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This is a published version of a paper published in *Folia Geobotanica*.

Citation for the published paper:

Johansson, V., Cousins, S., Eriksson, O. (2011)

"Remnant Populations and Plant Functional Traits in Abandoned Semi-Natural Grasslands"

Folia Geobotanica, 46(2-3): 165-179

Access to the published version may require subscription.

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Remnant Populations and Plant Functional Traits in Abandoned Semi-Natural Grasslands

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Abstract Although semi-natural grasslands in Europe are declining there is often a time delay in the local extinction of grassland species due to development of remnant populations, i.e., populations with an extended persistence despite a negative growth rate. The objectives of this study were to examine the occurrence of remnant populations after abandonment of semi-natural grasslands and to examine functional traits of plants associated with the development of remnant populations. We surveyed six managed semi-natural grasslands and 20 former semi-natural grasslands where management ceased 60–100 years ago, and assessed species response to abandonment, assuming a space-for-time substitution. The response of species was related to nine traits representing life cycle, clonality, leaf traits, seed dispersal and seed mass. Of the 67 species for which data allowed analysis, 44 species declined after grassland abandonment but still occurred at the sites, probably as remnant populations. Five traits were associated with the response to abandonment. The declining but still occurring species were characterized by high plant height, a perennial life form, possession of a perennial bud bank, high clonal ability, and lack of dispersal attributes promoting long-distance dispersal. Traits allowing plants to maintain populations by utilizing only a part of their life cycle, such as clonal propagation, are most important for the capacity to develop remnant populations and delay local extinction. A considerable fraction of the species inhabiting semi-natural grasslands maintain what is most likely remnant populations after more than 60 years of spontaneous succession from managed semi-natural grasslands to forest.

Keywords Clonal growth · Grassland abandonment · Land use change · Landscape history · Remnant population dynamics · Species-rich grasslands

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Plant nomenclature Mossberg and Stenberg (2003)

Introduction

Many studies on plant biodiversity (e.g., Pärtel et al. 1999; Pärtel and Zobel 1999; Cousins and Eriksson 2002; Eriksson et al. 2002; Öster et al. 2007) have been concerned with semi-natural grasslands, as they are the main remnants of the traditional agricultural landscape in northern and central Europe, and they are among the most species-rich habitats in this region. Due to land-use change, the total area of semi-natural grasslands in northern and central Europe has decreased considerably, in some regions by more than 90% over the last 100 years (Fuller 1987; Bernes 1994; Hodgson et al. 2005). Most of the semi-natural grassland area has been transformed to arable fields, forest plantations, or has been abandoned and left for spontaneous succession to forest. As a result of these changes in land use, many grassland species currently occur as small and isolated populations in the remaining grasslands. When grassland management is abandoned there is often a time delay in the extinction of species because of plant population inertia. The populations decline, but the rate of decline is so slow that populations may be present for several decades after grazing or mowing management has ceased. These plant species thus exist as remnant populations, that is to say populations that are decreasing in growth rate ($\lambda < 1$), but still remaining in the landscape (Eriksson 1996, 2000). For a species with remnant population dynamics, parts of the regional population thus consist of local populations that are declining towards extinction, although at a slow rate relative to landscape change. As a result, the present plant species distributions reflect the historical rather than the present landscape configuration (Lindborg and Eriksson 2004; Helm et al. 2006). Studies of abandoned semi-natural grasslands have indicated that perennial species, e.g., *Primula veris* (Brys et al. 2003), *Succisa pratensis* (Herben et al. 2006) and *Scorzonera humilis* (Colling et al. 2002), are likely to develop remnant populations. This may be one mechanism behind the finding by Sammuli et al. (2008) that grassland species in Estonia have not declined as much as would be expected from the decrease in grassland area. Annual plants in contrast, are strongly over-represented among species known to decline rapidly after cessation of grazing (Eriksson and Ehrlén 2001).

