Local and regional dynamics of *Succisa pratensis*

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Abstract† - Land use change is considered to be one of the biggest threats to global species diversity. In Sweden, abandonment of grazing is one of the most common reasons for decline in species richness in semi-natural grasslands. Semi-natural grasslands used to be the dominating vegetation type in rural Swedish landscapes. Today semi-natural grasslands often occur as more or less isolated fragments. The result for species that benefit from grazing is not only a smaller area of suitable habitat and higher extinction risks, but also a lowered ability to colonize new areas. *Succisa pratensis* is a long-lived perennial plant that benefits from grazing and is common in Swedish semi-natural grasslands. In this thesis, I have assessed the performance of *Succisa pratensis* at various spatial and temporal scales, in a Swedish rural landscape. To examine the local population dynamics, I performed demographic matrix modelling of populations at grazed and ungrazed sites. A regional level was then added, by incorporating data collected from a large number of populations and habitat types into the matrix models and extinction risks over 50 years were calculated. Further, a dynamic metapopulation model was created and the regional dynamics, in terms of colonisations resulting from long distance dispersal and population extinctions were examined. The effects of management history were incorporated into the model by using historical maps. In addition, I made an analysis of the impact of management history on the distribution and performance of four grassland species, using vegetation maps from 1945 and 2001. Local dynamics of *Succisa pratensis* was negatively affected by abandonment of grazing. The distribution and performance of *Succisa pratensis* in the study area confirm this result since recorded population sizes were ten times higher in grazed sites than in ungrazed. The turnover rate of the system was estimated to about one extinction or colonisation per year. Due to the slow dynamics, both locally and regionally, both the simulation study and in the analyses of vegetation maps suggested a pronounced legacy of management history in *Succisa pratensis* in the study landscape. Overall, the results of this thesis demonstrate the importance of management history for species in the rural landscape. This is an important issue for conservation ecology to take into account since it is essential for the development of optimal management strategies.
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Hotell Busarewski.
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List of papers

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

I. Mildén, M., Cousins, S. A. O. and Eriksson, O. The distribution of four grassland plant species in relation to landscape history of a Swedish rural area. Submitted manuscript.


My contribution to the papers with joint authorship is presented below.

I did the data collection for papers I - V and was responsible for most of the data analysis and manuscript preparation in papers I - IV. In paper I and V, the vegetation and historical maps were contributed by S. A. O. Cousins. In paper IV and V, T. Herben and Z. Münzbergová developed the dynamic metapopulation model as well as ran all the simulations and did the analyses of simulations.
Aims of the thesis

The distribution and abundance of plant species is affected by many factors. The actual configuration of suitable habitats will influence the performance and survival of populations and an often neglected factor, important for the configuration, is the history of the landscape. In this thesis, I have assessed the performance of *Succisa pratensis* at various scales, both in time and space. *Succisa pratensis* is most often found in semi-natural grasslands and one aim has been to analyse the impact of management history of these grasslands on the distribution and performance of populations. I also wanted to make detailed studies of the impact of grazing abandonment on plant performance and use this knowledge to forecast the development of the regional population of *S. pratensis* in the study area. Lastly, I wanted to elucidate the role of metapopulation dynamics for the regional distribution, e.g. to examine the impact of long-distance dispersal, by analysing a dynamic simulation model.

Introduction

*Management change in the rural landscape*

For more than a thousand years, hay meadows and grazed outland have been important habitats in Sweden. Heterogeneity and diversity of habitats in the rural landscape supported a diversity of species that were more or less dependent of management continuity. Many plant and animal species are well adapted to a life in semi-natural grasslands. Traditionally managed semi-natural grasslands contain an exceptionally high density of plant species, occasionally up to 40-60 species per m² (Kull and Zobel 1991, Eriksson and Eriksson 1997) as well as many threatened and declining fungi, insects and birds (Vessby et al. 2002). However, since the late 19th century, the rural landscape has undergone dramatic shifts. Increasing mechanisation, with ploughing and tractors, as well as artificial fertilizers have changed the conditions for the many species dependent on the traditional agricultural management. The new use of fertilizers has led to increased areas of crop fields and diminished needs for hay-making areas. The possibility to grow fodder as crops or import protein-
rich fodder has provided the possibility to keep cattle indoors all year round and this in turn has reduced the area of grazed semi-natural grasslands. New machinery has led to a need to “tidy up” the landscape and use large entities instead of the former more heterogeneous division of e.g. crop fields. The changes in the rural landscape are dramatic (Eriksson et al. 2002). For example, the area covered by semi-natural grasslands in Sweden has decreased by about 90% over the last 80 years (Bernes 1994). As a result, species diversity is decreasing. Remaining, still managed, semi-natural grasslands, often occur as more or less isolated fragments in a landscape dominated by arable fields, forests, roads, urban areas. Since changes in land-use and management are among the most important drivers behind the present and expected future global decline in biodiversity (e.g. Sala et al. 2001), understanding the effects of such drastic landscape changes on populations of plants and animals has become a key issue for conservation biology and landscape oriented ecology in general (Hansson 1992, Hanski 1999, Harrison and Bruna 1999, Eriksson and Ehrlén 2001, Turner et al. 2001).

