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Research article

Modelling the effects of landscape pattern and grazing regimes on the persistence of plant species with high conservation value in grasslands in south-eastern Sweden

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Abstract

Semi-natural grasslands in Sweden are threatened by land-use change and lack of management with attendant risk to their biodiversity. We present a model to explore the effects of grazing frequency and intensity on plant species persistence, and the relative effects of grassland size and pattern. We used a landscape modelling platform, LAMOS (LAndscape MOdelling Shell), to design a landscape model of vegetation dynamics incorporating the effects of local succession, dispersal and grazing disturbance. Five plant functional groups (PFG), representing various combinations of persistence and dispersal character, light requirements and disturbance responses, were defined to model species dynamics. Based on old cadastral maps three different landscapes were designed representing specific time-layers, i.e., a historical (17th to 18th century), a pre-modern (1940s) and a present-day landscape. Simulations showed that a threshold was crossed when grasslands decreased in area to about 10–30% of the modelled area, and as a consequence the biomass of grassland-specific PFGs was strongly reduced. These competition sensitive groups did not persist in the model even with intense grazing in the present-day landscape, where grasslands occupy 11% of the total area. However, all grassland species would have been able to persist in the historical landscape, where grasslands occupied 59% of the total area, even without grazing. Our results suggest that continuous but low-intensity grazing is more positive for grassland PFGs than discontinuous but highly intensive grazing. This effect was particularly strong when the frequency and/or intensity of grazing dropped below a threshold of 20%. Simulations using three landscape maps designed to explore effects of further fragmentation and habitat loss showed that the spatial pattern of remaining grasslands is important for the persistence of grassland-specific PFG. The model presented here is an advance towards more realistic grazing models to explore the effects of prescribed grazing and landscape fragmentation on the persistence species or plant functional groups.

Introduction

An important task for conservation biology is to evaluate the status of species inhabiting rare and fragmented habitats, and to design appropriate conservation plans. In northern and central Europe, semi-natural grasslands are not only among the most species-rich ecosystems (van der Maarel and Titlyanova 1989; Kull and Zobel 1991), they are also among the most threatened habitats. The biodiversity value of semi-natural grasslands is intimately linked with the fact that these grasslands have been managed for several hundreds of years by mowing or grazing and have not been fertilised or ploughed. Over the recent decades the area covered by semi-natural grasslands has declined steeply as a result of changes in land use associated with the changing socio-economic and political context in Europe. Indeed, during the last 150–200 years semi-natural grasslands in Sweden have been fertilised, cultivated, afforested or abandoned, so that approximately 90% of the semi-natural grasslands have disappeared. Due to habitat destruction, the remaining species-rich grasslands tend to be small and fragmented. So far, no fragmentation effects on plants have been identified in Sweden, but in Denmark Bruun (2000) found effects of fragmentation on small grassland remnants and suggested that it reflected the longer time of fragmentation in Denmark as compared to Sweden. In this context, and because declines in species specific to these habitats are already observed (Lennartsson and Svensson 1996; Kiviniemi and Eriksson 1999; Eriksson and Eriksson 2000; Lindborg and Ehrlén 2002), they must now be the focus for conservation plans.

That semi-natural grasslands need to be managed in order to maintain high species richness is well known. Repeated endogenous disturbance, caused by mowing and grazing, has shaped these ecosystems through evolutionary times (Holling 1986; Huston 1994). Several studies have indicated that the long continuity of management contributes to their high species richness (Eriksson et al. 1995; Pärtel et al. 1999; Austrheim et al. 1999; Cousins and Eriksson 2002). Hence, grassland habitats need to be grazed or mowed in order to maintain species richness (Peart 1989; Montalvo et al. 1993; Eriksson and Eriksson 1997; Poschlod and Bonn 1998; Kiviniemi 1999). Lack of management leads to encroachment of shrubs and trees and thus to species-loss (Grace 1999; Hansson and Fogelfors 2000; Cousins and Eriksson 2001). However, the question remains how often and with what intensity semi-natural grasslands need to be managed for typical grassland species to persist. Little is known either about how different landscape configurations affects species richness and persistence. Therefore we must address two specific questions: (i) In what way do variations in grazing frequency and intensity affect species persistence? (ii) What are the relative effects of grassland size and management regimes? Answers to these questions would give an indication how to best manage, conserve and restore semi-natural grasslands, and thus species richness within the rural landscape matrix.

In order to answer such questions, a generic understanding of the mechanisms of response of grassland species to grazing and landscape patterns must be gained. Grace (1999) lists some of the most important mechanisms controlling species diversity in herbaceous plant communities such as grasslands: disturbance, total community biomass, colonisation, species pool and spatial heterogeneity. The recognition that the response of plant species to predominant environmental factors and interactions with other organisms can be related to their biological characteristics has considerably advanced our understanding of these mechanisms (Lavorel et al. 1997; Grime 2001). Plant functional groups (PFGs) are user-defined groups of taxa with similar response to environmental resources and disturbance associated to shared biological traits (Gitay and Noble 1997; Lavorel et al. 1997). A growing number of empirical studies have recently contributed to the identification of PFGs for response to grazing (e.g., Bullock et al. 2001; Díaz et al. 2001; McIntyre and Lavorel 2001; Vesk and Westoby 2001) and to land abandonment (Tilman 1988; Bazzaz 1996; Prach et al. 1997). Among those functional traits relevant to these responses, and because local patterns of richness must be explained by including landscape-scale processes (Zobel 1992; Austin 1999; Grace 1999), seed-dispersal and colonisation abilities have recently become a focus of attention for studies of plant diversity and conservation (Strykstra et al. 1998; Eriksson 2000; Turnbull et al. 2000). In a synthesis of results from dispersal and colonisation studies in Swedish semi-natural grasslands and deciduous forests Eriksson (2000) presented a shortcut to assess temporal and spatial aspects of plant dynamics at the landscape scale. He assigned species into four different categories of spatio-temporal dynamics, where the first category contains species with poor ability to disperse in space and poor ability to persist in time. On the opposite end of the axis are species with a high ability to both disperse and persist. However, as a result of the competition-colonisation trade-off (Tilman 1994), most species are either poor ‘dispersers’ but fair ‘persisters’, or fair ‘dispersers’ but poor at persisting in a certain location. A species’ ability to persist in time and its ability to disperse in space can serve as focus for modelling plant species retention in fragmented landscapes. Expected fragmentation effects are that species with poor dispersal abilities would have trouble dispersing to distant habitats, and that local populations would decline and go extinct. However, some plant species have the potential to develop remnant populations (Eriksson 1996) and can persist despite unfavourable conditions and a negative population growth rate. Species that have the ability to develop remnant populations are likely to be successful if habitats were restored (Eriksson 2000; Cousins and Eriksson 2002).