If species are present at a landscape scale, but in slowly declining populations, this implies that there is an extinction debt (Tilman et al. 1994; Hanski 1999). In the case of the changing landscapes in northern and central Europe, where the most drastic changes have occurred during the last 100 years, the existence of such an extinction debt would imply that there will be a decline in species diversity in the near future. Indirect evidence (Lindborg and Eriksson 2004; Helm et al. 2006) suggest that the present plant species distribution in grasslands and former grasslands (where management has been abandoned) is more related to the habitat configuration existing about 50–100 years ago, than it is to the present-day landscape. This observation suggests a similar time scale for the decline to final disappearance of many grassland species after abandonment of management. Identifying extinction debts and remnant populations is important when assessing the degree to which biological surveys provide accurate estimates of the capacity of landscapes to

maintain biodiversity. It is also important to study the time-period it takes for a population or a community to come into equilibrium with a given landscape structure following disturbance (Vellend et al. 2006).

In this study, we examined the pattern of species decline in grasslands by comparing still managed grasslands with sites where grassland management (grazing) ceased 60–100 years ago. Some traits have been suggested to enhance the ability of plants to develop remnant populations (or generally respond slowly to vegetation change), such as the possession of long-lived life-cycle stages (Grime 1979; van Groenendael et al. 1994; Eriksson 2000), or broader tolerance to the environmental factors characteristic of late successional stages, for example shade. To assess the features that may promote development of remnant populations, we used information on plant functional traits (Westoby et al. 2002), related to different phases in the plant life cycle, reproduction, dispersal, recruitment and performance of established plants. The specific objectives were *i*) to investigate and quantify the occurrence of putative remnant populations of plants in abandoned semi-natural grasslands and *ii*) to examine if there are any functional traits of plants contributing to the development of remnant populations.

Methods

Study Area

The study was conducted in the parishes of Lid and Ludgo in the County of Södermanland, ca. 75 km SSW of Stockholm, Sweden (58°55' N, 17°6' E). The region was convenient for this study because it has a long history of management continuity and a well-built base of historical maps. Maps of this kind serve as an important source of information on the history of present-day vegetation patterns (Cousins 2001; Cousins and Eriksson 2008). Grazing by cattle is the dominating management of semi-natural grasslands today, as it was earlier during the 20th century. The design of the field survey was based on a selection of sites with still managed semi-natural grasslands (reference sites, Nr.=6), and sites which, according to information from old maps and aerial photographs, were managed as grasslands 60–100 years ago. These “abandoned sites” (Nr.=20) were left for natural succession, and are now mixed deciduous-coniferous forest, usually dominated by a mixture of pine (*Pinus sylvestris*) and birch (*Betula pubescens* and *B. verrucosa*). Shrubs like Common hazel (*Corylus avellana*) and Common juniper (*Juniperus communis*) are frequent in these forests and are a legacy of previous more open conditions. These forests are not grazed by livestock, but are to some extent affected by grazing and browsing from wild animals, e.g., roe deer and moose. The selected forest stands were all dry to mesic and relatively open with at least partly open canopies.

Sites were selected by analyzing historical maps from the 18th century, 1901 and the 1950s as well as aerial photographs from the 1980s (infra-red) and 2003 (black and white orthophotos). Aerial photographs were mostly used to exclude plantations, restorations and marshier areas, because these areas would differ too much from the study habitat. Identification of reference areas was conducted in the same way except for the additional criterion that the sites had to be included in the Swedish survey of

semi-natural pastures and meadows (Persson 2005). Grasslands in this survey were classified into different Natura 2000 habitats and all the selected reference areas belonged to the category “Fennoscandian lowland species-rich dry to mesic grassland” (code 6270, Anonymous 1992). These habitats are characterized by having a long history of grazing or mowing and a minimal to no influence of added nutrients. All sites were located within 100 km². The size range of the sites was 1.8–8.5 hectares for the reference sites, and 0.3–4.1 hectares for the abandoned sites. All geographical analyses were performed in Arcview GIS 3.2.

