Ann. Bot. Fennici 44: 416–426 ISSN 0003-3847 (print) ISSN 1797-2442 (online)
Helsinki 20 December 2007

The distribution of four grassland plant species in relation to landscape history in a Swedish rural area

Mikael Mildén, Sara A. O. Cousins & Ove Eriksson*

Department of Botany, Stockholm University, SE-10691 Stockholm, Sweden (corresponding author's e-mail: ove.eriksson@botan.su.se)

Received 15 Dec. 2005, revised version received 17 May 2006, accepted 11 July 2006

Mildén, M., Cousins, S. A. O. & Ove Eriksson, O. 2007: The distribution of four grassland plant species in relation to landscape history in a Swedish rural area. — *Ann. Bot. Fennici* 44: 416–426.

It is commonly agreed that landscape history is important for species distributions today. Here, we studied present-day regional population distribution and performance of four grassland species, the perennials *Ranunculus bulbosus* and *Succisa pratensis*, and the monocarpic "biennials" *Carlina vulgaris* and *Tragopogon pratensis*, in a Swedish rural landscape. We analysed the management history of their population patches, using vegetation maps from 1945 and 2001. Distributions of *Succisa pratensis* reflected the grassland occurrences in 1945 and *Tragopogon pratensis* was associated with the road network 60 years ago. Performance in different habitats also suggested an impact of land use on species distributions. For *Ranunculus bulbosus* and *Carlina vulgaris* the impact of landscape history was less obvious. Our results indicate that present-day distributions of some grassland species partly may be a legacy of previous semi-natural grassland patterns in rural Sweden, an insight that has valuable implications for assessments of long-term vulnerability of grassland species.

Key words: management history, semi-natural grasslands, time lag

Introduction

In Sweden, as in many other parts of Europe, traditional management such as mowing and grazing on unfertilized and unploughed grasslands (semi-natural grasslands) has declined rapidly over the last century (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). Remaining, still managed, semi-natural grasslands, often occur as more or less isolated remnants in a landscape dominated by arable fields, forests, roads, urban or built up 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*. 2000), 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 & Bruna 1999, Eriksson & Ehrlén 2001, Turner *et al*. 2001).

Traditionally managed semi-natural grasslands contain an exceptionally high density of plant species, occasionally up to 40–60 species per m^2 (Kull & Zobel 1991, Eriksson & Eriksson

1997). Besides the high plant species richness, these habitats host many threatened and declining fungi, insects and birds (Vessby *et al.* 2002). Thus, the remaining fragments of semi-natural grasslands attract a considerable conservation interest, and there is a Swedish national goal to maintain all present semi-natural grasslands.

An important, but often neglected, aspect of fragmentation is that many organisms, plants in particular, respond very slowly to environmental change, developing so-called remnant populations (Eriksson 1996). Such remnant populations may, due to their long life spans and limited requirements for space, persist in sub-optimal habitat for time spans in the magnitude of 50–100 years (Eriksson & Ehrlén 2001). This phenomenon leaves an historical imprint in the present-day vegetation and regional distributions of many species, which are thus legacies of past management and landscape structure (e.g. Koerner *et al.* 1997, Cousins & Eriksson 2001, 2002, Bellemare *et al.* 2002, Dupoeuy *et al.* 2002, Foster 2002, Lindborg & Eriksson 2004, Helm *et al.* 2006). This slow response implies that the present-day diversity is in a non-equilibrium state with the present landscape habitat configuration (Herben *et al.* 2006). Declining plant species thereby contribute to an extinction debt (Tilman *et al.* 1994, Hanski & Ovaskainen 2002), i.e. populations may be developing towards regional extinction even if the present management is maintained. On the other hand, existing remnant populations are potentially important in restoration programmes, since habitat fragmentation is expected to cause severe dispersal limitation of many species (e.g. Turnbull *et al.* 2000), implying that spontaneous recolonization of restored sites may take a very long time (Eriksson & Ehrlén 2001).

Although a general recognition of time lags in the response of plant populations to landscape changes may be considered well known, there are still difficulties in assessing historical effects on present-day diversity. In most cases we lack time-series of population development, and old vegetation surveys (which can be repeated) are scarce. In practice, indirect methods have to be used to detect historical effects in the vegetation. In this study, we have analyzed the regional distributions of four grassland species, as they appear in the present-day landscape, and compared the distributions with vegetation maps depicting the landscape in 1945 and 2001. We have also compared the performance of the present-day populations, occupying sites which are continuously managed, abandoned or re-created, respectively. The four species represent perennials (*Succisa pratensis* and *Ranunculus bulbosus*) and short-lived monocarpic perennials (“biennials”) (*Carlina vulgaris* and *Tragopogon pratensis*).

The main objective with this study was to assess whether the present distribution of the four species still preserves a relationship to semi-natural grassland configuration in the 1940s, although many of these grasslands no longer exist. For one of the species (*Tragopogon pratensis*), which is often found along road verges, we examined the present-day distribution in relation to historical, no longer existing roads. To examine whether land-use change affects populations negatively, we compared population size and flowering in grazed and ungrazed habitats in the present landscape. Furthermore, perennial plants have, on average, a life span that is more than six times longer than monocarpic (semelparous) plants (Ehrlén & Lehtilä 2002). Thus, although using only four target species makes it difficult to draw conclusions on the relationship between life span and response to landscape change, we expected that the two perennial species should have a slower response than the two monocarpic species, due to differences in life span (Eriksson 1996).