**Landscape change and plant performance**

Plant species are affected by the change of the rural landscape in various ways. There are two main effects of changed management. Firstly, habitats become fragmented, with smaller and more isolated patches as a result. Secondly, the quality of habitats becomes degraded, e.g. due to ceased grazing or eutrophication.

Longer distances between habitat patches may have several effects. With the rise of metapopulation theory (Hanski 1999), focus has largely been on colonisation and extinction dynamics in regional population sets. Fragmentation decreases the colonisation probabilities and at some point the dispersal between habitat patches is so low that colonisations do not balance local extinctions, leading to a decline of the number of populations. Fragmentation may also increase local extinction rates because smaller population sizes means increased negative effects of demographic and environmental stochasticity. Small and isolated populations are also susceptible to genetic stochasticity, inbreeding and Allee-effects, i.e. positive density dependence, as well as edge-effects (cf. Kiviniemi and Eriksson 2002, Lienert 2004).
Habitat deterioration from abandonment of grazing can cause lowered performance in all life stages of species that benefits from grazing. Increased density and cover of the vegetation may lower recruitment of seeds and will also change the conditions that give e.g. species with leaves arranged in rosettes advantages in a grazing or mowing regime. Lower fecundity and higher mortality in different life-stages may then change the fate of populations. Decreasing trends in population growth rates and population size will ultimately give increased extinction risks.

**Time-lags**

It is important to be aware of that a species response to management changes is likely to vary from species to species. Plants in particular, can respond very slowly to environmental change, developing so-called remnant populations (Eriksson 1996). Such remnant populations may, due to their long life spans persist in sub-optimal habitat for 50-100 years (Eriksson and Ehrlén 2001). This phenomenon leaves an historical imprint of past management and landscape structure in the present-day vegetation and regional distributions of many species (e.g. Koerner et al. 1997, Cousins and Eriksson 2001, 2002, Bellemare et al. 2002, Dupoeuy et al. 2002, Foster 2002, Lindborg and Eriksson 2004). Time-lags may hinder us to see a population decline until it is too late to take conservation measures. In this sense, time-lags can constitute an extinction debt (Tilman et al. 1994, Hanski and Ovaskainen 2002), i.e. populations that remain in the landscape may be moving towards extinction, even if conditions are not further changed. On the other hand, time-lags give conservation actions more time to restore habitats as the target species is still present. This is important when fragmentation has lowered the colonisation ability of the species in the landscape and recolonisations to restored habitats might be scarce (Turnbull et al. 2000, Eriksson and Ehrlén 2001).

**Metapopulation dynamics in plants**

During the last 10 years the application of metapopulation theory to plants have generated a great deal of discussion. On one hand, plants may seem particularly suitable for metapopulation analyses because of their immobility, strong spatial structure and restricted dispersal (Husband and Barrett
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1996). On the other hand, it has been argued that an application of metapopulation theory to plants implies several major problems. Plants do seldom live in habitats that are obviously restricted to discrete patches. Rather they live in continuous environments where gradients in suitability may be a better description of the spatial variation in the habitat. Another problem is the long life and slow turnover rate of most plant species (Husband and Barrett 1996, Eriksson 1996, Freckleton and Watkinson 2002, Ehrén and Eriksson 2003, Ouborg and Eriksson 2004). Additionally, there are methodological problems with the assessment of metapopulations in plants. The existence of a seed bank means that it is hard to interpret extinctions and colonisations of populations. How would we define a “recolonisation” from the seed bank? Other obstacles to a working metapopulation concept in plants is the difficulties to measure dispersal between patches, since long distance dispersal is hard to estimate but at the same time very important for the regional scale of ecology.

Still, there are good reasons to assume that metapopulation dynamics are important to understand when studying plant distributions. For example, plant distributions seem to be better explained if occasional long-distance dispersal is incorporated in the models (Higgins and Richardson 1999, Cain et al. 1998, Bullock et al. 2002, Vellend 2003, Higgins et al. 2003). Further, many regional distributions of plants show that larger and more connected habitat patches are more often occupied than small and isolated ones (Quintana-Ascencio and Menges 1996, Bastin and Thomas 1999, Dupré and Ehrén 2002). A likely explanation for such patterns is that regional colonisations depend on isolation of patches and local extinctions depend on habitat patch size.