Species Survey and Analysis of Population Decline

For each site, we inventoried ten 1-m² plots to obtain frequency data for the species. The plots were distributed over two transects per site. The first transect was placed across the longest section of each site and included six plots, and the remaining four plots were placed on a transect perpendicular to the first transect. The plots were evenly distributed along transects, so the distance between them depended on the size of the site. Although the sites were of different size, the same total area per site was sampled for the assessment of species frequencies. An inventory was also performed at each site by walking through the area, noting all additional species. By performing Pearson’s chi-square tests on the frequencies of the recorded species in managed and in abandoned semi-natural grasslands, respectively, species were assigned to four different categories, based on their response to abandonment of grassland management: increasing, not responding, declining but still occurring, and disappeared. Because the main objective of the study was to examine species that decline after abandonment of grassland management, and identify features that enable some of these species to remain as remnant populations, we focused on the two categories, declining but still occurring and disappeared.

To be included in the analysis a species had to be recorded in at least a total of five plots in the managed semi-natural grasslands. It should be noted that the distinction between species present and those disappeared was only based on above-ground organs. It cannot be excluded that some of the species categorized as disappeared were still present by a seed bank or underground organs. To proceed we had to make two assumptions, related to the interpretation of the results of the frequency analysis.

Firstly, we assume that all the species found to decline in frequency when comparing managed semi-natural grassland with abandoned grassland have a population growth rate (λ) below 1, and thus, by definition (Eriksson 1996) occur as remnant populations in the study area. Population growth rate was considered as the ratio $N(t+1)/N(t)$ over the investigated time interval. Although the data does not allow any detailed estimate of population growth rate, a decrease in frequency must imply that population growth is <1 . However, in principle, a significantly lower frequency in abandoned grasslands, found with the space-for-time substitution approach, could result from recent colonization, followed by a $\lambda > 1$. Alternatively, the present population may have declined initially, but then established at a new stable level ($\lambda \approx 1$). Although our data cannot be used to exclude these alternatives, we consider them unlikely, given that all the examined species (Table 1), are known as characteristic for semi-natural grassland (Ekstam and Forshed 1992). Secondly,

Table 1 List of species analyzed with regard to their response to abandonment of management in semi-natural grassland

Species	Response to habitat change	P-value
<i>Achillea millefolium</i>	-	<0.001
<i>Agrostis capillaris</i>	-	<0.001
<i>Ajuga pyramidalis</i>	n.s.	0.111
<i>Alchemilla glaucescens</i>	-	<0.001
<i>Anthoxanthum odoratum</i>	-	<0.001
<i>Anthriscus sylvestris</i>	n.s.	0.074
<i>Briza media</i>	†	<0.001
<i>Campanula persicifolia</i>	n.s.	0.358
<i>Campanula rotundifolia</i>	-	0.043
<i>Carex caryophyllea</i>	n.s.	0.256
<i>Carex leporina</i>	-	0.001
<i>Carex pallescens</i>	-	<0.001
<i>Carex panicea</i>	†	<0.001
<i>Carex spicata</i>	-	0.005
<i>Centaurea jacea</i>	-	<0.001
<i>Cerastium fontanum</i>	-	<0.001
<i>Dactylis glomerata</i>	+	0.011
<i>Danthonia decumbens</i>	-	<0.001
<i>Deschampsia cespitosa</i>	-	<0.001
<i>Deschampsia flexuosa</i>	+	<0.001
<i>Festuca ovina</i>	-	<0.001
<i>Festuca pratensis</i>	-	<0.001
<i>Festuca rubra</i>	-	<0.001
<i>Filipendula vulgaris</i>	-	<0.001
<i>Fragaria vesca</i>	n.s.	0.395
<i>Galium boreale</i>	n.s.	0.880
<i>Galium uliginosum</i>	-	<0.001
<i>Galium verum</i>	-	<0.001
<i>Geum rivale</i>	n.s.	0.541
<i>Helictotrichon pratense</i>	n.s.	0.202
<i>Helictotrichon pubescens</i>	n.s.	0.935
<i>Hieracium</i> sect. <i>Vulgata</i>	n.s.	0.200
<i>Hieracium umbellatum</i>	n.s.	0.942
<i>Hypericum maculatum</i>	n.s.	0.122
<i>Lathyrus linifolius</i>	n.s.	0.124
<i>Lathyrus pratensis</i>	-	<0.001
<i>Leontodon autumnalis</i>	†	<0.001
<i>Leucanthemum vulgare</i>	-	0.004
<i>Lotus corniculatus</i>	-	<0.001
<i>Luzula campestris</i>	-	<0.001
<i>Melampyrum pratense</i>	n.s.	0.706