Material and methods

Study area

The study was performed between 2000 and 2003 in the northern part (3.1 × 2.3 km) of the Nynäs nature reserve, situated ca. 100 km south of Stockholm, Sweden (58°50´N, 17°24´E). The area is a part of the hemiboreal Swedish rural landscape close to the Baltic coast, with bedrock consisting mainly of Precambrian gneiss. Soil layers in the area are mostly clay sediments in the cultivated valleys, and till is situated on slopes with bare bedrock exposed on the

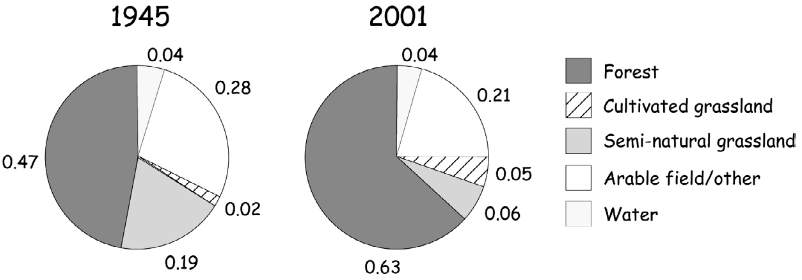

Fig. 1. Distribution of the major vegetation and management types in the Nynäs area in 1945 and 2001. Numbers indicate proportions (%) of the total study area. More detailed information is found in Cousins (2001).

tops (Cousins 2001). Mean temperature ranges between –3 °C in February and 16 °C in July, and annual mean precipitation is 550 mm (Alexandersson *et al.* 1991). The study area has undergone important changes in management during the 20th century, something that is clearly shown in the vegetation changes of the landscape (Fig. 1). Many former fields are now grazed, whereas semi-natural grasslands are turning into forest, due to abandonment.

Study species

We chose four grassland species that are characteristic of Swedish grasslands in the hemiboreal zone and southwards. *Ranunculus bulbosus* (Ranunculaceae) is a perennial found mainly in dry grasslands. It has a swollen stem base, probably as an adaptation to drought. Flowering occurs, from several stems with a height of up to about 20 cm, in early summer after which the leaves wilt. The seeds (achenes) weigh ca. 3.1 mg and have no apparent adaptation for animal or wind dispersal (Grime *et al.* 1988). *Succisa pratensis* (Dipsacaceae) is a perennial plant, mostly found in mesic or moist grasslands. In late summer it develops one to six flower heads on each of up to three stems of about 60–70 cm in height. The fruit is a hairy capsule that promotes adhesive seed dispersal with animals such as cattle. The seeds weigh ca. 0.9 mg (M. Mildén unpubl. data). *Carlina vulgaris* (Asteraceae) is a prickly, monocarpic short-lived perennial, which usually persists as a rosette during several years before it flowers and thereafter dies. It is mostly found in grazed dry grasslands, often on calcareous soils. The achenes weigh ca. 1.5 mg and have a small pappus enabling wind dispersal and they often remain in the fruiting heads until late autumn or winter (Löfgren *et al.* 2000, Jakobsson & Eriksson 2003). *Tragopogon pratensis* (Asteraceae) is a biennial or monocarpic perennial plant most commonly found in road verges and grasslands. During its first year, it has an upright rosette of long, grasslike leaves that in the second year produces one, commonly branched, stem up to one meter in height (M. Mildén unpubl. data). In road verges, it often has up to ten flower heads, while in grazed grasslands individuals are smaller with just a few flower heads. The achenes weigh ca. 11.2 mg and have a large pappus suitable for wind dispersal (Jakobsson & Eriksson 2003).

The species are henceforth referred to by their generic names only.

Inventory

The study area was carefully inventoried at the time of flowering of the four target species. Delimiting the patches was made at a fine scale, so that occupied patches of suitable habitat at least 10 m apart were counted as separate. The position of the patches was recorded with Global Positioning System (GPS). The number of flowering and vegetative individuals was counted at all patches, except for *Tragopogon* where we counted only flowering individuals. The reason was time-limitation in the field. A very large effort is needed to avoid overlooking small vegetative *Tragopogon*, due to their grasslike appearance.

Vegetation classification and maps

Aerial photographs were used to analyse the past and present land cover and to make vegetation maps. Black and white photographs from the

1940s (scale 1:20 000) and modern colour infrared (CIR) photographs (scale 1:30 000) were interpreted using a zoom-lens stereoscope. The vegetation was initially classified into 14 classes (for details *see* Cousins & Eriksson 2002) and the modern interpretation was verified by field checks. The interpretations were digitised and rectified to orthogonal projection and imported to a Geographical Information System, GIS (ArcView 3.2), resulting in two vegetation maps. The vegetation maps cover approximately an area of 7 km^2 (3.1 × 2.3 km) and has a resolution of five metres. The vegetation classes were then generalised into four classes; forest, cultivated grassland, semi-natural grassland, and other (Fig. 1). "Cultivated grasslands" are former arable fields that are now grazed (Cousins & Eriksson 2002). Information from older maps was used to identify cultivated grasslands 1945 (Cousins 2001). The aerial photographs from 1945 were also used to delineate roads and farm tracks.

