant in different situations.

Overall, these results suggest that the restoration progress can be coarsely evaluated using the species traits approach, but that responses of rare and threatened species or indicator species may be more useful in studying the success of grassland management for biodiversity (Cousins & Lindborg 2004, Lindborg & Eriksson 2005).

3.4.

Persistence of grassland plants in abandoned grasslands

In the grasslands of the river Rekijoki valley, the increase in solar radiation was positively correlated with total species richness, richness of grassland plants and richness of rare grassland plants (V). Increasing cover of trees had a negative effect on total species richness and that of rare grassland species. Total species richness and richness of grassland species declined with increasing time after abandonment, but richness of rare species did not show a similar trend. This was unexpected, because rare species are usually considered to be more sensitive to abandonment than common species (Schaffers 2002, Luoto et al. 2003b, Myklestad & Sætersdal 2004). According to the results the increase in the cover of trees after the end of grazing may be more detrimental to grassland plants than the lack of grazing per se (V).

The results emphasize the importance of high solar radiation, grazing and low cover of trees for plant species richness in mesic semi-natural grasslands (V). Plants appear to be less sensitive to overgrowth on steep slopes with high solar radiation. Similar results have recently been obtained by Baur et al. (2006) and Bennie et al. (2006). Bennie et al. (2006) also reported that the effect of nutrient enrichment on vegetation in managed chalk grasslands decreased with increasing slope angle and solar radiation. The steepest S-SW-exposed slopes are climatologically the most extreme sites, sharing high radiation and maximum temperatures (Stoutjesdijk & Barkman 1992). Thus, they provide the most favorable sites for species occurring close to their natural distribution limit (Grime & Lloyd 1973).

The present results provide some support to the hypothesis that many grassland species have a certain resistance to overgrowth and that annual management of semi-natural grassland may not always be necessary. Many species may occur in grasslands after several decades of abandonment (Milberg 1995, Eriksson 1996, Eriksson et al. 2002). However, there are contrasting results and several studies have shown sensitivity of many grassland plants to overgrowth even during short time periods (Hansson & Fogelfors 2000, Norderhaug et al. 2000, Eriksson et al. 2002).

The present results highlight the importance of semi-natural grasslands on steep slopes for grassland plants. One practical conclusion stemming from this is that abandoned semi-natural grasslands situated on south- and west-facing slopes should be prioritized in grassland restoration (V).

3.5

Restoration of mesic semi-natural grasslands

Restoration of plant communities is generally a slow process (Bakker 1989, Gibson & Brown 1992, Bakker et al. 2002). Only a few studies have been made of the restoration of semi-natural grasslands in northern Europe, and they have provided mixed results. Management of former arable land by grazing and / or mowing has given discouraging results (Tikka et al. 2001). Minor or major increase in plant species richness and desired plant species has usually occurred due to restoration of abandoned grasslands (Kotiluoto 1998, Huhta et al. 2001, Vinther & Hald 2001, Mitlacher et al. 2002, Hellström et al. 2003, 2006, Lindborg & Eriksson 2004b, Lindborg et al. 2005, Rosén & Bakker 2005, Öckinger et al. 2006) or clear cutting of forests (Pykälä 2004). In general, it appears that restoration of species richness can be achieved more easily than restoration of communities (Gibson & Brown 1992).

The main problem in restoration studies is that the full success of ecological restoration can be evaluated only after several decades of restorative management (Gibson & Brown 1992). Usually change of vegetation is slow (e.g. Kotiluoto 1998, Huhta et al. 2001, Hellström et al. 2003, 2006, but see Willems & Bik 1998). The temporal scale of restoration tends to be several times longer than the duration of studies investigating the success of restoration. However, it can be detected after only a few years of management whether restoration has started successfully (II). There is a strong indication that restoration should occur within the time scale of performed studies, but scientific studies tend to last only very few years. For this reason dispersal limitation has been emphasized as a major constraint in restoration (e.g. Stampfli & Zeiter 1999, Pywell et al. 2002, Hellström 2004, Lindborg 2006), although the temporal scale of restoration studies is too short for evaluating the phenomenon.

Increase of common grassland species and of plant species richness does not necessarily indicate success of restoration. Total species richness may actually be increased by dispersal of species of other habitats or non-native plants to managed sites. Several studies have shown that some increase in plant species richness can easily be achieved by various management methods in many kinds of habitats (e.g. Gibson & Brown 1991, Zobel et al. 1996, Pykälä 2004, Walker et al. 2004). Furthermore, when plant size decreases more individuals (and species) may occur in small sample plots (Oksanen 1996, Stevens & Carson 1999). Because grazing decreases the size of plant individuals, some increase in species density may occur even in sites managed poorly for biodiversity conservation. Because of these potential biases related to the total species richness, changes in species composition and species richness of rare and declining grassland species often provide better indicators of restoration success.