Table 1 (continued)

Species	Response to habitat change	P-value
<i>Phleum pratense</i>	-	<0.001
<i>Pilosella officinarum</i>	-	<0.001
<i>Pimpinella saxifraga</i>	-	<0.001
<i>Plantago lanceolata</i>	-	<0.001
<i>Poa pratensis</i>	n.s.	0.185
<i>Polygala vulgaris</i>	-	<0.001
<i>Potentilla erecta</i>	-	<0.001
<i>Primula veris</i>	n.s.	0.372
<i>Prunella vulgaris</i>	-	<0.001
<i>Ranunculus acris</i>	-	<0.001
<i>Ranunculus auricomus</i>	-	<0.001
<i>Ranunculus polyanthemos</i>	n.s.	0.131
<i>Rhinanthus minor</i>	-	<0.001
<i>Rumex acetosa</i>	-	<0.001
<i>Saxifraga granulata</i>	†	<0.001
<i>Stellaria graminea</i>	-	<0.001
<i>Succisa pratensis</i>	-	<0.001
<i>Taraxacum</i> sect. <i>Ruderalia</i>	-	0.001
<i>Trifolium medium</i>	-	0.011
<i>Trifolium pratense</i>	-	<0.001
<i>Trifolium repens</i>	-	<0.001
<i>Veronica chamaedrys</i>	-	<0.001
<i>Veronica officinalis</i>	-	<0.001
<i>Veronica serpyllifolia</i>	-	<0.001
<i>Vicia cracca</i>	-	<0.001
<i>Viola canina</i>	-	<0.001

- – decreased in frequency; + – increased in frequency; n.s. – no significant change; † – disappeared.
P-values are calculated from χ^2 analyses.

we assume that it is appropriate to make a space-for-time substitution. We thus assume that managed sites represent the state of the now abandoned sites, as it was 60–100 years ago. As recently has been discussed by Johnson and Miyanishi (2008) there are several potential problems with using a space-for-time substitution. The main reason is that the underlying assumption that all sites studies represent developmental stages following the same historical trajectory may not be valid. We acknowledge this problem but maintain that this method is useful to examine long-term processes that would otherwise be impossible to study. To reduce the risk of invalidating the assumption of the time-for-space substitution we have used sites that, according to old maps, previously were categorized as similar. Furthermore, we have restricted the study to a relatively small landscape area to reduce the risk that other factors such as soil conditions, management and weather conditions differ among the sites. This restriction in area was why we only had access to six reference

sites, whereas we used 20 abandoned sites. Thus, we chose an unbalanced design to reduce the risk of invalidating the assumption of the space-for-time substitution.

Population Decline and Functional Traits

Both declining and disappeared species respond negatively to abandonment of grassland management, but only species in the former category manage to persist after 60–100 years after abandonment (as explained above, probably as remnant populations). Thus, a comparison of functional traits between these two categories was used to identify traits potentially contributing to the development of remnant populations. However, only four species were recorded as locally disappeared (see [Results](#)). This is probably partly because we had access to only six reference sites (see the section above where we explain why only six sites were used), and thus several species were too infrequent to be recorded in at least five plots. Thus, the category of disappeared species was complemented by including species known to rapidly decrease in an early stage of succession after grassland management (Ekstam and Forshed 1992). To be selected these species had to fulfill two criteria: *i*) The species are typical for the focal habitat (dry-mesic grasslands) and known to decline rapidly after abandonment of management (listed on pages 50–56 in Ekstam and Forshed 1992); *ii*) The species have been recorded at semi-natural grassland sites in, or in a close vicinity of the study area (this study; Rydberg and Wanntorp 2001; O. Eriksson, unpubl.). This resulted in the addition of 41 species to the category disappeared (Table 2). In this table we note whether the species were recorded in this study (but in a frequency below five plots) or have been recorded in semi-natural grasslands elsewhere in the region. The justification of categorizing these species as “disappeared” was that no records of any of the species were from abandoned sites.