Performance

The performance of populations in different habitat types was analysed by comparing the population size and flowering frequency between grazed semi-natural grassland, abandoned grassland and grazed cultivated grassland. We classified the patches containing populations according to the vegetation map from 2001. As semi-natural grassland patches, we only included presently grazed semi-natural grasslands. As abandoned patches we considered all semi-natural and formerly cultivated grasslands that are presently not grazed, as well as ungrazed forest patches that were classified as semi-natural grassland in 1945. The cultivated grassland class consisted of all presently grazed former fields and cultivated grasslands. For *Tragopogon*, we added one class consisting of road verges.

For the statistical analyses of population performance we used the free statistics software R, version 1.9.0 for GNU/Linux (R Development Core Team, www.r-project.org). For testing the differences between grassland types, we used the Kruskal-Wallis rank sum test. Post hoc testing was made with the Wilcoxon rank sum test with Bonferroni correction of *p* values.

Analysis of species distributions

We mapped the positions of the present populations of the four species onto the vegetation maps from 1945 and 2001. For *Tragopogon* we also mapped the present species distribution in relation to road verges from 1945 and 2001. The analysis of historical distribution assumes that we infer a process extending over the last 60 years from a pattern that we see today. It is unrealistic to assume strictly that all present-day patches of the study species had the same locations in 1945; that would imply no dynamics at all during the 60-year period. However, spatially explicit simulation models of the regional population of *Succisa* in the study area (Herben *et al.* 2006, Mildén *et al.* 2006) suggest that the turnover is indeed slow, and that this species is not capable of tracking changes in landscape habitat configuration occurring over a time span in the magnitude of one century. Thus, we compared the difference in distribution of the populations among the vegetation types 1945 and 2001, assuming that a large fraction of the populations were present at the same sites, unless the sites were used as arable fields during the period from 1945–2001. In the former fields, colonisations have most likely occurred after transformation from fields to pastures.

We did not subject the differences in distributions between 1945 and 2001 to statistical tests. Instead, we decided to only describe the distributions of populations mapped on 1945 and 2001 landscapes. We summarized the changes in land cover, due to changing land use, in a transition matrix based on Cousins (2001), and compared these changes with the land-cover transitions for the patches of the four species. Since there were few patches of *Carlina*, and since the examined historical legacy for *Tragopogon* mostly concerned road verges, we only present the matrices for *Ranunculus* and *Succisa*. The conclusions we draw should be regarded as tentative, and, as historical studies in general, more open to alternative interpretations than usual in experimental ecology. A statistical analysis would necessitate a range of assumptions of population extinction, dispersal and colonisation, and that was beyond the scope of this study. For *Succisa*, modelling studies were performed, analysing how this spe-

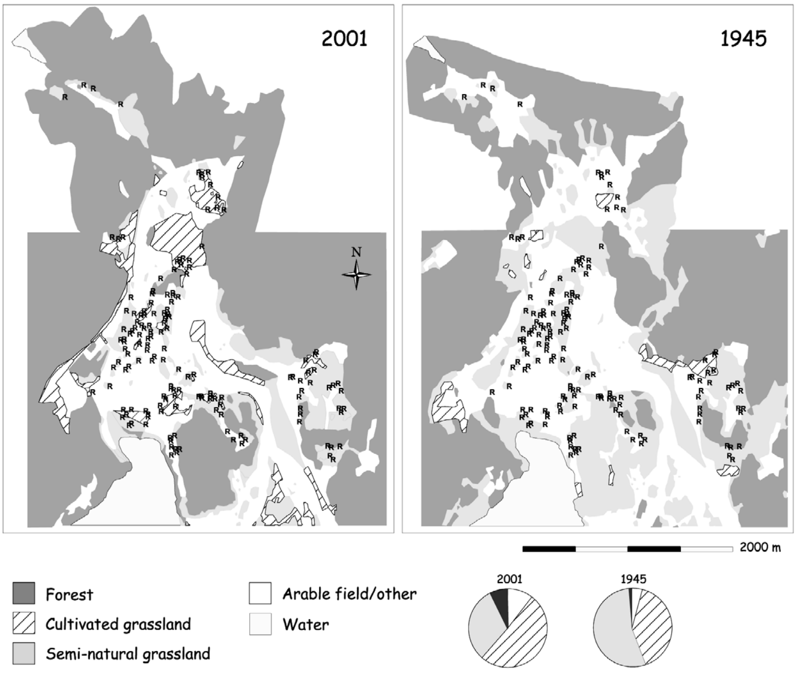

Fig. 2. The spatial distribution of patches of *Ranunculus bulbosus* in 1945 and 2001. Pie charts show the distribution of patches associated with vegetation management types in 1945 and 2001.

cies may respond to a range of different landscape scenarios, using different levels of population turnover and dispersal (Herben *et al.* 2006, Mildén *et al.* 2006).