To examine plant population performance and distribution on a regional scale we will need to take a number of factors into account. First of all, in a rural landscape land use as well as the management history of the landscape will be of great importance. Moreover, detailed studies of current performance in sites with different habitat and management types will be necessary. In the case of declining species, the specific dynamics of small populations also need to be investigated. For the regional dynamics, the issue of long distance dispersal will have to be addressed.
Methods

Overview
The field studies for this thesis were all performed in the rural landscape of Nynäs nature reserve during 2000-2003. For this area, I have used historical maps and inventories of the landscape as a background for the studies of *Succisa pratensis* and its dynamics. In paper I (The distribution of four grassland species in relation to landscape history of a Swedish rural area), I projected the distributions of four grassland species on the vegetation maps of 1945 and 2001 and recorded simple characteristics of the populations. This made it possible to analyse the difference in vegetation type between 1945 and 2001, for the current sites of the target species. In addition, it gave an opportunity to analyse the performance of populations with different management history over the last 60 years. In paper II (Slow response to habitat change - a demographic study of the grassland herb *Succisa pratensis*), I used recordings in permanent plots of six populations of *Succisa pratensis* over four years and performed demographic matrix modelling, to examine the effects of abandonment of grazing. In paper III (Size, structure and performance of 110 populations of *Succisa pratensis* - linking local dynamics to regional development), I made seed sowing experiments and seed collections from a large number of populations of *S. pratensis* in the study landscape. A greenhouse recruitment experiment and a common garden performance experiment were also carried out to investigate the performance differences between populations. With the demographic data from paper II, I then created matrices for eleven habitat types of the landscape and simulated the *S. pratensis* development in the area over the next 50 years. The demographic data from paper II was also used in a spatially explicit simulation model in paper IV (Metapopulation dynamics of a perennial plant, *Succisa pratensis*, in an agricultural landscape). This model used local dynamics within suitable patches, and distance dependent as well as distance independent dispersal between patches, to assess the regional distribution of *S. pratensis* as a metapopulation. To determine what was a suitable patch, I used seed sowing experiments and vegetation mapping together with Beals index (Beals 1984, Münzbergová and Herben 2004). In paper V (Long-term spatial dynamics of *Succisa pratensis* in a changing rural landscape: linking dynamical modelling with historical maps), the model from paper IV was used to simulate the
development of *S. pratensis* in the landscape during 1850-2050, using historical maps to create spatially explicit historical layers of suitable patches from 1850, 1900, 1945 and 2001. Below, I will in more detail describe the different methods that were used.

**Study species**

For the main part of this thesis, I have worked with *Succisa pratensis* Moench (Dipsacaceae) that is a long-lived perennial rosette plant (Fig. 1). In August and September, it flowers with several light purple flower heads. The seeds are covered by a hairy capsule, which may attach to the furs of animals such as cattle or roe deer (Römermann et al. 2005). *Succisa pratensis* is a relatively common plant species of managed semi-natural grasslands in Sweden and many other parts of Europe, for example Switzerland, while it is rare and endangered in other countries such as the Netherlands. It is known to benefit from grazing and mowing and to respond only slowly to habitat change such as abandonment (Regnell 1980, Ekstam and Forshed 1992, Schrautzer and Jensen 1998) and is thus an interesting species to study in relation to landscape history and land-use. Hooftman and Diemer (2002) found that isolation and size of populations had an effect on their performance and structure. Additionally, Vergeer et al. (2003a, 2003b) showed that small and isolated populations of *S. pratensis* exhibit lower genetic variability and a poor performance, something that was confirmed in other studies by Hooftman et al. (2003, 2004).

In paper I, I also made an inventory of three other grassland species: *Carlina vulgaris*, *Ranunculus bulbosus* and *Tragopogon pratensis*. I used these species to represent short-lived (*C. vulgaris* and *T. pratensis*) and long-lived species (*R. bulbosus* and *S. pratensis*), typical of Swedish grasslands. *Carlina vulgaris* L. (Asteraceae) is a monocarpic thistle, most often found in grazed, dry grasslands. It is often considered to be biennial, but in the study area it lives for several years before flowering. *Ranunculus bulbosus* L. (Ranunculaceae) is a buttercup with a swollen stem base, probably as an adaptation to drought, that is found in dry grasslands. *Tragopogon pratensis* L. (Asteraceae) is a biennial, living its first year as a rosette and flowering in the second year or sometimes even later. It is often found in road verges. In nutrient rich habitats it can become more than one meter tall.
Figure 1. Black and white reprint of *Succisa pratensis* from Bilder ur Nordens Flora by C. A. M. Lindman (1917).
Study area

I have worked in the northern part (3.1 × 2.3 km, 7.1 km²) of the Nynäsh nature reserve, situated c. 100 km south of Stockholm, Sweden (58°50′N, 17°24′E) (Fig. 2). The area is situated close to the Baltic coast and has a long management history (Cousins and Eriksson 2001). It is part of the hemiboreal Swedish rural landscape and as such it has undergone important changes in management during the 20th century. These changes include the modernisation of agriculture with the entrance of fertilizers and heavier machinery. To take advantage of the modern inventions to increase productivity, the sizes of fields and pastures have increased and the mosaic character of the older rural landscape has largely disappeared. Because of increased productivity, a smaller total area of crop fields is needed. This causes a domino effect; grazers are moved to the high-productive former crop fields, and high-diversity semi-natural grasslands that have been managed for centuries are now abandoned and turning into forest. In the Nynäsh nature reserve forest cover has increased from 4% to 17% of the total area since 1945, while semi-natural grassland has decreased from 47% to 26% during the same period (Cousins 2001, Mildén et al. paper I).

