

Functional traits and remnant populations of plants in abandoned semi-natural grasslands

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Cover: To the left: a managed semi-natural grassland site. Photo by Mathias Öster. To the right: example of an abandoned grassland site, 50-100 years after management has ceased. Photo by Veronika Johansson

Abstract

Many studies on biodiversity have been concerned with semi-natural grasslands, as they are the main remnants of the traditional agricultural landscape in Scandinavia. Species richness in these habitats is threatened by extinction, as habitat area decreases and is fragmented.

However, development of remnant populations may cause a time delay in the extinction of species. Different functional traits may contribute to this population inertia. To identify and better understand remnant populations, this study focused on functional traits of plants and more in detail on a model species (*Primula veris*), believed to be capable of developing remnant populations.

Inventories performed on 26 sites, in the southern parts of Södermanland, Sweden, showed that about 20 % of the species typical for managed semi-natural grasslands, significantly decreased in frequency after management abandonment. When comparing declining and disappearing species, regenerative and life-form traits were of larger importance than leaf traits. Species that decrease in frequency rather than disappear, more often possess a perennial life-cycle, a perennial subterranean bud bank, have higher clonal abilities and more often unassisted seed dispersal. When analysing the response of declining species separately to different functional traits, results showed that clonal ability was higher amongst species that declined less in frequency.

Demographic studies from 30 patches of *P. veris* showed that larger proportions of large individuals can be expected at sites where grazing has been abandoned. This is consistent with lower population growth rates, indicating the presence of remnant populations. Both canopy cover and litter were correlated to the proportion of large individuals. Although determining which of these environmental factors is most important for stage distribution was prevented by a colinear relationship, canopy cover most likely is the most influential factor for *P. veris* populations.

The results suggest that a considerable fraction of species inhabiting semi-natural grasslands maintain what are most likely remnant populations after more than 50 years of abandonment. If this interpretation is correct, it implies that there is an extinction debt in the present-day landscape. The results also provide a trait-based mechanism for the delayed response of plant species distribution to ongoing landscape change.

Sammanfattning

Naturbetesmarker är de huvudsakliga resterna av det traditionella jordbrukslandskapet i Skandinavien och därför viktiga ur bevarandesynpunkt. Artrikedomen i dessa habitat riskerar att minska i och med att stora mängder av habitatet har förstörts och fragmenterats. Men det finns en möjlighet att bildandet av restpopulationer kan skjuta upp dessa utdöenden.

Inneboende funktionella egenskaper hos växter kan bidra till denna tröghet hos populationer. Den här studien är inriktad på dessa funktionella egenskaper hos växter och mer ingående på en modellart, gullviva (*Primula veris*), för att kunna identifiera och få en bättre förståelse om restpopulationer.

Inventeringar i 26 områden, i södra Södermanland, visade att minst ca 20 % av de arter som är typiska för hävdade gräsmarker minskar i förekomst när skötseln upphör. Jämförelser mellan arter som minskade eller försvann visade att regenerativa och livsform-egenskaper är viktigare än bladegenskaper. Arter som minskar i frekvens istället för att försvinna har oftare en perenn livscykel, en perenn underjordisk knoppbank, förmåga att klona sig och frön utan spridningsattribut. Analyser av de minskande arternas respons till olika funktionella egenskaper visade att förmågan till klonbildning var högst hos arter med lägst procentuell minskning.

Demografiska studier från 30 lokala populationer av *Primula veris*, visade att en större proportion av storväxta individer kan förväntas där hävden har övergivits. Det här hänger samman med lägre tillväxthastigheter, vilket kan indikera förekomsten av restpopulationer. Både krontäcket och mängden marktäckande vegetation visade sig korrelera med andelen storväxta individer. Vilken av dessa faktorer som är viktigast för storleksstrukturen kunde inte klarläggas. Det är dock troligast att krontäcket är mest betydelsefullt.

Resultaten av studien visar att en stor del av de arter som förekommer i naturbetesmarker finns kvar som vad som kan tolkas som troliga restpopulationer trots att habitatet övergivits för mer än 50 år sedan. Det här kan innebära att det finns en utdöendeskuld i dagens landskap. Resultaten bidrar också med en egenskapbaserad mekanism till växters långsamma respons till förändringar i landskapet.