The following traits were examined: specific leaf area (SLA), leaf dry matter content (LDMC), seed mass, dispersal strategy, clonal ability, perennial subterranean bud bank production, plant height, leaf distribution and life-cycle.

Table 2 Species added to the category “disappeared” as they are known to rapidly decrease in an early stage of succession after abandonment of grassland management (Ekstam and Forshed 1992)

Species added to the category disappeared

Recorded during site inventory:

Antennaria dioica, *Arabis thaliana*, *Arenaria serpyllifolia*, *Bromus hordeaceus*, *Capsella bursa-pastoris*, *Carex pilulifera*, *Erophila verna*, *Geranium pulchellum*, *Hypochoeris maculata*, *Lolium perenne*, *Pilosella lactucella*, *Plantago major*, *Poa annua*, *Poa supina*, *Polygonum aviculare*, *Potentilla tabernaemontani*, *Scleranthus annuus*, *Trifolium arvense*, *Vicia tetrasperma*

Recorded on other surveys in semi-natural grasslands in the region (Rydberg and Wanntorp 2001; O. Eriksson, unpubl.):

Bellis perennis, *Botrychium lunaria*, *Carlina vulgaris*, *Cerastium semidecandrum*, *Cynosurus cristatus*, *Euphrasia rostkoviana* subsp. *fennica*, *Euphrasia stricta*, *Gagea minima*, *Gentianella campestris*, *Jasione montana*, *Linum catharticum*, *Matricaria matricarioides*, *Myosotis discolor*, *Myosotis ramosissima*, *Myosotis stricta*, *Potentilla cranzii*, *Rhinanthus serotinus*, *Satureja acinos*, *Taraxacum* sect. *Hamatum*, *Taraxacum* sect. *Erythrosperma*, *Trifolium campestre*, *Veronica verna*

Nomenclature is according to Mossberg and Stenberg (2003).

Information on SLA (m^2/kg) and seed mass (mg) was taken from a local database (H. Quested and O. Eriksson, unpubl.), and information on LDMC (mg/g) was provided by B. Marteinsdóttir and M. Öster (unpubl.). All these measurements were done in accordance with Knevel et al. (2005). The dispersal strategy was simplified into two categories: no dispersal traits (including myrmecochory, because we assumed that seed dispersal by ants occurs on local scale) and those with dispersal traits potentially promoting long-distance dispersal, including wind dispersal, exo-zoochory and endo-zoochory. Information on dispersal was taken from a local database (H. Quested and O. Eriksson, unpubl.). Information on clonal ability was used in two ways: as a dichotomy, possessing or not possessing clonal growth and propagation, and as a “clonal index”. The clonal index was calculated based on information on number of clonal “offspring” produced per parent and year, and lateral spread, gathered from the CLO-PLA3 database (Klimešová and Klimeš 2006, 2008). Number of clonal offspring was assigned to four different categories (0–3), representing 0, 1, 2–10 and >10 offspring produced per year, respectively. Lateral spread was assigned to three different categories (0–2), representing <0.01, 0.01–0.25, >0.25 m/year, respectively. The clonal index equals the sum of the category values for number of clonal offspring (0–3) and lateral spread (0–2). Where multiple records of lateral spread and number of clonal offspring were found, the highest value was selected to represent the maximum capacity of the different species to reproduce clonally. It was also taken into account that some plants have more than one clonal growth organ (CGO), rhizomes/stolons, adventitious roots/root splitters and bulbs, and therefore may achieve a higher clonal index. If a species possessed more than one CGO, its final clonal index was the sum of estimates for all CGOs.