Inventory

All papers in this thesis are based on thorough inventories of the target species in the study area. During 2000 - 2003, I repeatedly inventoried all species; Carlina vulgaris, Ranunculus bulbosus, Succisa pratensis and Tragopogon pratensis, and recorded various population parameters such as population size and density. All populations were mapped with GPS, using a GIS based approach (ArcView 3.2 and Quantum GIS 0.6), so that they could easily be projected on present and historical maps. Since I largely focused on the dependence of population performance on habitat type, delimitation of the patches was made at a fine scale. My working definition of a population, or occupied patch, was a group of plants separated by a distance of at least 10 m from the next group of plants. Further, a continuous distribution of plants growing in an environment that was regarded as two different habitat types, was counted as separate populations or patches. For example, a population growing on both sides of a fence, where one half was grazed and the other not, was divided into two. In this way, I was able to predict the future of the population in a more proper way, assuming that the environmental factors are most important for plant performance (paper III).
Figure 2. Vegetation map of the northern part of Nynäs nature reserve in southern Sweden. Populations of *Succisa pratensis* are indicated on the map.
Assessment of suitable patches of Succisa pratensis

To model the metapopulation dynamics of *Succisa pratensis*, I did not only examine the species distribution but I also wanted to identify patches that were suitable but presently unoccupied (paper IV and V). To do this, the inventory was extended to search for empty patches. I took care to include patches that according to my judgement ranged from clearly suitable to probably unsuitable. In all these patches, floristic surveys were made, and seed sowing experiments (see below) conducted. Suitability of habitat patches was assessed based on presence of other plant species assembled from the floristic lists of all inventoried sites (i.e. occupied and unoccupied) using Beals index, that express the probability of occurrence of species at a patch, using number of joint occurrences with other species (Beals 1984, Münzbergová and Herben 2004). This resulted in about half of the unoccupied patches being defined as suitable. In order to find out how well predictions of habitat suitability based on floristic co-occurrences agreed with the results of the seed introduction experiments, the relationship between Beals index value and establishment success in the sowing plots was examined (paper IV).

**Historical maps**

For the work with historical vegetation maps (paper I and V), I relied largely on previous work by S. A. O. Cousins (see Cousins 2001b) who has worked with the Nynäshamn area from various perspectives. I have been able to use her vegetation maps of the area from 1945 and 2001. Both these maps were based on aerial photographs (for details see Cousins and Eriksson 2002). Vegetation was classified into 14 classes and the map of 2001 was verified by field-checks. Additionally, for paper V, I used a map of the landscape from 1850, which was based on the old cadastral maps, that were actually a land-use map and thus not based on vegetation as the two more recent maps. However, a reasonably realistic picture of the landscape could be drawn from the knowledge of what areas were mown and grazed in 1850, together with topographic data. Maps have been imported to a Geographical Information System, GIS (ArcView 3.2 and Quantum GIS 0.6), to make handling and analyses of the data easier.
Historical analyses of species distributions

In paper I, a simple method of analysing historical impact on present species distributions was used. I wanted to examine landscape change in relation to four species distributions. Since I did not have access to the distributions of the target species in 1945, I used the locations of today's populations and examined the history of the spots by recording what vegetation type they belonged to in 1945 and 2001.

Tracking suitable habitat through the centuries

For the simulation study of the *S. pratensis* distribution from 1825 to 2000 (paper V), it was necessary to create historical layers of maps that represented the landscape in terms of suitable and not suitable habitat patches. For this purpose, I used the digitalized map from 1850 as a starting point. This map is a land-use map, in contrast to the available vegetation maps from 1945 and 2001. I made the fairly coarse assumption that all grassland parts of the infields (i.e. mown meadows, probably with grazing in late autumn) were suitable for *S. pratensis*. Even outland (i.e. the peripheral areas where cattle were let out grazing) were included in the suitable habitat category. The second map layer (1900) could not be directly based on a historical map, but was extrapolated from the 1850 and 1945 layers, based on common historical knowledge on the development of the rural landscape. Thus, what had become arable fields in 1945, was subtracted from the suitable areas already in 1900. For former grassland areas that had turned into forests in 1945, a “poor” habitat class was constructed, that I assumed to be abandoned, but still supporting remnant populations. For the 1945 layer, I interpreted midfield islets, village areas and abandoned grasslands as poor habitat, and in 2001 areas that were grassland in 1945 but forest in 2001 were categorized as poor habitat. Additionally, all poor habitat from 1945 was classified as unsuitable in 2001.