Introduction

Destruction and fragmentation of natural habitats is one of the largest threats to existing biodiversity. When habitats are fragmented species are expected to be at a larger risk of local extinction due to, for example, demographic and environmental stochasticity (Lande 1993), inbreeding (Young et al. 1996), edge-effects (Murica 1995) and Allee-effects (Stephens and Sutherland 1999). At a landscape scale, increasing fragmentation also implies that species may have difficulty to reach suitable sites. Thus, colonization is expected to decrease. The results of these processes are a general decline in species richness, but it is unclear to what extent this occurs (Hanski 2000).

Many studies on biodiversity have been concerned with semi-natural grasslands, as they are the main remnants of the traditional agricultural landscape in Scandinavia (Cousins 2001). Semi-natural grasslands are among the most species-rich habitats in northern and central Europe (Eriksson et al. 1995, Pärtel et al. 1999). However, the species richness in these habitats is threatened as the area of the habitat decreases and is fragmented. Most of the grassland area has been lost in favour of arable fields and forests and the remaining semi-natural grasslands are mainly situated on shallow soils, less than 50 cm deep. These soils were not possible to cultivate, and afforestation (plantation) has therefore been avoided (Cousins 2001). Of the grasslands existing in the 19th century, there are only 10% left today (Bernes 1994). About 270 000 ha of semi-natural grasslands are still managed today (Persson 2005) and the remaining grasslands have been left for succession (Cousins et al. 2002).

Many grassland-species may currently occur in populations that are too small or isolated from other sites for long-term persistence. There may, however, be a time delay involved in the extinction of species, because of plant population inertia. Inherent traits of some plant species causing this inertia, like the ability of producing a seed bank or having a long-lived life-cycle, may buffer unfavourable environmental conditions and variability, causing a long time to species extinction even in declining populations. These plant species are thought to exist as remnant populations, that is to say populations that are decreasing ($\lambda < 1$), but remain in the landscape due to long-lived life-cycle stages (Eriksson 1996).

The general view of populations with low growth rates is that they have low levels of recruitment and hence consist mostly of adult individuals (Oostermeijer et al. 1996; Colling et al. 2002). An opposite pattern showing a population mainly consisting of small individuals does however not entirely exclude it from being a remnant population since different plant species have different traits and strategies. For example, remnant plants with a clonal life

cycle could still have a large amount of small vegetative plants despite a low recruitment and sexual reproduction (Warburton et al. 2000). To preserve energy in a suboptimal habitat, or as a strategy to avoid herbivores, plants also possess the capacity of shrinking in size. Previous 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. Annual plants in contrast, are strongly over-represented among species known to decline rapidly after cessation of grazing (Eriksson and Ehrlén 2001).

If remnant populations are widespread in the landscape they might be a contributing factor to the so called 'extinction debt' (sensu Tilman et al. 1994) and implies a future cost in terms of species extinctions. The concept extinction debt has its origin in the metapopulation theory (Levins 1969, Hanski 1999). In the case of the changing landscapes in northern Europe, where the most drastic changes have occurred during the last 50-60 years, the existence of an extinction debt would imply that the actual decline in species diversity will accelerate in the near future. Indirect evidence (Helm et al. 2006; Lindborg and Eriksson 2004) 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 extinction for many grassland species after abandonment of management. To examine whether extinction debts actually exist, we require either long-term data on species loss following habitat fragmentation (e.g. Helm et al. 2005) 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 contributing to an extinction debt (Vellend 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). Some species might pass their critical level, in terms of minimum available habitat, faster than others. Solé and Bascompte (2006) describe this

critical level, the extinction threshold, in a fragmented landscape as the amount of unoccupied patches at metapopulation equilibrium. Such an extinction threshold (Hanski and Ovaskainen 2002), implies that dispersal becomes so unlikely that it can not counterbalance extinctions of local populations, ultimately resulting in metapopulation extinction. This could lead to regional populations being doomed to extinction despite currently showing a positive growth rate at local sites.