Results

The landscape habitat structure changed markedly between 1945 and 2001 (Fig. 1 and Table 1). Forest cover increased from 47% to 63% of the total area, while semi-natural grasslands decreased from 19% to 6%. Generally, these changes were due to abandonment of grazing in semi-natural grasslands. These grasslands developed into forest. Another important change was the decreased cover of arable fields (changing from 26% to 19%) and a corresponding increase in cultivated grassland (changing from 2% to 5%).

We found 173 patches of *Ranunculus*, 108 patches of *Succisa*, 31 patches of *Carlina* and 408 patches of *Tragopogon* distributed in the landscape (Figs. 2–5). The *Ranunculus* patches in 1945 were mostly associated with semi-natural grassland (54%) and cultivated grassland (40%) (Fig. 2). In 2001, 31% of the patches were in semi-natural grassland, while 51% were located

Table 1. Transition matrix for general land-cover change in the study area. The figures in the matrix show the proportion (%) of each 1945 land-cover type that had become transformed to new 2001 land-cover types. “Grassland” denotes semi-natural grassland.

	Grassland	Arable field	Water	Forest	Cultivated grassland	No management
Grassland	**40.8**	16.1	0	26.9	11.1	5.1
Arable field	5.3	**84.1**	0	1.6	8.1	0.8
Water	8.2	0	**88.3**	1.2	0	2.2
Forest	30.9	6.9	0	**62.1**	0	0
Cultivated grassland	22.5	46.1	0	0	**0**	31.4
No management	0	0	0	0	0	**0**

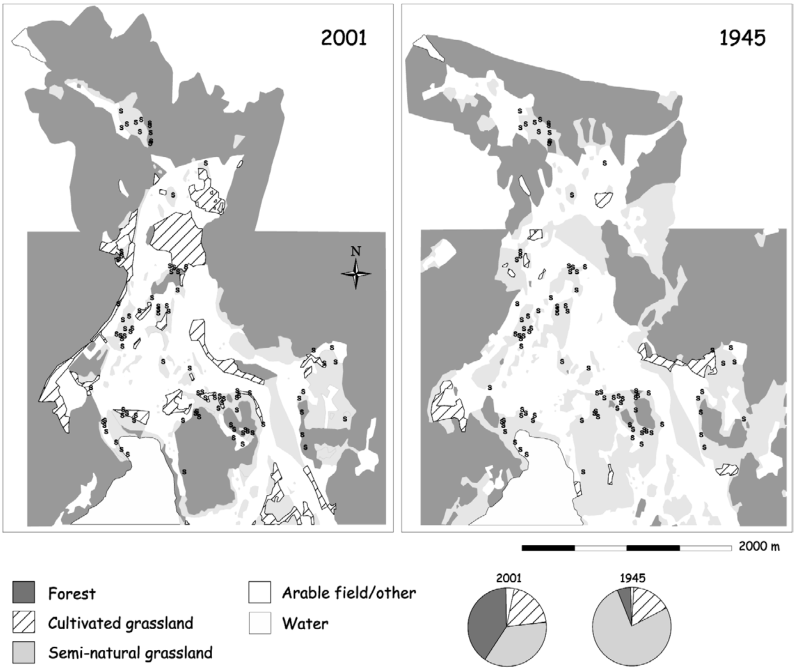

Fig. 3. The spatial distribution of patches of *Succisa pratensis* in 1945 and 2001. Pie charts show the distribution of patches associated with vegetation management types in 1945 and 2001.

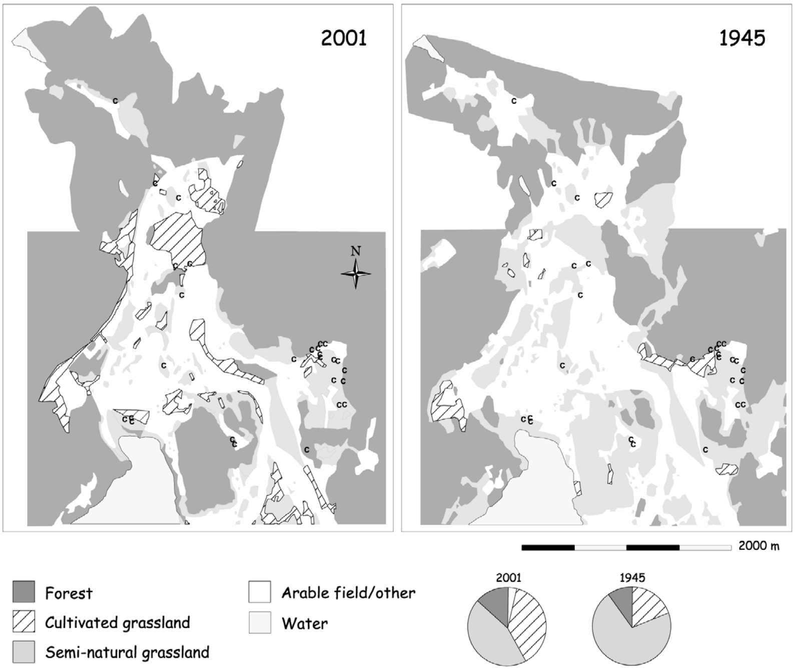

Fig. 4. The spatial distribution of patches of *Carlina vulgaris* in 1945 and 2001. Pie charts show the distribution of patches associated with vegetation management types in 1945 and 2001.

at sites classified as cultivated grassland. A small fraction (8%) was located in forest. For *Succisa*, 36% of the patches in 2001 were located in semi-natural grassland (Fig. 3). Of these patches, 77% were classified as semi-natural grassland in 1945. Proportions of patches classified as forest were 6% and 41% in in 1945 and 2001, respectively. The proportion of patches located in cultivated grassland increased slightly from 17% in 1945 to 20% in 2001.