Local dynamics

The demographic study of local dynamics in *Succisa pratensis* populations was fundamental to this thesis for several reasons. It was needed for a detailed analyses of the effects of abandonment of grazing on the performance of *S. pratensis* (paper II). It was also used as the core of the simulations of the landscape development in paper III, and it was further used in our simulations in paper IV.
and V. For the demographic study (paper II), I selected six populations of *S. pratensis*, representing typical habitats of *S. pratensis* in the landscape. Three of the sites were currently grazed, while two were abandoned since 40-70 years and one was situated in a road verge that was not mown. The grazed sites were either dry, mesic or moist, while the ungrazed sites were mesic and moist. The road verge site was a mixture of moist and mesic habitats. In all sites, I established permanent plots, initially with at least 250 plants at each site. Each individual plant was recorded once every year during flowering from 2000 to 2003. I analysed the demographic data using both simple projection of transition matrices and stochastic simulations and calculated the population growth rates (λ) and elasticity values, and I used Life Table Response Experiment (LTRE) analyses (Horvitz et al. 1997, Caswell 2001). Elasticity values measure the sensitivity of proportional changes in lambda to matrix elements, while (LTRE) to examine how differences in matrix elements contributed to variation in lambda between sites, years and grazing regimes. In paper II, I used the complete dataset to analyse the mechanisms behind population decline after abandonment. The matrices used in paper IV and V, were based on the data from 2000 to 2002 only, which resulted in partly different conclusions concerning the effects of abandonment.

**Performance effects of population size, density and habitat type**

Population performance may differ for several reasons. Studies have reported genetic effects of population size and isolation (cf. Vergeer 2003a, Hooftman et al. 2004). In paper III, I wanted to set up experiments under controlled conditions to examine whether the size, density or environment of the mother population could explain differences in plant performance. A greenhouse germination experiment with seeds from mother plants from 49 populations of *S. pratensis* was performed, and the fraction of seeds germinating was analysed. Seedlings were then transferred to larger pots in a common garden for a performance study, where differences in flower number and plant size were investigated.

**Seed sowing experiment and seed collection**

I wanted to assess the recruitment and seedling survival in sites of different habitat and management type. This information was then used to assess the seed bank of *S. pratensis* (paper II), evaluate the
assessment of empty suitable patches that were made with Beals index in paper IV (see above), and to extend the analyses of the local dynamics to incorporate also the small populations growing in abandoned sites (paper III). The seed sowings were performed in 2000 and 2001. At 37 sites, chosen to represent a variety of habitat types, I added 50 seeds each to 3 sub-plots. The number of seedlings in each sub-plot was recorded in early summer and autumn in 2001, 2002 and 2003. I further wanted to investigate the effect of population size, population density and habitat type on seed set in the landscape. In order to do so, in the autumn of 2001 I made seed collections of up to thirty flower heads from each of 55 populations of \textit{S. pratensis} in the study area.

\textit{Dynamics on a regional scale}

In paper III, the results of seed collections and recruitment as well as seedling survival in different habitats, were used in combination with the matrices created in the demographic study in paper II, to predict the development of \textit{Succisa pratensis} in the study area during 50 years. The underlying question for the adjustment of matrices in paper III, was if the six populations in the demographic study was really representative also for the small abandoned populations and newly founded populations growing in former fields. Addressing this question, I created new matrices by adding the information from seed collections and sowings. In this way, I created population matrices for 11 habitat types, based on current management (grazing), historical management (former fields or semi-natural grassland) and soil moisture (dry, mesic or moist). All \textit{Succisa pratensis} populations in the area were assigned to one habitat type and subjected to stochastic simulations for 50 years with starting vectors based on the current population structure and size.

\textit{Dynamic metapopulation model}

In collaboration with T. Herben and Z. Münzbergova, I developed a dynamic simulation model for \textit{S. pratensis} in paper IV. The model was also used in paper V. The model was based on a grid map of the study landscape, constructed of cells of $5 \times 5$ metres, where suitable patches were placed according to their real positions, size, and shape. All patches were assigned a management type (grazed or ungrazed) and local population dynamics were simulated at each patch with the population matrices obtained from the first two years of the demographic permanent plot study.
Environmental stochasticity was simulated by using several matrices for one habitat quality and random choosing of matrices for each interval. Density dependence and demographic stochasticity were included in the model (for further details see paper IV). We used two types of dispersal in the model: distance-dependent and distance-independent. The majority of seeds were subjected to distance-dependent dispersal (mainly thought of as wind dispersal) and mean dispersal distance was estimated as the product of plant height and wind speed divided by the terminal velocity (Soons and Heil 2002). To mimic rare long distance dispersal events (for example adhesive dispersal), we used distance independent dispersal of a low fraction of seeds. This was simulated as a random “rain” of seeds over the cells in the grid, and therefore the probability for a suitable patch of receiving a seed was proportional to its area.

Dynamic modelling with historical maps
To examine the influence of the historical landscape configuration and management through dynamic modelling, the model that was parametrised in paper IV was extended to handle changing grid map layers. In this way, we could in paper V use historical layers of *S. pratensis* suitable habitat (see above) and simulate different scenarios in a changing landscape over 175 years and evaluate the results against the distribution of the species in year 2000.