The information on the ability for each species to produce or not produce a perennial subterranean bud bank was also gathered from CLO-PLA3 database. To be categorized as possessing a perennial subterranean bud bank, a species should produce buds below or at the soil surface and the bud bank should be perennial, and not only seasonal. Data on mean plant height (m) was taken from a local database (H. Quested and O. Eriksson, unpubl.), and was measured according to Weiher et al. (1999). Descriptions on leaf distribution and life-cycles were attained from Mossberg and Stenberg (2003). Leaves were classified as either regularly distributed along the stem (scattered) or partly concentrated at the plant base (semi-rosette) or as shoots near the ground (rosette). Dicyclic shoots bearing a rosette in the first year of plant life and tall leafy shoot in the second year were classified as semi-rosettes. Species were assigned to two life-cycle categories: perennial or annual/biennial.

The analyses were performed in two ways: firstly by comparing declining species with disappeared species regarding each trait, and secondly, by relating the functional traits to the proportional species decline (only using the species that were declining but still occurring).

To examine functional traits with continuous values, SLA, LDMC, seed mass, and mean plant height, logistic regressions were performed, with species declining or disappearing as a binary response variable. For categorized traits: dispersal strategy, clonal ability, perennial subterranean bud-bank production, leaf distribution and life-cycle, analyses were made using Pearson’s chi-square test.

For all the significantly declining species the proportional decline (%) was calculated. Regression analyses were then performed to examine the relationships

between decline and SLA, LDMC, seed mass and plant height. ANOVA was used to examine decline in relation to dispersal strategy, perennial subterranean bud-bank production, leaf distribution and life cycle. The effect of clonal ability was examined with Spearman rank correlation test, using the clonal index.

All statistical tests were done using the freeware R 2.7.2 (R Development Core Team 2008).

Results

A total of 274 species were recorded in the study sites. Of these species, 221 were found in the managed semi-natural grassland and 229 in the abandoned semi-natural grasslands. Forty-five species were unique to managed semi-natural grasslands and 53 species were unique for abandoned sites. There was on average 25 species per m² (range 12–40) in managed semi-natural grassland sites and 14 species per m² (range 5–28) in abandoned grasslands. To be selected for further analysis of species decline, the species had to be recorded in a total of at least five plots in managed sites. This resulted in 67 species left (Table 1): increasing ($n=2$), not responding ($n=17$), decreasing ($n=44$) and disappeared ($n=4$). Species marked as significantly declining but still occurring (-) or locally disappeared (†) were used in the further analyses. As mentioned in the “Methods” section, we added 41 species to the category disappeared.

Of the nine traits examined, five were significantly associated with the grouping into disappeared and declining but still occurring. Species that declined, but still occurred at abandoned sites, were characterized by high plant height, a perennial life form, possession of a perennial bud bank, and a high clonal ability (Fig. 1). Possession of dispersal attributes promoting long-distance dispersal was more frequent among the species that disappeared (Fig. 2). There was a marginally non-significant ($P=0.066$) positive relationship between seed mass and the likelihood that species declined but still occurred at abandoned sites. In contrast, leaf traits were not related to species response to grassland abandonment: SLA ($P=0.31$) and LDMC ($P=0.856$), and the same was found for leaf distribution ($P=0.195$).

In the analyses of the species that declined but still occurred in the abandoned grassland, only one trait, clonal ability, was found to be significantly associated with the proportional decline. The higher the clonal ability, as measured by the clonal index, the smaller was the decline after abandonment of grassland management (Fig. 3). There was a marginally non-significant ($P=0.068$) negative relationship between plant height and proportional decline, suggesting that taller plants resist decline better than smaller plants. Life cycle was not possible to analyze because only one of the declining but still occurring species had an annual/biennial life cycle.