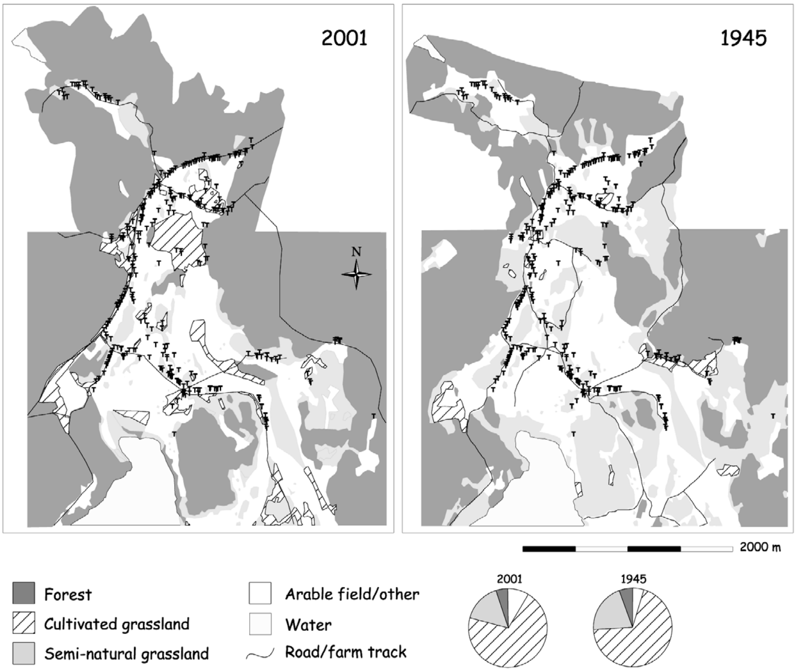

Fig. 5. The spatial distribution of patches of *Tragopogon pratensis* in 2001 in relation to present-day road verges and road verges, which existed in 1945. Pie charts show the distribution of patches associated with vegetation management types in 1945 and 2001.

A comparison between the transitions for *Ranunculus* and *Succisa* patches (Table 2) with the overall land-cover change (Table 1) revealed a few notable differences between these species. For *Ranunculus*, a large fraction of the semi-natural grassland patches 1945 was transformed to cultivated grassland 2001 (40%; Table 2A) whereas a small fraction (12%, Table 2A) was transformed to forest. For *Succisa*, a comparably smaller fraction of the semi-natural grassland patches 1945 was transformed to cultivated grassland (14%; Table 2B) but the fraction transformed to forest was higher (45%; table 2B). The overall land-cover change indicated that the transitions from semi-natural grassland to forest (26.9%; Table 1) was intermediate between the changes experienced by the *Ranunculus* and *Succisa* patches, respectively, whereas the transitions to cultivated grasslands (11.1%; Table 1) was much lower than for the *Ranunculus* patches.

Table 2. (**A**) Transition matrix showing land-cover changes from 1945 to 2001 for the patches of *Ranunculus bulbosus*. (**B**) Transition matrix showing land-cover changes from 1945 to 2001 for patches of *Succisa pratensis*. The figures in the matrix show the proportion (%) of each 1945 land-cover type that had become transformed to new 2001 land-cover types. The number of present-day populations occurring in each 1945 land-cover type is shown in parentheses.

	Forest	Semi-natural grassland	Cultivated grassland	Arable field/other
A				
Forest (2)	**50**	50		
Semi-natural grassland (94)	12	**41**	40	6
Cultivated grassland (70)	1	20	**77**	1
Arable field/other (7)	0	0	71	**29**
B				
Forest (6)	**67**	33	0	0
Semi-natural grassland (83)	45	**37**	14	4
Cultivated grassland (18)	17	28	**56**	0
Arable field/other (1)	0	100	0	**0**

For *Carlina*, the distribution of vegetation classes (Fig. 4) for the patches in 1945 very much resembled that of *Succisa* (Fig. 3). Most patches (71%) were at that time situated in semi-natural grassland, while 10% and 19% were situated in forest and abandoned fields, respectively. In 2001, the fraction of *Carlina* patches in forest (13%) had not increased notably, but 38% of the patches were located in cultivated grassland. From 1945 to 2001, the fraction of patches in semi-natural grassland decreased to 45%.

For *Tragopogon,* 60% of the patches were situated directly along road verges and 74% in close connection to roads (Fig. 5). Of the 64 patches that were not found close to roads in 2001, 27 (42%) were positioned in close connection to roads existing in 1945.