Land use-related questions are difficult to address experimentally in a thorough manner because of the large spatial and temporal scales involved to capture responses in a meaningful manner (Turner et al. 1995; With 1997; Weber et al. 1998; Lindborg and Ehrlén 2002). As a result, in nature reserves and conservation areas, grassland management is often carried out by trial and error as only few studies have used comparative management regimes of sufficient duration (Hansson and Fogelfors 2000; Hulme et al. 2001). Spatially explicit modelling appears as the tool of choice to circumvent these problems and provide managers with decision support systems grounded in solid scientific knowledge (Turner et al. 1995; Jeltsch et al. 1997). Landscape models addressing pattern and process in herbaceous vegetation can be classified into two groups, corresponding to two different sets of objectives. A first group of models have explored the mechanisms of maintenance of species diversity as a result of the interactions between species functional traits (e.g., competitive ability, reproductive output, dispersal ability and longevity) (Palmer 1992; Colasanti and Grime 1993; Moloney and Levin 1996; Schippers et al. 2001; Plotnick and Gardner 2002). These models provide important insights into the degrees of landscape fragmentation and disturbance regimes suitable to maintain highly diverse grassland communities. However, being theoretical models they must simplify reality and are a long way from practical management questions. The second group of models have examined the response of particular grassland systems to changes in management regimes. The vast majority of these models appear to have been developed in semi-arid regions, where they have been motivated by urgent questions of management to prevent or restore degradation (e.g., Pickup 1994; Wiegand and Milton 1996; Jeltsch et al. 1997a, b; Reynolds et al. 1997; Weber et al. 1998). While focusing on the outcome of different management regimes, they have highlighted important processes responsible for the observed responses. Despite the large number of empirical studies in European grasslands that have shown the importance of different mechanisms of species persistence (Harper 1977; Grubb 1977; Grime 1979; Zobel 1992; Grace 1999; Hulme et al. 2001 and many others). Such models are few and only available for particular species or locations (e.g., Hunt 2001; Rees and Hill 2001), and mechanisms of grassland species persistence in fragmented landscapes have not been addressed systematically in a spatially explicit context.

In this study, we modelled grazing effects on the persistence and spatial distribution of five plant functional groups in different landscape types submitted to a range of grazing regimes. Five plant functional groups relevant to the dynamics of vegetation following the extensification of grassland management were defined. These groups represented the range of persistence and dispersal characteristics (cf., Eriksson 2000), light requirements and grazing responses represented in semi-arid grasslands of South-Eastern Sweden (Ekstam et al. 1988; Ekstam and Forshed 1997). Using simulations we explored how often grazing is needed and how intense the grazing must be for model grassland species to persist in patches or in the landscape depending on their biology, in particular their dispersal abilities. We also examined what effect landscape changes resulting from different land-use trajectories (fragmentation, habitat loss and abandonment) might have on the persistence of grassland-specific species.

The model

We used the landscape modelling platform LAMOS (LAndscape MOdelling Shell; Lavorel et al. 2000) to design a model of vegetation dynamics incorporating effects of local succession, dispersal and grazing disturbance. This platform makes it possible to put succession point models within a spatially explicit context (Noble and Gitay 1996) by taking into account explicit fluxes of seeds and disturbance between pixels of a map. Landscapes are represented as raster images of fixed extent and grain. In this study we used a resolution of 20 m for a map of 50 × 50 pixels, representing a total area of 100 ha.

Successional dynamics

To analyse the effects of grazing in grasslands, local succession within each map pixel was simulated using the model FATE (Functional Attributes in Terrestrial Ecosystems; Moore and Noble 1990). FATE is a semi-quantitative model derived from the Vital Attributes model (Noble and Slatyer 1980), which considers the biology of individual plants or functional groups as the driver of vegetation dynamics. FATE can be considered as a good compromise to capture essential processes of community dynamics while remaining relatively simple, easy to parametrise and providing an adequate representation of disturbance-driven dynamics (Pausas 1999). Rather than modelling the dynamics of each individual plant, FATE focuses on groups of individuals with the same effective age within a functional group (cohorts). In the model, plants pass through four discrete life-stages: propagules, germinants, immature plants and mature plants. Each life-stage has different responses to environmental conditions and to disturbance. To account for these responses FATE is divided into three submodels: life-history, competition and disturbance (Figure 1).

The *life-history* submodel manages the transitions between life-stages, based on the germination requirements, maturation time and the life span of each functional group. Propagules can be seeds, vegetative reproductive structures and seedlings with or without dormancy. Germination of a propagule is enforced depending on the environmental conditions and the germination requirements of the PFG. Immature plants are plants that have successfully recruited but not yet reproduced. Further transitions to maturity and senescence are determined by the life-history schedule. Production of seeds for dispersal by mature plants is based on fixed fecundity values for each PFG.

Competition submodel: In grasslands many herbs and grasses respond to light availability, and are outcompeted by larger species if the grassland is abandoned. Shade-tolerant species take over and suppress the light-requiring species. Huston and Smith (1987) demonstrated that by varying plant characteristics, such as size, growth rate, shade tolerance and fecundity, various successional patterns could be produced as a result of light competition. Similarly, FATE considers the interaction between the biology of species and light competition as a driver of vegetation dynamics. There are three levels of light availability, low, medium and high determined by the vertical stratification of species. Plants of the same age and functional group can belong to one of four discrete strata, and are only able to change stratum depending on life-stage (they increase by ageing or decrease by disturbance). Hence immature and mature plants of a same PFG may occupy different strata based on a proportional size parameter. Plants do not compete for light within cohorts or with other functional groups within the same stratum. Instead the abundance of plants in the superior strata governs the light resource in all inferior strata by determining which PFGs (shade-tolerant or intolerant) can be present at which abundance. Actual abundance of a species in a stratum is then a function of the light resource available and its potential maximum abundance (i.e., how much cover could this PFG achieve for 100% light availability?). In LAMOS, this actual abundance is then used to calculate the biomass of each PFG in the pixel by multiplying it with its potential biomass (the biomass achieved for a monospecific cover).

The *disturbance-response submodel* deals with events such as fire or grazing, or any other event, which destroy plants and thus release resources. In this implementation of LAMOS, we considered grazing as the single active disturbance. Depending on its biology and life-stage and on grazing intensity, a plant may be unaffected, killed, or may resprout. The reduction in plant size by biomass loss is translated into a reduction in cohort age, where plants are set back to an age before or after the age of maturity. Although FATE includes the possibility to represent seed banks and their response to disturbance, we did not use any seed bank since typical perennial grassland species of our system do not tend to accumulate seeds in the soil.

Grazing disturbance

In LAMOS, disturbance is modelled as an event determined by three processes: initiation, spread and effects on vegetation. The disturbance submodel handles the first two processes that are of a truly spatial nature in the landscape, while local disturbance effects are addressed by the life-history submodel (see above). In this model we used a simple implementation of the disturbance submodel in order to represent grazing by cattle in a pasture situation (as opposed to free range), where location, extent and intensity of grazing are imposed as part of the management regime within a set cadastral plan. This requires a ‘static’ approach, where grazing is superimposed on a vegetation map in a fixed manner determined by the distribution of semi-natural grassland amongst the landscape matrix. To do this, we used a GIS-based approach where the location of grazing starts is imposed through a map of grazed plots. Arable fields were also modelled by using a mask to exclude vegetation from establishing in these pre-designated areas. The rest of the landscape matrix was left to secondary succession.