Species richness of new pastures was 20% higher in 0.25-0.8 ha and 40-50% higher in 1 m^2 scale compared to abandoned grasslands (II). However, species numbers in new (restored) and abandoned pastures did not differ significantly (II), possibly because of the rather low statistical power of a posteriori tests. Total, grassland and indicator species richness both per m^2 and per grassland patch in new pastures were between the numbers of old and abandoned pastures. The results presented here suggest an increase of ca. one species per m^2 per year after resumed grazing (II). Numbers of species with high and low Ellenberg nitrogen indicator values in new pastures were between those of old and abandoned pastures (III). The frequencies of most grassland species in restored new pastures were between those observed in old and abandoned pastures (III), as was also the species composition of new pastures (II). Thus, the present study showed rather promising results of restoration of abandoned grasslands by cattle grazing in private farms (II, III), although there is much between- and within-site variation in the management regimes of grasslands managed by farmers. Restoration of semi-natural grasslands by private farmers with the agri-environment scheme may be useful and potentially effective (II, Rosén & Bakker 2005).

However, rare species showed poor response to resumed grazing, which may be due to unsuitable management quality or the short time period of restoration. Several problems in management quality (see also Pykälä & Heikkinen 2005, Schulman et al. 2006) were observed such as use of supplementary forages, grazing with cultivated pastures and low grazing intensity (II). Poor management quality retards, hampers or may even prevent restoration progress. It is therefore possible that populations of several rare grassland plants will not recover with current cattle grazing regimes (II, III). Management regulations in the agri-environment scheme must be followed and also defined more precisely for successful restoration. Recent studies suggest that the use of minerals may cause a clear increase in the amount of soluble phosphorus in grassland soils (Virkajärvi 2005). This causes a major problem in the management of Finnish semi-natural grasslands for biodiversity. Furthermore, for many grassland plants mowing is a better management method than grazing (Tamm 1956, Ekstam & Forshed 1992, Norderhaug et al. 2000, Wahlman & Milberg 2002). To be fully effective, restoration should be based on site-specific considerations and management should be performed according to the present and desired species composition of the site (Vandvik et al. 2005). Detailed information concerning the quality of restoration efforts is generally lacking in restoration studies. This makes it impossible to evaluate how severely unsuitable or insufficient management quality affects the success of restoration.

In Finland it is rather difficult to tailor high quality management for certain vegetation types and declining plant species, because the financial support for management of semi-natural grasslands is on a rather low level compared to financial support for other agricultural measures such as arable cultivation. Less than 3 % of the total amount of money spent in the Finnish agri-environment scheme has been used for biodiversity-oriented measures (Puurunen et al. 2004).

It is possible that the total success of restoration would fail even with high quality management, i.e. that the species composition of traditional semi-natural grasslands cannot be achieved. Some studies have shown negative vegetation changes (Berlin et al. 2000) and disappearance of demanding species (Fischer & Stöcklin 1997) even in semi-natural grasslands that have been continuously traditionally managed. These changes have been attributed to atmospheric nitrogen deposition, minor changes in management and changes in the landscape surrounding semi-natural grasslands (Berlin et al. 2000).

However, numerous studies have demonstrated that restoration of abandoned semi-natural grasslands is worthwhile as it can result in increase in plant species richness, population size of rare and threatened species and dispersal of rare and threatened species to restored sites (e.g. Zobel et al. 1996, Kotiluoto 1998, Vinther & Hald 2001, Willems 2001). Different grassland plants have different ecological demands. Thus, restoration of the grassland species pool in a certain landscape would require a number of different management regimes applied at different grassland sites. Moreover, restoration of semi-natural grasslands is further complicated by the fact that responses of insect communities to grazing differ from those of plant communities (Pöyry et al. 2004). The peak in insect species richness occurs at a lower grazing intensity than in plant species richness (Pöyry et al. 2004, 2006). Thus, different grazing intensities in different grassland patches are needed for management of grassland biodiversity (Pöyry et al. 2004, 2005).

3.6

Explanations for high plant species richness of traditionally grazed and mowed areas

There are many explanations why traditional grazing and mowing are beneficial for plant species richness (VI). Numerous studies have shown that decrease of competition, biomass and nutrient availability, suppression of growth of trees and shrubs and enhanced recruitment of plants in grazed and mown areas are important for explaining why they are rich in species. Several other explanations presented have been less intensively studied, and their importance is insufficiently known. At present the relative importances of different explanations is not clear (VI). Furthermore, different factors are not isolated from each other, but are interactive (Olff & Ritchie 1998). The interactions between the different factors are probably of great importance and should be studied in more detail. In practice, in many cases the relative impacts of different factors may be very difficult to differentiate (VI).