We found significant differences in population performance between habitat types (Table 3). Both *Ranunculus* and *Succisa* had different population sizes in semi-natural, abandoned and cultivated grasslands. *Ranunculus* populations were significantly smaller in abandoned grassland than in cultivated grasslands, but semi-natural grassland patches, despite the high median population size, did not have a significantly larger median population sizes. For *Succisa*, semi-natural grassland patches supported populations that were approximately tenfold in size as compared with those in abandoned and cultivated grasslands. There was no difference in population size of *Carlina* among habitat types. In *Tragopogon*, plant stands in road verges were significantly smaller than those in semi-natural and abandoned grasslands.

Flowering frequency (Table 3) varied significantly between habitat types in *Ranunculus* and *Succisa*, where abandoned grasslands had twice as high frequency as semi-natural and cultivated grasslands. There was no difference in flowering frequency between habitat types in *Carlina*.

Discussion

For three of four investigated species: *Ranunculus*, *Succisa* and *Carlina*, the patches presently occupied were to a higher extent classified as semi-natural grassland in 1945 than in 2001. In 2001, the fraction of patches of these species in semi-natural grassland is generally halved in comparison with that in 1945. The pattern for

Table 3. Population size and flowering frequency of the four study species in managed semi-natural grasslands, abandoned grasslands, and cultivated grasslands (former arable fields). P values (Kruskal-Wallis rank sum test) indicated significant differences among all grassland types. Different letters indicate significant ($p < 0.05$, Wilcoxon rank sum test with Bonferroni correction) differences between grassland types. Flowering frequencies for *Tragopogon* were not presented, since the inventory only recorded flowering individuals.

	Grassland type	Median population size (range)	Flowering frequency
Ranunculus bulbosus (n = 149)	semi-natural	75^{ab} (10–5000)	0.30^{b}
	abandoned	30^{a} (10–1000)	0.63^{a}
	cultivated	100^{b} (6–4000)	0.36^{b}
		$p = 0.025$	$p < 0.001$
Succisa pratensis (n = 94)	semi-natural	400^{a} (2–20000)	0.26^{b}
	abandoned	30^{b} (1–3000)	0.49^{a}
	cultivated	40^{b} (1–6000)	0.22^{b}
		$p < 0.001$	$p < 0.001$
Carlina vulgaris (n = 27)	semi-natural	31 (3–180)	0.29
	abandoned	10 (5–76)	0.28
	cultivated	31 (20–176)	0.27
		ns	ns
Tragopogon pratensis (n = 244)	semi-natural	25^{a} (3–50)	–
	abandoned	10^{a} (1–200)	–
	cultivated	5^{ab} (1–40)	–
	road verge	3^{b} (1–150)	–
		$p < 0.001$	

Succisa, where 45% of the patches that in 1945 were semi-natural grassland, in 2001 are situated in vegetation classified as forest, suggests that present forest populations are remnants from previous grassland populations. The patterns for *Ranunculus* and *Carlina* are not as easy to interpret. A large fraction of the *Ranunculus* patches occurred in cultivated grasslands, which indicates that *Ranunculus* is able to colonize areas that have periodically been used as crop fields. For *Carlina* we found only 31 small patches, both in semi-natural and cultivated grasslands, generally in edge zones and on bare soil.

There was a difference in the land-cover transitions from 1945 to 2001 between patches of *Ranunculus* and *Succisa*. The transformation of the semi-natural grasslands where *Ranunculus* patches occurred 1945 was more directed to cultivated grassland, and less to forest, as compared with the semi-natural grasslands where *Succisa* occurred 1945. These differences in transitions for patches of *Ranunculus* and *Succisa* indicate that the sites occupied by these two species in 1945, differed so that the *Ranunculus* patches occurred at what is likely to be more productive sites (that are most likely to have been cultivated) whereas *Succisa* patches occurred at what is likely to be less productive sites (that are most likely to simply have been abandoned). Apart from indicating a difference in habitat preferences for these species, the difference also suggest that *Succisa* will be more prone to occur in remnant populations in forests that are previously abandoned grasslands, simply because *Succisa* was present at such sites that developed into forests.

Tragopogon differs from the other semi-natural grassland plants since a large fraction of the *Tragopogon* patches are situated in close proximity to roads. It is, though, particularly noteworthy that almost half of the populations not located along roads in 2001 were located at sites associated with roads and farm tracts present in 1945. This association with historical roads occurs despite the fact that *Tragopogon* is a short-lived species, and therefore has the potential of a high population turnover.

The analyses of population performance generally confirm that semi-natural grasslands are the core habitats for at least two of the species. Both *Succisa* and *Ranunculus* perform better in patches with continuity of grazing management, although *Ranunculus* also shows good performance in cultivated grassland. Population size of both *Succisa* and *Ranunculus* is reduced after abandonment. This reduction is not likely to reflect differences in the size of habitat areas, since even in semi-natural grasslands the patches make up only a small fraction of the habitat area. For example, the average patch size of *Succisa* in semi-natural grasslands (the largest patches among the study species) was ca. 0.05 ha, whereas the semi-natural grasslands they inhabit were on average 2.9 ha (S. A. O. Cousins unpubl. data). Thus, the changing management regime is the most plausible cause for the reduced population size. Flowering, in contrast, increased after abandonment, most likely as a result of a decreased fraction of recruiting individuals. Some earlier studies of abandonment showed decreasing populations of *Succisa* (Regnéll 1980, Schrautzer & Jensen 1998), while others did not find any decrease in population size (Billeter *et al.* 2003). However, the latter study was performed in low-productive highland fens, whereas our study, as well as Regnéll (1980) and Schrautzer and Jensen (1998), was performed in more productive areas, something that may influence the effects of abandonment and speed of succession.