Grazing starts have a fixed frequency throughout the simulation, corresponding with the periodicity of grazing for a single pasture (if the pasture is grazed

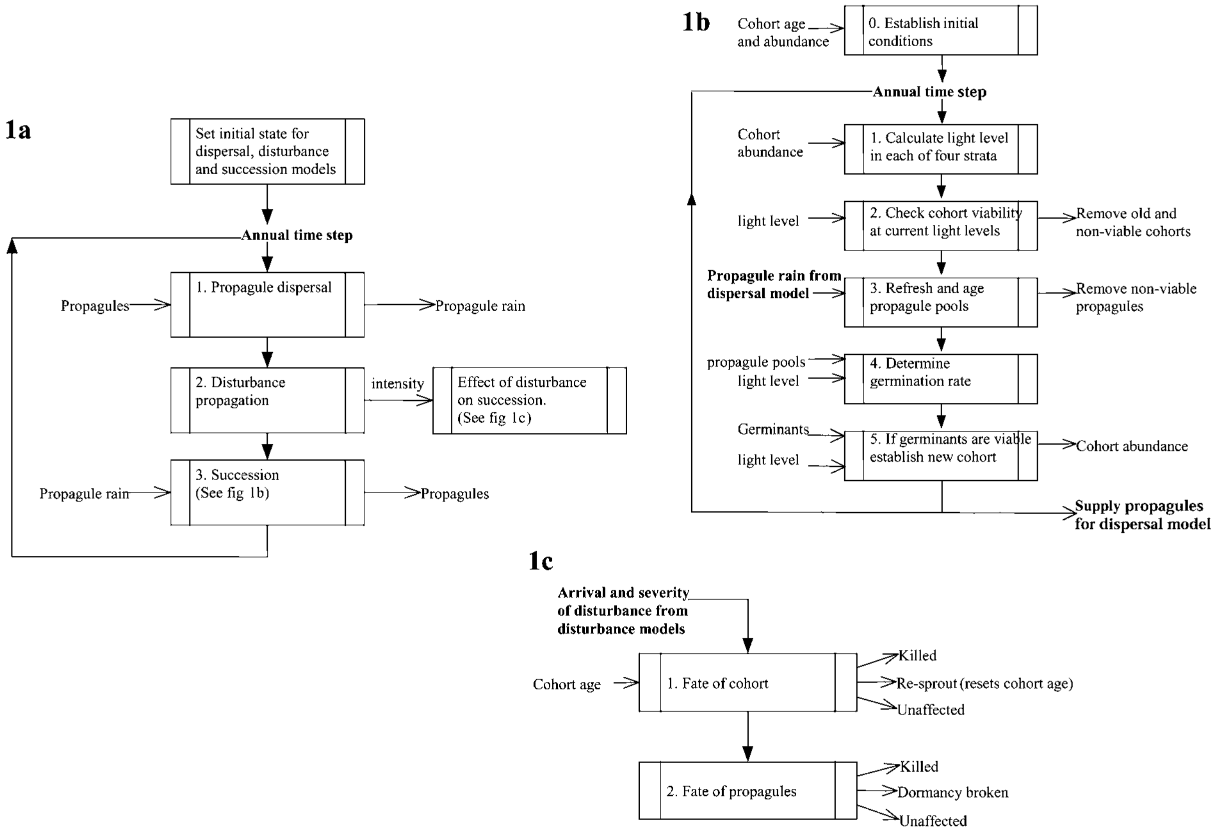

Figure 1. (a) Sequence of events in a LAMOS simulation. After setting the initial conditions for dispersal (propagule map), disturbance (time since last disturbance) and succession (cohort abundance and age), the simulation enters an annual time step. Propagules are distributed across the landscape by the dispersal model taking a map of propagules and producing a map of propagule rain. Next, a disturbance propagation model visits all selected cells and calls the succession model to respond to the disturbance at the given intensity level. Once disturbance is complete, succession is called for each cell in the landscape. Succession determines the current state of the vegetation, recruiting from the propagule rain and updating the propagule map to be supplied to the dispersal model at the next time step. (b) Schematic diagram showing the sequence of events in FATE affecting vegetation succession. For each PFG: (1) The abundance in each stratum of mature and immature cohorts is used to establish a light profile through four strata. (2) Cohorts that are old or cannot survive at the current light level within their respective stratum, are removed from the simulation. (3) Seed pools are replenished from propagules distributed by an external seed dispersal model. The seed pools age and emptied for PFGs that display pulse germination. (4) A germination rate is determined based upon the number of propagules available and the amount of light at ground level. (5) The abundance of germinants is determined from the available light and a new cohort created. (c) Schematic diagram showing the effect of disturbance on vegetation in FATE. The intensity of a disturbance is set at three levels; low, medium and high. For each level, the fate of a cohort can be set for three separate age classes. Within each age class a proportion of the cohort can re-sprout or be killed, the remainder being left unaffected. When a proportion of a cohort re-spouts, its effective age is reset to a set value.

every year, every ten years, etc.). As a simplifying assumption, for each simulation year the probability of grazing occurring was equal to the average frequency. The extent of grazing was then fixed to that of the pasture plot by using a ‘cookie-cutter’ technique, with a fixed extent of a single pixel around starting pixels. For simplicity, we considered that grazing was homogenous within each grazed pasture (see Jeltsch et al. 1997b). Grazing intensity within each grazed pasture was hence fixed by management as a probability for a pixel within the grazed area to be actually consumed. Finally, the actual severity of grazing that plants are subjected to inside each grazed pixel was calculated as the average of palatabilities of PFGs present in the pixel, weighted by their biomass (Wiegand and Milton 1996). This formulation of grazing pressure makes it possible to account in a coarse manner for grazing behaviour, where grazing pressure at a small scale is a function of the overall composition of the vegetation rather than imposed individualistically on species present (Landsberg et al. 1999).

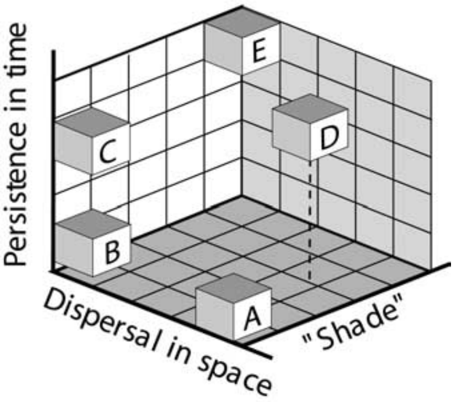

Figure 2. A conceptual model of positions of the plant functional groups (PFG) in a space-time diagram including the susceptibility to poor light conditions (i.e., resources in the model). The model has been modified from Eriksson (1996, 2000). The early successional PFGs, A, B and C, are located in the front of the cube, which indicates that they are intolerant to poor light conditions. PFG B and C have poor dispersal abilities in space. PFG A is short-lived but have better dispersal ability mainly due the large amount of seeds it produces. PFG D has a good dispersal in space, it persists in time and it is not sensitive to shade. PFG E is a long-lived secondary successional perennial with poor dispersal abilities in space.

Seed dispersal

The second spatially explicit landscape-scale process taken into account in the model was seed dispersal away from parental sites. We used an exponential decay around cells where a PFG is present. Spatial distributions of seeds produced in a pixel were captured by two parameters: the fraction of seeds that stay within the same pixel where they were produced (short distance dispersal), and the slope of the decay of frequency away from the source pixel for seeds dispersed at longer distances (see Moloney and Levin 1996). The intensity of the seed rain was determined by the fecundity of PFGs.