Discussion

If remnant populations are widespread in the landscape they might be a contributing factor to the so-called ‘extinction debt’ (Tilman et al. 1994), which implies a future cost in terms of species extinctions. To examine whether an extinction debt actually exists, we require either data on species loss following habitat fragmentation (e.g.,

Fig. 1 The relationship between plant species response (declining but still occurring vs disappeared) to 60–100 years of abandonment of management in semi-natural grasslands in Sweden, and species traits: **a** Perennial vs annual/biennial life cycle ($\chi^2=31.8$, $P<0.001$), **b** effect of plant height on the probability of decline but still occur (logistic regression, $P=0.001$), **c** Possession of a perennial bud bank ($\chi^2=13.4$, $P<0.001$), **d** Possession of clonal ability ($\chi^2=7.1$, $P=0.008$)

Helm et al. 2006) or data from multiple similar landscapes with varying histories of fragmentation (Berglund and Jonsson 2005; Vellend et al. 2006). Scarcity of these kinds of data has resulted in few empirical studies that underpin the existence of extinction debts in natural populations. Most studies to date examine and discuss theoretical models for predicting extinction debts (e.g., Loehle and Li 1996; Hanski 2000). Others have tested for deviations from statistical predictions of species richness (e.g., based on species-area curves) assuming the extinction debt was already paid off (e.g., Berglund and Jonsson 2005). Focusing on species richness could however mask important differences among species in their likelihood of

Fig. 2 The relationship between plant species response (declining but still occurring vs disappeared) to 60–100 years of abandonment of management in semi-natural grasslands in Sweden, and possession of attributes promoting long-distance seed dispersal ($\chi^2=5.0$, $P=0.026$)

contributing to an extinction debt (Vellend et al. 2006). Dispersal strategies and life-cycle characteristics, for example, might cause some species to have lower rates of stochastic extinctions, while other species showing higher rates of stochastic population extinction are expected to pay off their extinction debt quite rapidly (Ovaskainen and Hanski 2002). Lindborg (2007) found that short-lived plants are positively associated with current grassland connectivity and grassland area, whereas long-lived species remain unrelated to current grassland connectivity and area.

Fig. 3 The relationship between plant species decline after 60–100 years of abandonment of management in semi-natural grasslands in Sweden, and clonal ability measured as an index based on number of clonal propagules produced and lateral spread per year (see text for an explanation) ($\rho=-0.306$, $P=0.049$)

Instead, long-lived species are more associated with the properties of the historical landscape. This indicates the existence of time-lags in semi-natural grassland, which provides a rationale for studies on the mechanisms behind such time-lags.

The first objective of this study was to investigate and quantify the presence of remnant populations (Eriksson 1996) in habitats that have developed from semi-natural grasslands where management had been abandoned. We could document that about 20% (44 of 221) of the species found in managed semi-natural grassland sites were significantly declining in frequency, but still occurred in abandoned sites after 60–100 years without grazing management. However, the frequency data did only allow analysis based on 67 species, so 20% is probably a conservative estimate of the fraction of species that decline without going extinct within this time frame. We recognize that it is difficult to determine whether all these declining species are in fact remnant populations. A decrease in frequency does not necessarily imply that species presently have a negative population growth rate and demographic studies of each species would be necessary to reach a more firm conclusion about the status of the populations. It is, however, reasonable to assume that species typical for managed semi-natural grasslands that are declining in frequency as a response to ceased grazing but are still present more than 60 years after abandonment of grazing, are those that most likely develop remnant populations.

The second objective of this study was to identify if there are certain functional traits of grassland plants, which are associated with the development of remnant populations. For this analysis, we assumed that the 44 species identified as declining but still occurring, actually occur as remnant populations in former, presently abandoned, grasslands.