Results and discussion

*Paper I - Landscape history and plant distribution*
The distribution of the four grassland plant species was correlated with the management 50 years ago. The clearest correlation to the landscape of 1945 was for *S. pratensis*. While 77% of the sites were classified as semi-natural grassland in 1945, only 36% were classified as semi-natural grassland in 2001. The corresponding fraction classified as forest was 6% in 1945 and 41% in 2001. While we do not know anything about the distribution of *S. pratensis* in 1945, we know that the species is long-lived and therefore assume that many of the existing populations did in fact exist 50 years ago. As the figures suggest, a number of sites with *S. pratensis* are presently not grazed.
Median population size on still managed sites was 400 compared to 30 at abandoned sites and 40 at cultivated grasslands (former crop fields that today are grazed). The fact that *S. pratensis* is found on cultivated grasslands, is promising for the future of the species, since it implies that colonisations of previously inhabitable sites occur. The small median population size at cultivated sites may thus be a sign of the low age of these populations. Alternatively, *S. pratensis* perform worse in nutrient rich grasslands and recently restored grasslands as shown by Vergeer et al. (2003a) and Pywell et al. (2003).

Another interesting result of paper I was the distribution pattern of *T. pratensis*. This species is not a typical grassland plant as for example *S. pratensis* and its populations were to 74% found in close connection to roads. Still, of the 64 populations that were not found close to present roads, as many as 27 (42%) were located close to roads that existed in 1945. It has to be noted that this historical legacy is observed despite the short life-span of *T. pratensis*. Models that take the historical configuration of the landscape into account can thus give an increased knowledge, compared to models only considering the present dynamics of the species (cf. Lindborg and Eriksson 2004)

**Paper II - Demography of S. pratensis**

The demographic analyses of populations at grazed and ungrazed sites showed important differences between the two management types. The mean stochastic population growth rate (λ) of grazed sites was 1.03 (ranging from 0.94 to 1.27) and of ungrazed sites 0.90 (ranging from 0.72 to 1.04. Earlier studies, e.g. Regnéll (1980), have reported negative effects of abandonment for *S. pratensis*, but the rate of decline has not been studied in great detail.

Populations at ungrazed sites were found to have a higher flowering frequency, a higher seed set per flower head and higher germination of seeds, but also an overall higher mortality at all stages. Survival of large vegetative plants had a high elasticity in both grazed and ungrazed habitats, but at ungrazed sites stasis of flowering plants were equally important. The pattern with high elasticities for the survival of adult plants is commonly found in perennial plants. I found that LTRE values for the effect of grazing were high for the same stages as had shown high elasticity values. Further,
there was no support for low-sensitivity transitions being more affected by abandonment than other transitions. The lower $\lambda$-values were caused by an overall decrease in performance in all stages. Thus, there was no evidence that populations are buffering the effects of abandonment such that the most affected transition stages have the lowest impact on population growth. Rather, the response to abandonment is slow because of the relatively long-life span of \textit{S. pratensis} and the moderate impact that abandonment have on populations in short time-scales.

Grazed populations had a larger fraction of adult plants, which is likely to be the result of the lower seed set and lower mortality in those populations. Accordingly, the more even stage distribution in populations at ungrazed sites, mirrors the fact that more seedlings enter the populations and that higher mortality keeps the fraction of adult plants low. Bühler and Schmid (2001) as well as Billeter et al. (2003) recorded a smaller fraction of \textit{S. pratensis} seedlings at sites with high grazing intensities in high-altitude fens in Switzerland. They attributed the scarcity of seedlings to the lower seed set per plant individual, which in turn is the result of loss of stalks through grazing. The observed population structures of populations in grazed sites in my study, were closer to the stable stage distributions and thus to equilibrium than populations at ungrazed sites, suggesting that the populations at ungrazed sites have been declining for some time. In a study like this, the estimation of the seed bank is often a source of uncertainty. The estimated seed bank survival of 0.4 to 3 percent survival in two years is fairly well in accordance with studies reported in Thompson et al. (1997). Additionally, the impact of the seed bank on the fate of the populations was very limited.

Overall, the results suggest that populations at ungrazed sites are slowly declining, while the still managed populations maintain their size or increase slowly. In fact, the observed mean $\lambda$ of 0.90 means that a population of 10,000 plants will go extinct in 87 years, a quite probable scenario of the populations of \textit{S. pratensis} in grasslands that were abandoned about 60 years ago. In this respect the results of the demographic study support the observed patterns of \textit{S. pratensis} in paper I.

\textit{Paper III - Landscape performance of S. pratensis}

In the greenhouse recruitment and common garden performance study, there were significant
differences between populations concerning plant size, flower head number and recruitment. However, no effects of population size, density or habitat type were found. The lack of effect of population size on the performance in the study is in contrast with previous studies that have found that smaller and more isolated populations of *S. pratensis* in the Netherlands had lower genetic variability and a poorer performance (Vergeer et al. 2003a, 2003b). Hooftman et al. (2003, 2004) also found effects of population size and isolation on genetic variability in Swiss populations of *S. pratensis*. The absence of effects in our Swedish landscape may be due to the fact that the distribution of *S. pratensis* is even less fragmented than in Switzerland and that recent fragmentation events may not yet have had any strong negative effects on genetic diversity and performance of populations.

In the seed collection study, number of seeds per flower head was positively correlated to population size. This could be interpreted as an Allee effect, i.e. a lowered performance with population size that can be the result of for example pollen limitation in small or sparse populations. The seed sowing experiment found differences in recruitment between dry and moist habitats, something that was expected since *S. pratensis* is commonly considered to be a wetland species and has been reported to have a higher recruitment in moist soils (Isselstein et al. 2002). It is also well worth noting that recruitment was recorded in sites that have formerly been used as crop fields, supporting the observation from paper I that *S. pratensis* is able to colonise also these restored habitats.