Plant functional types in grasslands of South-Eastern Sweden

To represent the diversity of strategies present in semi-natural grasslands, we used five plant functional groups, corresponding to four different dispersal categories presented by Eriksson (1996, 2000). In addition, to represent species typical of different successional stages we included in the description of PFGs a characterisation of their shade and grazing tolerance. A conceptual model of the PFGs position in a space-time and light resource diagram can be seen in Figure 2. Table 1 shows how the parameters of the PFGs were set, for life-history, palatability and dispersal. The initial conditions used for the model simulations are based on experience from plant ecological studies in landscapes in south-eastern Sweden. Based on our experience of primary and secondary patterns in these grassland communities and of grazing effects on different species we parametrized the PFGs to a realistic vegetation community dynamic. Three PFGs, A, B and C, are ‘typical’ perennial grassland species. Annuals were not modelled since hemi-boreal grasslands primarily contain perennials (Eriksson et al. 1995). ‘A’ is a grazing-tolerant biennial with good dispersal qualities and poor competitive abilities. ‘B’ is a short-lived perennial with poor dispersal abilities and poor competitive abilities. ‘C’ is long-lived with poor dispersal abilities, but it is slightly less sensitive to low resources. This is a PFG likely to develop remnant populations. All the three grassland PFGs need abundant light to germinate and to survive (Table 2). The last two PFGs are also long-lived perennials. ‘D’ has a good dispersal range and ‘E’ is a very long-lived PFG with poor dispersal abilities, both being grazing-intolerant but shade-tolerant. ‘E’ has a greater shade-tolerance than ‘D’ and both are secondary successional PFGs (Table 2). To simplify the model, all PFGs were given the same maximum potential abundance, i.e., medium, and the same size ratio of juveniles to adults (1:4). Some typical grassland species in Sweden with similar characteristics as PFG A are *Carlina vulgaris* and *Myosotis ramoslisima* (annual). *Plantago media* and *Polygala vulgaris* could represent PFG B, and *Primula veris* and *Ajuga pyramidalis* are examples of PFG C species. *Filipendula ulmaria* and *Poa nemoralis* could characterise PFG D and, *Convallaria majalis* and *Anemone nemorosa* could be representative species of PFG E.

The five PFGs also differ in the response of their different life-stages to grazing (Table 3). The three typical grassland PFGs (A, B and C) resprout when they are grazed, whether the grazing is severe or medium. B and C are not affected at all when the grazing is mild. Although C and D have the same life span, D is more negatively affected by grazing than C. When the grazing is severe most individuals of D are killed and few resprout. D is less affected when the grazing is milder. Mature individuals of E are not affected by grazing. On the other hand, all germinant and immature individuals of PFG E are killed when the grazing is severe. Most individuals are killed when the grazing is medium, and only half are killed when the grazing is mild.

Table 1. Five model species representing plant functional groups (PFG) typical for different stages of succession in hemiboreal grasslands. The PFGs are designed with different life-histories and strategies. Dispersal abilities of functional groups modelled with a kernel-mode a certain proportion of the seeds stays ‘at home’ while another proportion spread away from the plant.

PFG	Lifespan (yrs)	Maturation time (yrs)	Potential biomass (tha^{-1})	Potential fecundity	Occupying strata when Mature	Occupying strata when Immature	Palatability	Proportion short dispersal distance	Dispersal distance
A	2	1	0.02	4000	0	0	0.8	0.3	0.9
B	10	3	0.05	2000	0	0	0.8	0.8	0.95
C	100	9	0.1	1000	1	0	0.7	0.8	0.95
D	100	9	0.5	1000	2	0	0.5	0.5	0.5
E	300	30	1.0	500	3	0	0.4	0.8	0.95

Table 3. Effects of disturbance on each PFG. There are three intensity levels of disturbance, severe, medium or mild. Either all, most, half, few or none of each PFG life stage are affected by disturbance. They may resprout (R.) when they are set back to a certain age i.e., resprouting age (R. age).

		Disturbance severe			Medium			Mild		
PFG		Killed	R.	R. age	Killed	R.	R. age	Killed	R.	R. age
A	Propagules	none			none			none		
	Germinants	few	all	0	few	all	0	few	all	0
	Matures	most	all	1	half	all	1	few	all	1
B	Propagules	none			none			none		
	Germinants	most	all	2	few	all	2	none		
	Immatures	most	all	3	few	all	3	none		
	Matures	most	all	3	few	all	3	none		
C	Propagules	none			none			none		
	Germinants	most	all	5	few	all	5	none		
	Immatures	most	all	10	few	all	10	none		
	Matures	most	all	20	few	all	20	none		
D	Propagules	none			none			none		
	Germinants	most	few	3	half	half	3	few	most	3
	Immatures	most	few	6	half	half	6	few	most	6
	Matures	most	few	45	half	half	45	few	most	45
E	Propagules	none			none			none		
	Germinants	all	none		most	few	5	half	half	5
	Immatures	all	none		most	few	10	half	half	10
	Matures	none			none			none		

Table 2. Survival at different life-stages depending on resource levels and disturbance severity. The resource levels can be low, medium or high. Germination rates can be all, high, moderate, low or none. The other life-stages, germinants, immatures and matures, either survive or die.

PFG	Life stage	Resources Low	 Medium	 High
A	Germination rate	none	none	all
	Germinants	no	yes	yes
	Immatures	no	yes	yes
	Matures	no	yes	yes
B	Germination rate	none	low	high
	Germinants	no	yes	yes
	Immatures	no	yes	yes
	Matures	no	no	yes
C	Germination rate	none	low	high
	Germinants	no	yes	yes
	Immatures	yes	yes	yes
	Matures	no	yes	yes
D	Germination rate	mod.	high	mod.
	Germinants	yes	yes	yes
	Immatures	yes	yes	yes
	Matures	yes	yes	yes
E	Germination rate	high	high	mod.
	Germinants	yes	yes	yes
	Immatures	yes	yes	yes
	Matures	yes	yes	yes

Simulations

Model landscapes

The persistence of grassland species was analysed in three different artificially designed landscapes, each representing a specific time-layer, i.e., the historical landscape of the 17–18th centuries, the pre-modern landscape of the mid-twentieth century and the modern landscape of today. The design of the three landscapes, i.e., the area extent of various land-covers, was based on real data from an area in south-eastern Sweden (Cousins 2001). These data are derived from cadastral maps from the 17th and 18th century, aerial photographs from 1945, and aerial photographs from 1981 complemented with field checks to determine present-day conditions.

In order to analyse persistence under historical landscape patterns, we ran a series of simulations for landscape maps having the same statistical properties as found in our empirical data. The grassland extent and distribution for each time-layer were randomly distributed in the respective landscape, mimicking actual grassland size and pattern (Figure 3). In the historical 200–300 years old landscape, there are no areas left to succession. The landscape consists of 10 patches of semi-natural grasslands that cover 59% of the total area. The matrix around the grasslands consists of arable fields with no seed sources for grassland species. In the pre-modern, mid-twentieth century landscape some grassland patches have disappeared altogether in comparison with the historical landscape. Grasslands have diminished to 29% of the total area. Large grassland patches have decreased in size, and a few new small patches have been randomly distributed in the landscape. In the pre-modern landscape a very small area is left to secondary succession (6%). In the modern, present-day landscape most of the larger grassland patches are significantly smaller than at previous dates, and as there are fewer patches. Altogether the modern landscape contains 9 patches of grassland (11% grassland of the total area). A larger area is also left to secondary succession (23% of the total area).

Grazing scenarios

In order to inform conservation managers about how often and how much an area needs to be grazed for all the species to survive in the landscape, we carried out a partial sensitivity analysis of the effects of different grazing intensities and frequencies. This analysis was restricted to specific combinations of landscape patterns and grazing parameters relevant to the management questions relevant to our region.

A first set of simulations examined changes in the abundance of different PFGs in the historical, the pre-modern and the present-day landscape configurations, resulting from the switch from annual intense grazing (frequency = 1.0, intensity = 1.0) to no grazing at all. The objective of these simulations was to analyse the persistence of sensitive grassland species in an historical perspective in order to compare it to today's situation.