The overall conclusion is that traits that imply persistence of vegetative (clonal) life-cycle stages, i.e., an ability to maintain an established population without completion of the reproductive life cycle, are those most strongly associated with the ability to develop remnant populations. Traits such as a perennial life cycle, clonal propagation, and possession of a perennial bud bank were found associated with remnant populations. These results support the suggestions made by van Groenendael et al. (1994) and Eriksson (1996, 2000), that life cycles with alternative loops enable species to buffer unfavourable conditions and maintain populations even if seed production, seed dispersal and seedling recruitment are hindered. These results confirm the findings by Ozinga et al. (2007) that there is a positive relationship between possession of clonal propagation and persistence. A high plant height was associated with remnant populations, possibly as a result of benefits related to competition for light. Regenerative traits related to seed dispersal and seedling recruitment (seed mass) were also related to the response of species to abandonment, although only weakly so for seed mass. Heavier seeds are commonly favoured under conditions of nutrient shortage and shade (Leishman et al. 2000), and it has been known for long that seed size is generally increasing when open grasslands develop into forest communities (Salisbury 1942; Hodkinson et al. 1998). Furthermore, persistent species were more commonly lacking attributes favouring long-distance dispersal, as compared to species which disappeared, possibly reflecting the suggested trade-off between dispersal and persistence (Grime 1979; Tilman 1994; Westoby et al. 2002). The likely mechanism behind this pattern is not clear, but it may reflect that many species in open grassland habitats rely on wind-

dispersal or exo-zoochory, but at the same time lack the life-cycle features that enable them to maintain populations after abandonment of grazing management.

The leaf traits, SLA and LDMC, were included in the analysis because they have been shown to indicate a range of features related to resource capture and usage, and growth rate (Westoby et al. 2002; Garnier et al. 2004; Wright et al. 2004). In particular, we expected that species response to the changing light environment that accompanies abandonment of semi-natural grasslands would be related to these leaf traits. We included both SLA and LDMC, as there are indications that LDMC may be a more accurate predictor of resource capture and usage than the more commonly used SLA (Wilson et al. 1999). In contrast to life-cycle traits such as clonality and life span, SLA and LDMC were not associated with the response of species after grassland abandonment. No patterns were found when comparing these leaf traits in declining and disappearing species, or in the analysis of declining species only. A possible explanation for the lack of coherent pattern is that advantages for plants of having lower SLA (higher LDMC) for increasing efficiency in resource usage (Westoby et al. 2002) are balanced against advantages of higher SLA (lower LDMC) in competition for light. However, if this explanation was valid, the distribution of leaves would be expected to differ between declining and disappearing species. Species with high-placed photosynthetic parts (leaves) would be favoured during succession from open grassland to forest. Such a relationship was not found. This indicates that there are several alternative strategies for light capture and resource usage following abandonment of grassland management. For example, species with scattered, high-placed leaves might be able to over-shadow species with lower placed leaves (e.g., rosette-species), but at the same time it is possible for rosette species to expand in a way that makes it hard for other species to overshadow them.

Population extinction due to abandonment of grazing in traditionally managed grasslands is an ongoing process in the landscapes transformed by modern agriculture and forestry. This process affects not only rare and short-lived plants but also long-lived and common perennials (Brys et al. 2003). The population dynamics of annual/biennial species, compared with perennial species, is often characterized by higher turnover rates, and the persistence of populations is dependent on frequent recruitment (e.g. Lindborg 2007). Annual and biennial species are therefore more vulnerable and respond more quickly to habitat transformation than perennial species. Our results suggest that traits that allow plants to maintain populations by utilizing only a part of their life cycle, mainly traits associated with clonal propagation, delay the process of decline and contribute to create systems of remnant populations. In addition to the delay directly caused by life-cycle characteristics, the species niche requirements, manifested by, for example, physiological features, not examined here, may contribute to the slow population response to land-use changes. The results also suggest that a considerable fraction of the species inhabiting semi-natural grasslands maintain what are most likely remnant populations after more than 60 years of spontaneous succession from managed semi-natural grasslands to forest. If this interpretation is correct, it implies that there is an extinction debt in the present-day landscape, based on populations of grassland species that are following a trajectory towards extinction, albeit slowly. Our results also provide a trait-based mechanism for the delayed response of plant species distribution to ongoing landscape change.

Acknowledgements We are grateful to K. Hylander, J. Klimešová and two anonymous reviewers for comments on the manuscript, and to the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning for financial support.

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Received: 19 March 2009 / Revised: 28 December 2009 / Accepted: 1 February 2010 /
Published online: 11 September 2010