In contrast to *Succisa* and *Ranunculus*, *Carlina* does not exhibit a strong association with management as judged by the population performance. We suspect that *Carlina* mainly occured in refuges in the study landscape and thus was strongly affected by abandonment of semi-natural grasslands in the past. This interpretation is supported by a study by Klinkhamer *et al.* (1996), who found that *Carlina* in productive sites in the Netherlands have a shorter life span and produce fewer seedlings, something that speed up turnover of populations and lower recruitment. Löfgren *et al.* (2000) further pointed out that *Carlina* populations in central Sweden need high disturbance to be able to maintain positive growth rates.

The species that showed the clearest relationship to the historical landscape is *Succisa*. This is probably due to the fact that *Succisa* populations do not go extinct very fast, despite their marked response to abandonment of grazing. In grazed semi-natural grasslands, it had a tenfold larger size of its populations as compared with that at abandoned sites. Presently, *Succisa* has a large fraction of its populations in forest, a habitat that it probably cannot colonize and where populations are unlikely to be persistent. The present distribution pattern thus indicates a time lag of about 50 years in response to landscape change. This result is in agreement with the findings of model simulations of the regional *Succisa* population (Herben *et al*. 2006). The models even suggest that current distribution partly reflects the distribution in the early 19th century, more than 150 years ago. This slow response is a possible mechanism behind an extinction debt (Tilman *et al*. 1994, Hanski & Ovaskainen 2002), i.e. species that still occur in a landscape although slowly moving towards regional extinction. These findings for *Succisa* have implications for conservation biology. In order to assess the conservation status of a species it may not be sufficient to study present distributions, without accounting for possible relationships to historical landscapes. On the other hand, the relatively large populations of *Succisa* in colonized patches of cultivated grassland suggest possibilities for restorations. Since a large part of the semi-natural grassland pastures have been abandoned and grazing cattle moved to former crop fields, this may be an important habitat type for the future regional population of *Succisa*. Earlier studies indicated that *Succisa* perform worse in nutrient-rich grasslands (Vergeer *et al*. 2003) and recently restored grasslands (Pywell *et al*. 2003). In contrast, our results indicate that *Succisa* is able to colonize patches located on such grasslands. The regional population will be dependent on both the decay rate of abandoned semi-natural grasslands and the rate with which grazed cultivated grasslands turn inhabitable for the species. It is thus not clear whether the observed historical legacy in the distribution of *Succisa* is sufficient for concluding that an extinction debt exists.

Colonization and extinction rates are likely to be low in many vascular plants. Moreover, there are few old inventories or time series of data that provide links between long-term population dynamics and landscape history. Here, we have examined effects of landscape history using data that are often available, i.e. vegetation maps or aerial photographs from the study period, and a recent survey of the target species. Even though not a perfect substitute for more detailed data, this approach gives a possibility to recapture the development of the species in the landscape. We believe that we were able to give a fairly good description of the last 50 years of dynamics of *Succisa*, *Ranunculus, Tragopogon* and *Carlina* with this indirect method. The results of this study illustrate the need for considerations of landscape history as well as the properties and behaviour of target species in order to make reliable predictions for conservation status of many species.

Acknowledgements

We are grateful to H. Berg, D. Franzén and two anonymous reviewers for comments on the manuscript and to A. Caruso, J. Dahlgren, A. Hult, S. Rosengren and A. Weise for assistance in field. This study was financially supported by the EU project TRANSPLANT (EVK2–CT–1999–00004).

References

Alexandersson, H., Karlström, C. & Larsson-McCann, S. 1991: *Temperature and precipitation in Sweden 1961–1990. Reference normals*. — SMHI Reports, Meteorology and Climatology 81, Norrköping.

Bellemare, J., Motzkin, G. & Foster, D. R. 2002: Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. — *Journal of Biogeography* 29: 1401–1420.

Bernes, C. (ed.) 1994: *Biological diversity in Sweden. A country study*. — Swedish Environmental Protection Agency, Monitor 14.

Billeter, R., Hooftman, D. A. P. & Diemer, M. 2003: Differential and reversible responses of common fen meadow species to abandonment. — *Applied Vegetation Science* 6: 3–12.

Cousins, S. A. O. 2001: Analysis of land-cover transitions based on 17th and 18th century cadastral maps and aerial photographs. — *Landscape Ecology* 16: 41–54.

Cousins, S. A. O. & Eriksson, O. 2001: Plant species occurrences in a rural hemiboreal landscape: effects of remnant habitats, site history, topography and soil. — *Ecography* 24: 461–469.

Cousins, S. A. O. & Eriksson, O. 2002: The influence of management history and habitat on plant species richness in a rural hemiboreal landscape, Sweden. — *Landscape Ecology* 17: 517–529.

Dupoeuy, J. L., Dambrine, E., Laffite, J. D. & Moares, C.

2002: Irreversible impact of past land use on forest soils and biodiversity. — *Ecology* 83: 2978–2984.