In a second set of simulations we analysed the effects of spatial and temporal components of the grazing regime on grassland species persistence in the present-day landscape. This analysis aimed to guide management from the current situation towards regimes that would allow maximum retention of grassland-specific species. We constructed a series of grazing scenarios varying both the frequency and

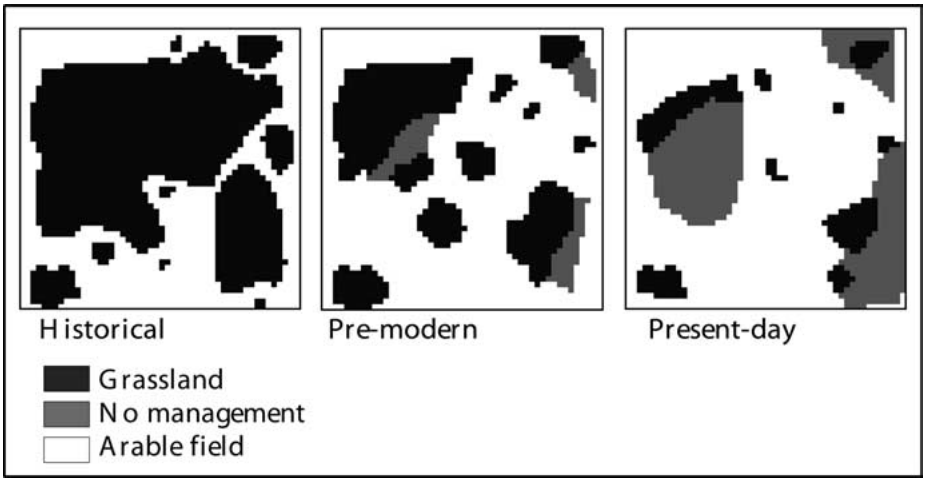

Figure 3. Different landscape patterns representing a historical (200–300 year old), a pre-modern (50 year old) and a present-day landscape. Grazing occurs within grasslands only. None of the PFG can grow on arable fields.

intensity parameters. First we explored the effects of grazing return intervals. Pastures were grazed at different intervals with a frequency ranging from annual to centennial, using a fixed grazing intensity of 100% i.e., the total grassland area is grazed at each grazing event. Second, the effects of the intensity of grazing (i.e., how much of the stocked area is actually grazed) were also analysed by decreasing the grazing pressure from high (100%) to moderate (e.g., 50%) and very low or absent ($< 5\%$). Finally we ran simulations for nine possible combinations of low to moderate grazing intensities (50%, 25% and 10%) and low to moderate grazing frequencies (50%, 25% and 10%, i.e., every 2, 4 or 10 years). These regimes are probably the most realistic to represent the current management of semi-natural grasslands in Sweden.

The last set of simulations was conducted to unravel the interaction between species life-history and grazing frequency. These simulations were guided by the fact that life history schedules of longer-lived species are not always well known and that they may vary across regions depending on environmental conditions and the composition of the species pool. We tested the hypothesis that many uncompetitive species could persist in the present-day landscape as long as the time between grazing events is shorter than the time required by secondary-successional species to reach maturity, i.e., to flower and set seeds. Answers to this hypothesis would help developing boundary conditions for management in different regions. In all previous simulations PFG E was parametrized to reach maturity at 30 years. We would then expect that the early successional species would have higher biomass if the time required by secondary-successional species to reach maturity were longer than the recurrence period of grazing event. Using the present-day landscape to provide initial conditions we performed a series of simulations where the time required for PFG E to reach maturity was varied, from the normal 30 years to 15, 20, 40 and 45 years. The grazing frequency was set to 5%, i.e., a grazing event every twenty years, and grazing intensity to 100%.

All simulations were run 10 times and each run consisted of 1000 steps. Results presented are mean values for final landscape composition. Because FATE is a deterministic model and grazing was prescribed from the cadastral map variance across simulations was minimal and no statistical analyses were conducted.

Landscape fragmentation scenarios

To explore further, and more systematically, the combined effects of landscape configurations and management regimes on the persistence of PFGs a series of scenarios were applied in the present-day landscape, representing fragmentation, habitat loss and deterioration of habitat management (Figure 4). The 'present-day landscape' was changed by reducing grassland and arable field areas. In the first landscape (X) the grassland area was reduced from 11% to 5.8% and only seven grassland patches were left. The grassland habitats were thus even more fragmented. In the next landscape (Y) grassland habitats were lost. We kept 7.4% grassland divided into three patches, which

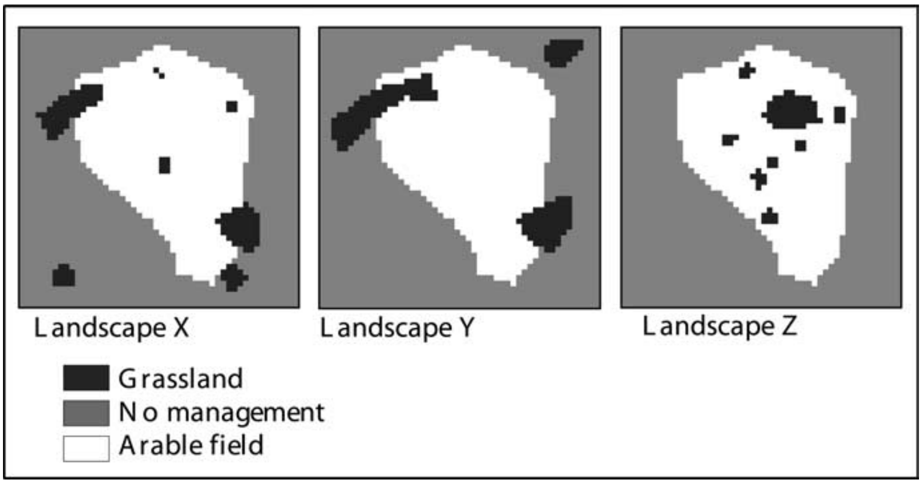

Figure 4. Three landscapes where the grassland patches are more fragmented compared to the present-day landscape. In landscape X the patches are smaller and fewer, in landscape Y only the three largest grassland patches of the present-day landscape remain, and in landscape Z only grasslands occur in midfield islets isolated in arable fields where no succession occur.

were originally the three largest grassland patches in the present-day map. However, all patches were now adjacent to areas without management, allowing for easy colonisation by successional species. These two first landscape scenarios are typical for the landscape changes occurring in more forested areas in Sweden. In the third landscape (Z) arable fields surrounded all grassland patches. There were eight grassland patches reduced to 3.7% grassland of the total area. This landscape scenario is most common in intensive agricultural landscapes. The persistence of the sensitive grassland species was analysed in all three landscapes both with grazing at 100% frequency and intensity or with no grazing.

All landscapes were generated and geographical analyses performed in a raster-based geographical information system (IDRISI).