Olff & Ritchie (1998) classified causative processes affecting high plant species richness in grazed areas into processes contributing to enhanced local colonization or reduced local extinction rates. Mowing and livestock grazing appear to increase the persistence of both individuals and populations of many plant species and decrease local extinctions of plant populations (VI).

Studies on the effects of grazing and mowing on plant species richness have usually been performed on small spatial scales. Several mechanisms presented promote small-scale species richness, but their effects on larger scales may be more complex. The scale dependence of different factors cannot be properly evaluated. The importance of grazing and mowing on regional scale plant species richness has been emphasized in some studies (Jensen & Schrautzer 1999, Dullinger et al. 2003). It was suggested that a landscape with more than half of the area traditionally grazed and/or mowed has the highest plant species richness (VI).

Extinction of plant populations due to livestock grazing appears to be rare in areas with a long evolutionary history of grazing by large herbivores (Milchunas & Noy-Meir 2002). To cause an extinction, herbivores must consume a high proportion of a species occurring at low abundance (Maron & Vilá 2001). This behaviour is only likely to occur in the case of specialized herbivores (Levine et al. 2004). This suggests that extinction of local populations may be higher in sites grazed by sheep than by cattle or horses.

Evolutionary and mitigation factors are emphasized in explaining the high plant species richness of grazed and mowed areas (VI). Furthermore, equalizing factors are very important in explaining the strong small-scale spatial variation in plant species richness. Grazing and mowing cause a shift towards conditions that have occurred during the evolutionary history of European plant species, as key ecological factors (nutrients, pH and light) are modified towards historical conditions (VI). Grazing and mowing mitigate deleterious human effects on plant species richness, e.g. by partially compensating natural disturbance dynamics suppressed by humans and mitigating the effects of nutrient-enrichment (I). However, in other continents than Europe, where there is a lack of evolutionary history including grazing by large herbivores, grazing (and presumably also mowing) have predominantly negative effects on plant species richness (Milchunas et al. 1988, Milchunas & Lauenroth 1993).

4 Conclusions

The hypothesis that livestock grazing has partially compensated for several natural disturbances has important consequences for nature conservation (I): (1) a large proportion of European species originally adapted to natural disturbances may currently be dependent on livestock grazing and / or mowing. (2) grazing and mowing are key management methods to mitigate the effects of nutrient-enrichment on biodiversity. The severity of nutrient-enrichment and disturbance suppression have increased during recent decades, probably with the result that the existence of many species is currently more dependent on grazing and mowing management than previously. (3) The cessation of grazing and mowing does not restore the species composition of natural ecosystems, but on the contrary may increase the deviation of species composition from natural ecosystems.

In mesic semi-natural grasslands most plant species benefit from cattle grazing, and the number of intolerant species is low (II, III). Indicator species of biologically valuable grasslands and rare species are generally also more abundant in grazed than in abandoned grasslands. Cattle grazing can be used as a partial surrogate of mowing. However, several grassland species prefer mowing and their populations can only be restored by moving. Consequently, increase of area of both grazed and mowed mesic semi-natural grasslands is required in order to halt the decline of farmland plant species richness.

Several of the studied species traits appear to be related to grazing (IV). Thus species trait responses to grazing may be related to how effectively natural factors limit plant growth. The species trait approach can be used in analyzing the effects of grazing on species composition and progress of restoration on a coarse scale. However, for a more detailed analysis of restoration success other methods such as change in species composition and in population sizes of indicator and threatened species are also needed.

Rare grassland plants are not necessarily more sensitive to abandonment than common ones (V). However, the sensitivities of rare species may differ between different geographical areas and habitat types. In northern European agricultural landscapes, steep S-SW-facing slopes are the most suitable sites for many grassland plants and should be prioritized in grassland management and restoration.

The full success of grassland restoration can only be evaluated after several decades of management. However, the potential and likely direction of the restoration progress can be evaluated after only a few years of management (II, III). Restoration of semi-natural grasslands by farmers is potentially a useful and effective method to halt the decline of biodiversity in agricultural landscape. However, several constraints in the restoration were identified in this thesis

(II). Financial constraints may be the most severe, as agricultural subsidies directed to biodiversity-friendly management are low compared to other subsidies. Due to financial constraints the quality of management is generally not sufficient.

High plant species richness of traditionally mowed and grazed areas is explained by numerous factors operating on different spatial scales (VI). Particularly important for maintaining large scale plant species richness are evolutionary and mitigation factors. However, the relative importance of different factors is poorly known. Studies on small spatial scales strongly dominate, and there is a clear need for studies concerning large scale effects of grazing and mowing.

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Maintaining plant species richness by cattle grazing: mesic semi-natural grasslands as focal habitats