Eriksson, Å. & Eriksson, O. 1997: Seedling recruitment in semi-natural pastures: the effects of disturbance, seed size, phenology and seed bank. — *Nordic Journal of Botany* 17: 469–482.

Ehrlén, J. & Lehtilä, K. 2002: How perennial are perennial plants? — *Oikos* 98: 308–322.

Eriksson, O. 1996: Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. — *Oikos* 77: 248–258.

Eriksson, O. & Ehrlén, J. 2001: Landscape fragmentation and the viability of plant populations. — In: Silvertown, J. & Antonovics, J. (eds.), *Integrating ecology and evolution in a spatial context*: 157–175. Blackwell, Oxford.

Eriksson, O., Cousins, S. A. O. & Bruun, H. H. 2002: Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. — *Journal of Vegetation Science* 13: 743–748.

Foster, D. R. 2002: Insights from historical geography to ecology and conservation: lessons from the New England landscape. — *Journal of Biogeography* 29: 1269–1275.

Grime, J. P., Hodgson, J. G. & Hunt, R. 1988: *Comparative plant ecology: a functional approach to common British species*. — Unwin Hyman, London.

Hanski, I. 1999: *Metapopulation ecology.* — Oxford Series in Ecology and Evolution.

Hanski, I. & Ovaskainen, O. 2002: Extinction debt at extinction threshold. — *Conservation biology* 16: 666–673.

Hansson, L. 1992: Landscape ecology of boreal forests. — *Trends in Ecology and Evolution* 7: 299–302.

Harrison, S. & Bruna, E. 1999: Habitat fragmentation and large-scale conservation: what do we know for sure? — *Ecography* 22: 225–232.

Helm, A., Hanski, I. & Pärtel, M. 2006: Slow response of plant species richness to habitat loss and fragmentation. — *Ecology Letters* 9: 72–77.

Herben, T., Münzbergová, Z., Mildén, M., Ehrlén, J., Cousins, S. A. O. & Eriksson, O. 2006: Long-term spatial dynamics of *Succisa pratensis* in a changing rural landscape: linking dynamical modelling with historical maps. — *Journal of Ecology* 94: 131–143.

Jakobsson, A. & Eriksson, O. 2003: Trade-offs between dispersal and competitive ability: a comparative study of wind-dispersed Asteraceae forbs. — *Evolutionary Ecology* 17: 233–246.

Klinkhamer, P. G. L., de Jong, T. J. & de Heiden, L. H. 1996: An eight-year study of population dynamics and life-history variation of the “biennial” *Carlina vulgaris*. — *Oikos* 75: 259–268.

Koerner, W., Dupouey, J. L., Dambrine, E. & Benoit, M. 1997: Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. — *Journal of Ecology* 85: 351–358.

Kull, K. & Zobel, M. 1991: High species richness in an Estonian wooded meadow. — *Journal of Vegetation Science* 2: 715–718.

Lindborg, R. & Eriksson, O. 2004: Historical landscape connectivity affects present plant species diversity. — *Ecology* 85: 1840–1845.

Löfgren, P., Eriksson, O. & Lehtilä, K. 2000: Population dynamics and the effect disturbance in the monocarpic herb *Carlina vulgaris* (Asteraceae). — *Ann. Bot. Fennici* 37: 183–192.

Mildén, M., Münzbergova, Z., Herben, T. & Ehrlén, J. 2006: Metapopulation dynamics of a perennial plant, *Succisa pratensis*, in an agricultural landscape. — *Ecological modelling* 199: 464–475.

Pywell, R. F., Bullock, J. M., Roy, D. B., Warman, L., Walker, K. J. & Rothery, P. 2003: Plant traits as predictors of performance in ecological restoration. — *Journal of Applied Ecology* 40: 65–77.

Regnéll, G. 1980: A numerical study of successions in an abandoned, damp calcareous meadow in S Sweden. — *Vegetatio* 43: 123–130.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M. & Wall, D. H. 2000: Biodiversity — global biodiversity scenarios for the year 2100. — *Science* 287: 1770–1774.

Schrautzer, J. & Jensen, K. 1998: Quantitative und qualitative Auswirkungen von Sukzessionsprozessen auf die Flora der Niedermoorstandorte Schleswig-Holsteins. — *Z. Ökol. Natursch.* 75: 64–73.

Tilman, D., May, R. M., Lehman, C. L. & Nowak, N. A. 1994: Habitat destruction and the extinction debt. — *Nature* 371: 65–66.

Turnbull, L. A., Crawley, M. J. & Rees, M. 2000: Are plant populations seed-limited? A review of seed sowing experiments. — *Oikos* 88: 225–238.

Turner, M. G., Gardner, R. H. & O’Neill, R. V. 2001: *Landscape ecology in theory and practice*. — Springer-Verlag Inc., New York.

Vergeer, P., Rengelink, R., Copal, A. & Ouborg, J. 2003: The interacting effects of genetic variation, habitat quality and population size on performance of *Succisa pratensis*. — *Journal of Ecology* 91: 18–26.

Vessby, K., Söderström, B., Glimskär, A. & Svensson, B. 2002: Species-richness correlations of six different taxa in Swedish seminatural grasslands. — *Conservation Biology* 16: 430–439.