Initial vegetation distribution patterns

To fill the model landscapes with plants, i.e., PFGs, an image, with randomly distributed 1-to-5-value pixels of equal frequency, was created in IDRISI. Each value was then assigned to a PFG. In order to ensure the potential of secondary-successional PFGs to encroach grasslands as a result of changes in management regime, a small number of secondary-successional PFGs must be readily present in grasslands. The same condition applies to grassland PFGs in unmanaged areas. Hence, secondary successional species had to be included in the initial conditions of grasslands, albeit in a small proportion. This corresponds well with reality as the old cadastral maps showed that even highly managed grasslands contained a mixture of herbaceous species and trees. Field checks in current grasslands and unmanaged areas also confirmed the ecological validity of this prerequisite. To achieve this the random image was reclassified twice. The first reclassification yielded an image in which the ratio between grassland PFGs (A, B, C) and secondary-successional PFGs (D, E) was set to approximately 4:1. The second reclassification yielded a ratio of grassland PFGs to secondary-successional species PFGs of approximately 1:3. The two reclassified images were then combined with the images showing the artificial historical, pre-modern and present-day landscapes, so that grasslands in the artificial landscapes contained a dominance of the grassland PFG assemblage (A, B, C), but also a minor proportion of the secondary-successional PFG assemblage (D, E). Similarly, unmanaged areas in the artificial landscapes contained a dominance of the secondary-successional PFG assemblage (D, E), but with a minor proportion of the grassland PFG assemblage. Finally there had to be seed present from the different PFGs in the initial landscape. Each of the historical, pre-modern and present-day landscapes were classified into five Boolean images showing all pixels of a particular PFG in each image. This image was then used as an initial seed distribution image for each PFG, thus there were a higher proportion of seeds from secondary-successional species in forests and a higher proportion of grassland seeds in grazed areas.

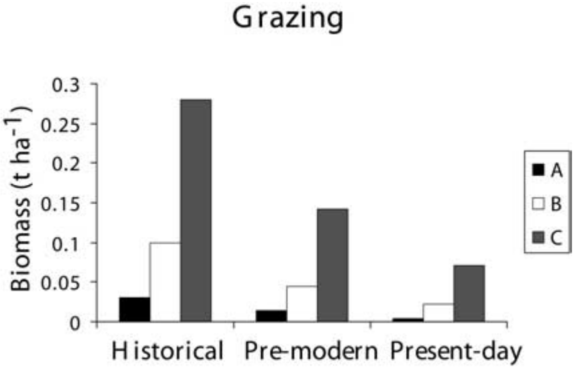

Figure 5. Effects of grazing on grassland species (PFGs) in a historical, pre-modern and present-day landscape. PFG D and E were left out of the charts for clarity, as their biomass were so much larger. However, they were included in all simulations.

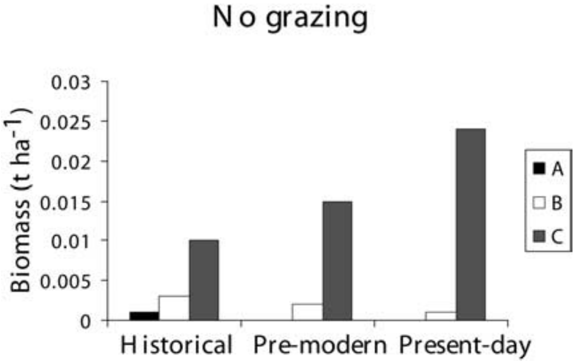

Figure 6. Effects on grassland species (PFGs) when grazing have ceased in a historical, pre-modern and present-day landscape. PFG D and E were left out of the charts for clarity, as their biomass were so much larger. However, they were included in all simulations. The biomass of C increased in the absence of grazing, and when grassland area was reduced, which relates to a long life-span and an ability to withstand encroachment by secondary-successional species.

The initial abundance of each PFG in each pixel was assigned in order to provide realistic conditions for the simulations. Hence, all pixels corresponding to PFG A and PFG B were assigned the quality 'many individuals within all age cohorts'. Pixels corresponding to PFG C were assigned the quality 'medium number of individuals within all age cohorts'. Pixels corresponding to PFG D were assigned the quality 'few individuals within all age cohorts', and finally, pixels corresponding to PFG E were assigned the quality 'few, but all individuals within the age cohorts 200–250 years'.

Results

Effect of historical landscape patterns on the persistence of grassland species

An area reduction from 59% grassland of total area 200–300 years ago to 11% grassland of total area today led to a sharp decrease in the mean abundance of typical grassland species groups A, B and C (Figure 5). This reduction was greatest for PFG A, which appeared more sensitive to area reduction than the other two species groups. Thus, even with intensive grazing management the present-day landscape would not allow these species to persist as significant populations. On the other hand, the less dramatic decrease of grassland area between the historical and pre-modern periods (from 59 to 31% of the landscape) resulted in equal reductions (of about 50%) in abundance of all three species groups. In this situation, the maintenance of an intensive grazing regime would have been enough to maintain some integrity of the grassland species.

When grazing was discontinued for the 3 historical landscape situations A was able to persist in the historical landscape but not in the pre-modern or the present-day landscape (Figure 6). B was able to maintain itself, though at lower abundance. The biomass of C increased in the absence of grazing, and when grassland area was reduced. These responses are related to the relative shade tolerance of the PFGs. A and B are both intolerant to shade, but immature B persisted under unfavourable shade conditions. The lower sensitivity of C relates to its long life-span and its ability to withstand the encroachment by secondary-successional species (D and E).

Grazing management

Variations in grazing intensity under a constant annual frequency had little effect on the biomass of PFGs A, B and C when intensity decreased from 100% to about 20% (Figure 7a). However, when the intensity decreased below 20% the biomass of all three PFGs dropped substantially. In the absence of any grazing PFG, A went extinct and the biomass of PFG B decreased to only 4% of the biomass for a 100% grazing intensity. Concurrent with the decrease in biomass of PFGs A, B and C for intensities below 20%, the biomass of PFGs D and E increased with decreasing grazing intensity (results not shown graphically). PFG D reached its highest abundance for an intensity of 5%.

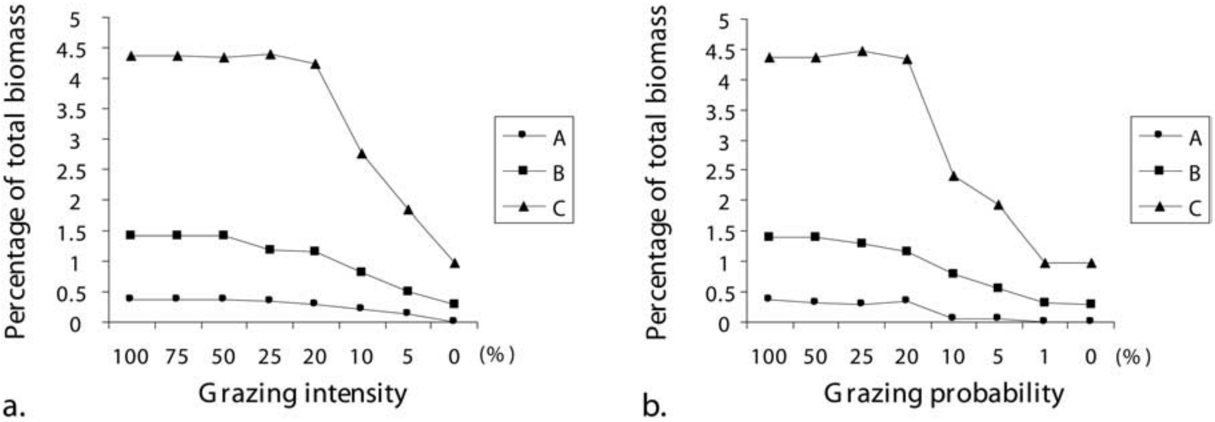

Figure 7. Effects of different grazing intensity (a) and frequency (b) in the present-day landscape. PFG D and E were left out of the charts for clarity, as their biomass were so much larger. However, they were included in all simulations.