From the original set of six habitat types (Paper II) a new set of matrices for eleven habitat and management types was created. Matrices were adjusted according to seed set, seedling recruitment and seedling survival in the seed collection and seed sowing experiments. The largest differences between adjusted and non-adjusted matrices in the original set, was in ungrazed mesic semi-natural grasslands, where $\lambda$ decreased from 1.04 to 0.87. Mean population growth rates ranged from 0.74 to 1.13 in the eleven habitat types. In the study landscape, 47 out of 110 populations were given a $\lambda$ lower than one. Fifteen populations had a risk of extinction that was higher than 50% in 20 years. These populations were in general very small and had a median size of 3 adult individuals. The 38
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Populations with high risk of extinction within 50 years had a present median population size of 15 individuals. Overall, about 10% of the *S. pratensis* individuals in the current regional population are situated in populations predicted to go extinct within the next 50 years. Despite the ongoing change in management regimes, the projections thus suggest that *S. pratensis* will persist and thrive in the study landscape during the next decades as long as management is maintained. The proportion of populations facing extinction during the coming 50 years was only 35%, and those were mostly very small populations. This corresponds to an extinction rate of 0.7% per year for *S. pratensis* in the current landscape, indicating a very slow turnover in the system.

**Paper IV - Metapopulation dynamics of *S. pratensis***

In the study system, 137 patches were identified as suitable for *S. pratensis*. There was a significant, positive relationship between the Beals index value and seedling germination and seedling survival in the seed sowing experiment, giving support to the method of assigning suitability. It is important to bear in mind that these approaches to assess patch suitability are not equivalent, but rather complementary. Seed sowing experiments focus on the establishment processes, while vegetation surveys incorporate several aspects of habitat quality and patch history.

Simulation results showed that the colonisation and extinction dynamics of *S. pratensis* were slow with about one colonisation or extinction per year and the time frame for the population system to attain equilibrium in a constant landscape was several thousands of years. Most of the turnover took place in small and isolated patches, and extinction occurred mostly soon after colonisation. Sensitivity analyses demonstrated that occasional long-distance dispersal had a large influence on population turnover rates whereas regular short-distance dispersal had little effect. This result is largely an effect of the distance between suitable patches being generally longer that the distance that can be achieved by wind dispersal for *Succisa pratensis* in our study system. A fraction of one out of 10,000 seeds dispersing over long distance had a great impact on colonisation rates and patch occupancy in the landscape. Caswell et al. (2003) reached a similar conclusion, when examining the effects of local processes and long- and short-distance dispersal on wave-speed in a landscape. In terms of conservation, the importance of rare long-distance dispersal events implies that more
attention should be paid to potential long-dispersal agents such as cattle and wild animals or even agricultural machinery.

Our model also allowed us to assess how demographic processes affect not only local population growth but also regional dynamics. In a metapopulation context, fecundity was more important, compared with growth and survival, than when considered only within populations. Thus, fecundity, which was of minor importance for local population growth, became relatively more important regionally, in terms of effects on regional population size, number of occupied patches and population turnover. In contrast, the influence of survival, which was locally important, decreased in a regional context. With dispersal, a higher fecundity enhanced colonisation success by providing more seeds and thereby chances of successful colonisation, while survival only kept local extinction rates low. Hence, demographic processes that are unimportant in a local population context may still be important for metapopulation performance.

**Paper V - Spatial modelling and historical maps**

In this study, an attempt was made to explain the current distribution of *S. pratensis* using the dynamical, spatially-explicit model from paper IV together with historical maps. We tested if predictions for the current species distribution are affected by assumptions about its early 19th century distribution, and tried to determine whether recent history and current processes are dominant, and how past landscape changes determine current distributions.

The number of patches and the fraction of the landscape available for *S. pratensis* decreased consistently (Fig. 3), with an almost fivefold decrease in the area between 1850 and 2000. This is in accordance with most descriptions of the development of the rural landscape and the semi-natural grasslands (cf. Bernes 1994). Simulations showed that landscape changes are likely to have had a strong effect on habitat occupancy patterns and population sizes of *S. pratensis* over the past 175 years. Initial distribution of *S. pratensis* within the landscape had a major effect on the outcome of the simulations both in qualitative and quantitative terms and the fit between the predicted occupancy and the actual *S. pratensis* distribution is enhanced by the inclusion of the historical
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information. This is true particularly for simulations starting with initially low occupation, where
the plant was able to benefit from easier spread in the much less fragmented 19th century landscape.
The results indicate that the time frame available has been too short for *S. pratensis* to spread in the
landscape, and that it is likely to have been present in considerable amounts in 1825. Current habitat
occupancy or species richness related to connectivity of an historical landscape configuration has
been demonstrated in other systems: for example, the site connectivity 50 and 100 years ago
explained about 50% of the among-site variation in species richness in semi-natural grasslands in
Sweden (Lindborg and Eriksson 2004). Similar results were obtained by Bruun et al. for semi-
natural grasslands (2001), by Bellemare et al. (2002) for herbaceous vegetation typical of primary
forests, and by Vellend (2003) for species richness of the ground flora in forests.