A: Frequency \ Intensity	50	25	10
50	0.24	0.16	0.14
25	0.17	0.14	0.08
10	0.09	0.08	0

B: Frequency \ Intensity	50	25	10
50	1.18	0.99	0.51
25	0.98	0.61	0.32
10	0.45	0.32	0.32

C: Frequency \ Intensity	50	25	10
50	4.36	3.28	1.84
25	3.31	2.11	1.16
10	1.68	1.17	1.02

Figure 8. Matrices of the effects of low frequency grazing combined with low intensity of grazing of the three grassland plan functional groups. Values are given as the percentage of total biomass.

As with the changes in grazing intensity there were hardly any changes in biomass of grassland PFGs as grazing frequency decreased down to 20% for a constant intensity of 100% (Figure 7b). Again, as the frequency drops below 20% all grassland PFGs declined rapidly, and PFG A was most severely affected – it was eradicated at 1% grazing frequency. PFGs D and E followed exactly the same trend as following decreases in grazing intensity. Similar biomass values for the three PFGs under equal values of grazing frequency or intensity suggest that temporal or spatial reductions of grazing would have similar effects on the persistence of these grassland species. This result is to be considered with caution in relation to the probabilistic treatment of grazing in our model. Under a 50% grazing intensity each pixel has a 50% chance to be grazed every year, while with a 50% grazing frequency, all pixels are grazed half of the time. These probabilities result in equal average values for each pixel, i.e., being grazed once every two years.

However, a combined reduction in grazing intensity and frequency suggested that these two components of the grazing regime are not fully interchangeable. While for an equal value of frequency a decrease in intensity had a sensibly equivalent effect to a decrease in frequency for the same fixed intensity (as shown in the two previous sets of simulations), concurrent decreases in intensity and frequency had more detrimental effects on the persistence of grassland PFGs than a decrease in frequency or intensity alone (Figure 8). Grassland species reached a higher biomass for a continuous but low-intensity grazing, than when grazing was discontinuous but highly intensive. Conversely, low intensity but continuous grazing was more successful at keeping secondary-successional PFGs at low densities than infrequent intense grazing. These effects were particularly strong when either or both frequency and intensity dropped below the 20% threshold.

Simulations with a grazing return interval of 20 years showed that A could not persist in the landscape and both B and C were negatively affected when the maturation age of the secondary-successional PFG E was reduced from 30 to 15 or 20 years to reach maturity (Figure 9). All grassland PFGs benefited from an increase in the time required for E to reach maturity to 40 years. However, as the time was increased to 45 years only A and B showed a positive response. PFG

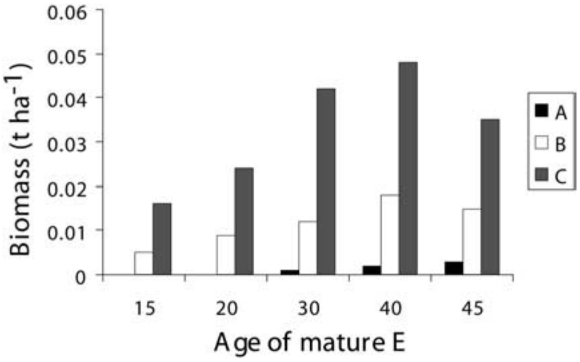

Figure 9. The maturity age of E was varied and simulated with 5and E were left out of the charts for clarity, as their biomass were so much larger. However, they were included in all simulations. Observe that the age of 30 years is the used age for all other simulations.

D was fairly stable in all simulations, and, as expected, the biomass of E decreased with prolonged maturation – there was a decrease by 20% from 15 years to 45 years.

Persistence in fragmented grassland patches

The analysis of the effects of habitat loss and fragmentation revealed that the different PFGs responded differently to landscape changes. PFG A could not persist in any of the three fragmented landscapes, and went extinct after 20 to 30 time-steps whether grazing was present or not (Figure 10). With grazing PFG B survived in all landscapes, although there was a considerable decrease in biomass in comparison with the present-day landscape. However, the decline in biomass did not show a linear relation to the decrease in grassland area. There was a greater biomass loss in landscape Y than in landscape X, despite the larger grassland area in landscape Y. In landscape Z PFG B also survived when grazing was discontinued. The biomass of PFG C remained on a comparatively high level in all landscapes if the grasslands were managed by grazing. However, in a non-grazing situation there was a considerable decrease in the biomass of PFG C in the landscapes where grassland patches were located in direct connection with unmanaged areas with secondary-successional PFGs (landscapes X and Y). In landscape Z, where grassland patches were isolated in a matrix of arable fields (i.e., no successional species), the biomass of PFG C differed only to a minor extent between grazed and non-managed situations.

Discussion

We simulated the effects of different grazing regimes and grassland patterns on five Plant Functional Groups chosen, based on a model on persistence and dispersal characteristics presented by Eriksson (1996, 2000), to which we added considerations of grazing tolerance and shade tolerance. In our simulations for the his, the extra-sensitive grassland species could persist even with hardly any grazing at all. However, with the reduction of the grassland area to levels of the present-day landscape, there were dramatic negative effects on the grassland PFGs.

The ecological basis for the model is based on long field experience and experimental work on how different grassland-specific or secondary succession species behave in our systems (Ekstam and Forshed 1997; Kiviniemi 1999; Lindborg and Ehrlén 2002; Cousins and Eriksson 2002). Although the response and detailed conservation requirements of each species are unique, landscapes cannot be planned for single species. Therefore we must find similarities between species to generate rules for sustainable landscapes (Opdam et al. 2002; see Lindenmayer et al. 2002). Using PFGs as 'model-plants' for simulation modelling or the development of management indicators is one way to meet this challenge (Díaz et al. 2002). A handful of caricatural PFGs may answer more questions on grassland management and conservation at a broad landscape scale than individual species models. We would like to acknowledge, however, that the ecological basis for details of the model needs further exploration. There are still many gaps in knowledge on some of the processes underlying the species response to grazing or abandonment. Specifically, a mix of short intensive and long-term studies would be needed to determine and empirically validate various input parameters, such as those used for dispersal ranges, the age to reach maturity as well as how long a plant can remain as a remnant in an inhospitable habitat. Improved estimates of dispersal abilities would be essential as dispersal distance appears as a critical parameter for species persistence in spatially-explicit metapopulations (van Dorp et al. 1997; With and King 1999). Data from long-term controlled grazing trials at different frequencies and intensities (Wahren et al. 1994; Collins et al. 1998; Bullock et al. 2001; Pettit and Froend 2001) and controlled experiments including seed addition experiments (Ehrlén and Eriksson 2001) and competition experiments (Suding 2001) would help us refine our understanding of the mechanisms of species replacement during extensification. Currently, management experiments with cattle grazing grasslands at different intensity and frequencies, including historical levels (since the 16th century), have been initiated, and effects on target species and biodiversity are being monitored. Demographic behaviour of several typical sensitive grassland species and secondary succession species will also be investigated across landscape types presenting varying patterns of fragmentation and patch isolation.

The simulation of the effects of different grazing management regimes in the present-day landscape suggested that the community composition crosses a threshold when grazing frequency or intensity drop below 20%. As the threshold is passed, the secondary-successional species start to increase at the expense of grassland species. This is congruent with the findings in semi-natural grasslands of southern Sweden that species composition remained unchanged whether grasslands were mowed every third year or every year (Hansson and Folgelfors 2000). On the other hand, Ryser et al. (1995) found in Switzerland, that grasslands cut every second year had more species than grasslands cut every fifth year. It is thus possible that grassland management with a recurrence period of three to four years can delay vegetation change, while a lower management frequency cannot impede successional development (Wadsworth et al. 2000). Complementary simulations where we changed the maturity age of PFG E showed that a grazing event occurring more frequently than the time required by secondary successional species to reach maturity delays the vegetation change. Such scaling properties relating species life-histories and the effects of disturbance regimes (Turner et al. 1993), are likely to be of general interest for the development of management strategies.

The most realistic scenario concerning management of Swedish grasslands today is unfortunately that both grazing intensities and grazing frequencies are low. In our simulations we detected a less negative impact on the biomass of grassland species if the grasslands are managed through low-intensity grazing every year, than if they are grazed with higher intensity but less frequently. Hence, one may infer that extensive grazing on comparatively large areas is more important for the persistence of grassland species than intensive grazing on smaller areas. These results are of interest for insect conservation too, as many butterflies, beetles and bumblebees prefer a longer grass sward than is provided in intensively grazed grasslands (Weibull 2002).

In this study we have not dealt with fragmentation *per se*, i.e., the actual process of dividing areas into smaller pieces, but rather with habitat loss. Metapopulation models predict a non-linear effect of habitat loss – species will become extinct when the amount of remaining habitat falls below a critical threshold governed by the dispersal abilities of the species (Harrison and Bruna 1999; Hanski 1999). We found that a threshold appears to have been crossed between the pre-modern period and present-day. In that time, grasslands decreased from 31% to 11% of the total area, and as a consequence the biomass of grassland PFGs is strongly reduced. In order to have viable populations of sensitive grassland species we need to restore and recreate grasslands. In a review of habitat fragmentation and biodiversity, Andrén (1997) concluded that animal species are affected when there is 10–30% suitable habitat left in the landscape. Similarly, McIntyre et al. (2000) proposed a maximum threshold of 30% intensively managed land and minimum of 30% semi-natural areas for the maintenance of biodiversity and landscape processes in sub-tropical grassy woodlands of Australia. Interestingly, joining these theoretical syntheses with ours indicates that if 30% of the original habitat area could be preserved or restored in a landscape we would probably be able to preserve both animal and plant species associated to that habitat.

To proceed with an effective conservation strategy we need to find out how much needs to be restored and in what type of matrix. Different types of matrix surrounding the suitable habitats differ in permeability and suitability for species. The landscape should therefore be considered as a continuous set of more or less suitable habitats (Wiens 1997; McIntyre and Hobbs 1999). Many modelling studies have so far considered the matrix in a categorical manner as inhospitable (e.g., Hanski 1999). However, in order to adequately preserve species within a landscape conservation management needs not only to focus on the conservation of suitable habitats as an isolated entity but also to improve conditions of the landscape matrix (McIntyre and Hobbs 1999). Our results suggest that isolated grassland patches may have better conservation prospects than patches imbedded in secondary successional vegetation. If the grasslands were surrounded by arable fields where secondary-successional species cannot establish, grassland species may still persist even when grazing is discontinued and even if the

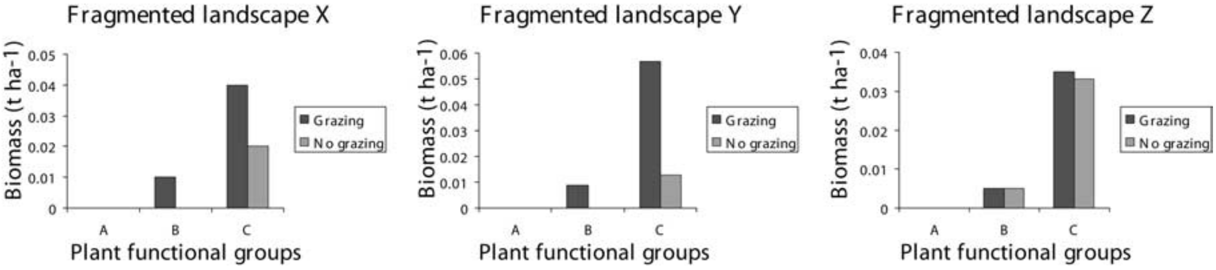

Figure 10. The effect of grazing and no grazing in three different fragmented landscapes (see Figure 3). PFG D and E were left out of the charts for clarity, as their biomass were so much larger. However, they were included in all simulations.

patches are fairly small. This result suggests that the constitution of arable buffers around remnant grasslands fragments could be important for their conservation. In the field we observed that small midfield islets were managed as grasslands in the 17th and 18th century, but have not been managed for several decades (Cousins 2001), usually have many grassland species (Cousins and Eriksson 2002). Many of these species are grassland specialists that are confined to these habitats (Cousins and Eriksson, 2001). An implication of this modelling study is that the isolation of midfield islets within arable fields may be one reason why grassland species persist in these patches, as the secondary-successional species have not been able to colonise. However old midfield islets, now imbedded in forest, tend to have a different vegetation structure compared to those in arable fields (Cousins, unpublished), suggesting that competition for light and the availability of seeds are the most important factors limiting colonisation by successional species. Médail et al. (1998) studied isolated plant communities in Mediterranean France and found that within each study site, edges and forested core areas were occupied by different functional groups, associated with different levels of isolation and disturbance.

The model presented here was intended as a first attempt to estimate the long-term influence of landscape and grazing management on the persistence of plants in semi-natural grasslands of south-eastern Sweden, and in similar communities that are widespread in northern and northwestern Europe. It is one step towards developing more realistic grazing models to explore the effects of prescribed grazing and landscape patterns on plant species or plant functional groups. Further developments should address grazing management in a more realistic manner so as to allow for a better representation of the effects of actual grazing frequencies and stocking rates. In particular previous models have shown that spatial heterogeneity created and perpetuated by grazing can be an important component of vegetation dynamics (Pickup 1994; Weber et al. 1998). Grazing seasonality is also a critical factor that would need to be incorporated (Sternberg et al. 2000; Hulme et al. 2001).

One of the most important tasks for conservation biologists is to develop useful methods for assessing the status of endangered species. Landscape modelling studies are one of these as they can be used to produce guidelines and general rules on a multi-species level. Although spatially explicit models have been criticised for being too sensitive and for incorporating too many parameters that are poorly known (Ruckelshaus et al. 1997; Harrison and Bruna 1999), these types of models may still be a useful tool for assessing at once the status of multiple species in changing landscapes (Turner et al. 1995). As Eriksson and Kiviniemi (1999, p. 324) stated “unrealistic’ models can be useful if they are found to produce results that catch the essence of species status’. The usefulness of a model such as LAMOS lies primarily in the potential of testing formal hypotheses about the processes operating in complex landscapes, and in being a complement or inspiration for field studies and experiments (With and King 1997). On one hand, as in the more theoretical models of community diversity (e.g., Moloney and Levin 1996; Plotnick and Gardner 2002), we were able to explore sensitivities of community composition to variation in key biological, management and landscape parameters. On the other hand, the ability to incorporate GIS-based historical land use maps into a relatively simple modelling structure made it possible to test fairly specific management-relevant hypotheses. For instance the finding that small grassland patches surrounded by arable fields have more sensitive grassland species than grassland patches surrounded by forest or abandoned land was not necessarily intuitive, and has considerable bearings on future conservation strategies.

Despite a thorough search of relevant journals and conservation literature we found only one model addressing mechanisms of grassland species persistence in fragmented landscapes in a spatially explicit context (van Dorp et al. 1997). Most modelling studies in a landscape context have been animal or single species oriented or have focused on forest and fire dynamics. Opdam et al. (2002) also confirmed that studies using models are clearly underrepresented in spatial planning and conservation at a landscape scale. We believe that our model can help ecologists in understanding the mechanisms that affect biodiversity in managed grasslands subjected to land use change.

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