**Figure 3.** Distribution of habitat suitable for *Succisa pratensis* in four map layers of a
rural landscape of southern Sweden.
Concluding remarks

*Succisa pratensis* is a long-lived species, common for Swedish semi-natural grasslands. As such it is particularly suitable to study in relation to land use history. In this thesis, I have tried to examine both local and regional, as well as long-term and current dynamics of *S. pratensis*, all with an emphasis on effects of grazing. The studies have included demographic matrix modelling, common garden studies, dynamic modelling and the use of historical maps.

The observation that *S. pratensis* is found in many different habitats, often outside pastures and even in forest, might lead to the question of how dependent it really is on grazing or mowing. From the results achieved in my studies it seems obvious that grazing is crucial for the survival of *S. pratensis* populations, even if the processes are indeed slow. A reasonably large population of *S. pratensis* might persist for up to 100 years after abandonment and in some places maybe even longer. Still, the effects of abandonment of grazing are negative and populations in abandoned areas will eventually go extinct. The slow response of *S. pratensis* to management change leads to an imprint of land use history on the current distribution. More surprisingly, also the short-lived *Tragopogon pratensis* showed a connection to past landscape configuration, in terms of old roads. An historical perspective is thus a valuable complement to studies of species distribution and performance.

The regional dynamics of *S. pratensis* were shown to be very slow with less than one extinction or colonisation per year. Over short to moderate time frames, the regional population size thus clearly depends more on local dynamics than on regional dynamics. The transient environment and the non-equilibrium of the regional population mean that *S. pratensis* in the study area do not constitute a metapopulation in the strict sense. We could still see a higher impact of fecundity and a decreased impact of survival of adult plants when the regional level of dynamics was added to the model. This fact show that the regional scale does add insights to the analyses of species dynamics. Further, colonisation and extinction dynamics may in the long term be important for a species to track changes in the landscape. In the study area, a large part of the regional population of *S. pratensis* is
still situated in grazed grasslands, but depending on the development of e.g. agricultural policies and economics, the ability to colonise former fields might prove to be crucial.

In my study system, an interesting development of research would be to include the genetic level of dynamics. A genetic approach could, if successful, provide a different historical map of relationships between the current populations in the landscape. To include many assessments of history in a study system like this is important, since the historical aspect is indeed very hard to examine even if historical maps are available. If a map of similarities between populations could be constructed, we would possibly have the opportunity to see past configurations and dispersal routes of the landscape, adding valuable information to the current knowledge.

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Sammanfattning

Förändringar i markanvändning anses som ett de största hoten mot den globala biodiversiteten. I Sverige är upphört bete en av de vanligaste orsakerna till sjunkande artrikedom i våra naturbetesmarker. Naturbetesmarker och slätterängar var länge de dominerande vegetationstyperna i det svenska jordbrukslandskapet, men idag återfinner man ofta dessa marker bara som isolerade fragment avskurna av skogar, åkrar, vägar och bebyggelse. För arter som är betesberoende betyder det inte bara att de får mindre yta att leva på och på så vis högre risk att dö ut, utan de har också sämre chanser att nå och kolonisera nya områden.


Studierna visar tydligt att ängsvädden påverkas negativt av uteblivet bete, även om förändringar sker väldigt långsamt. Om ett område slutar betas dör en population med 1000 växter ut på ungefär 70 år enligt resultaten från populationer på obetad mark. Det innebär naturligtvis att vi kommer att kunna hitta ängsvädd på många platser i landskapet som inte betas längre och som till och med kan vara bevuxna med skog. På det sättet kan man säga att ängsväddens utbredning visar spår av det historiska landskapet, något som också tydligt syntes i den historiska analysen. När jag beräknade
utdöenderisker för populationerna i området, visade det sig att 38% riskerade att dö ut inom 50 år, men att de bara innehöll 10% av individerna i hela landskapet. Den största delen av all ängsvädd i norra Nynäs växer alltså idag på mark som betas. Dessutom visade inventeringarna att ängsvädd har lyckats kolonisera områden som förut använts som åkrar men som nu betas av kor. Detta är en intressant utveckling eftersom det visar att dessa marker långsamt blir tillgängliga för växtarter som annars är känsliga och behöver näringsfattig mark för att kunna klara sig.

Resultaten i avhandlingen visar tydligt att arters utbredning i landskapet till stor del beror på hur marken har brukats genom historien. Ur ett bevarandeperspektiv är det viktigt att tänka på hur markanvändningen sett ut i ett område när man gör en bevarandeplan, eftersom det kan öka våra chanser att göra rätt val och lyckas rädda hotade arter. Att arter svarar långsamt på förändringar i markanvändning ger oss också stora möjligheter att hinna reagera och ändra dagens skötsel så att den tar hänsyn till de arter och miljöer vi vill bevara.
Tack till