Fragmentation and disturbance of demographic processes in habitats lead to a reduction in population sizes for many species. This reduction in population size is thought to exhibit altered population structure and since vital rates in plants are usually stage-dependent, the structure of a population may be indicative for its demographic future (Brys et al. 2003). A correlation between population size structure and population growth rates would imply that it is possible to use size structure as a measure of viability, where a large proportion of adult individuals are consistent with a decreased growth rate, like for remnant populations.

Identifying extinction debts and remnant populations in nature 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 when studying 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). Ignoring this could result in preservation of areas that in the long-run would be incapable in sustaining biodiversity and threatened species.

The objectives of this study were (i) to investigate and quantify the abundance of remnant populations of plants in abandoned semi-natural grasslands by studying decreasing species that persist despite a changing habitat, (ii) to examine if there are any distinctive functional traits of plants contributing to the development of remnant populations, and finally (iii) to study the population dynamics of a model species, *Primula veris*, using available demographic data, with respect to remnant dynamics in relation to succession.

Methods

Abundance of remnant populations in abandoned semi-natural grasslands and functional trait analyses

Study area and regional history

The study was conducted in the parishes of Lid and Ludgo in the County of Södermanland, ca 75 km SSW of Stockholm, Sweden (N 58° 55', E 17° 6'). The region was convenient for this study since it has a long history of management continuity and a well-built base of historical

maps. Maps of this kind may serve as an important source of information on the historical background of present-day vegetation patterns (Cousins 2001).

There are grasslands in this area that with certainty have been managed since late Iron Age (Viking Age; J. Berg, pers.com). There was an increasing permanency of arable fields during this time and the traditional management of grasslands by collecting winter-fodder became more common (Cousins 2001). The Viking age locations of farms can also be verified by name-settings, grave fields, and rune-stones. It is believed that the cultural landscape in southern Sweden to a large extent was established during this time and that the oldest historical maps depict to a large extent this early grassland distribution (Widgren 1983). Human settlement in the area can be traced back as far as to the Bronze Age (1700 BC – 500 BC), mainly by remnant grave cairns, but it is however unclear whether settlements and grasslands were permanent during this time (J. Berg, pers.com).

Geographical analysis

A large proportion of the semi-natural grasslands in Sweden was abandoned during the past 100-150 years and the study region was not excluded from this process. To be able to study the effect of ceased management on plants, I compared inventories of semi-natural grasslands still open and grazed with areas with grasslands abandoned during the 20th century. Sites were selected by analysing historical maps from the 18th century (skifteskartor), 1901 (häradskartan) and aerial photographs from the 1950s (cadastral maps), 1980s (infra-red) and 2003 (black and white). Abandoned sites and reference areas (managed semi-natural grasslands) were divided into two categories: areas previously used as outlands (e.g. grazed forests; $N_{\text{abandoned}}=10$ and $N_{\text{managed}}=3$) and areas that had remained more open (e.g. meadows and pastures; $N_{\text{abandoned}}=10$, $N_{\text{abandoned}}=3$). Since most of the changes in management have occurred during the last 100-150 years, I did not expect to find any significant differences between areas managed during 18th and 19th centuries. For that reason I used the time-layer from the 19th century as a starting point. Maps from the 18th century were however used, since they are more detailed and in some ways more reliable when it comes to the presence of meadows and pastures (S.A.O. Cousins, pers.com). These types of habitats were not considered as important for taxation when making the 19th century maps, in contrast to e.g. arable fields. Consequently low-productive areas were often classified as grazed forest or residual properties on these maps. Aerial photographs (infra-red, and black and white) were mostly used to exclude plantations, restorations and wetter areas, since these areas would differ too much from the study habitat (Fig. 1). 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).

The different categories were however combined to one group of abandoned areas (n=20) and one group of reference areas (n=6), since no difference in species richness could be found between them ($P_{\text{abandoned}}=0.46$; $P_{\text{reference}}=0.44$; see Appendix 1A for coordinates). All sites were located within 100 km². The size range of the sites was 1.87 - 8.52 hectares for the reference sites, and 0.25 - 4.05 hectares for the abandoned sites. All geographical analyses were performed in Arcview GIS 3.2.

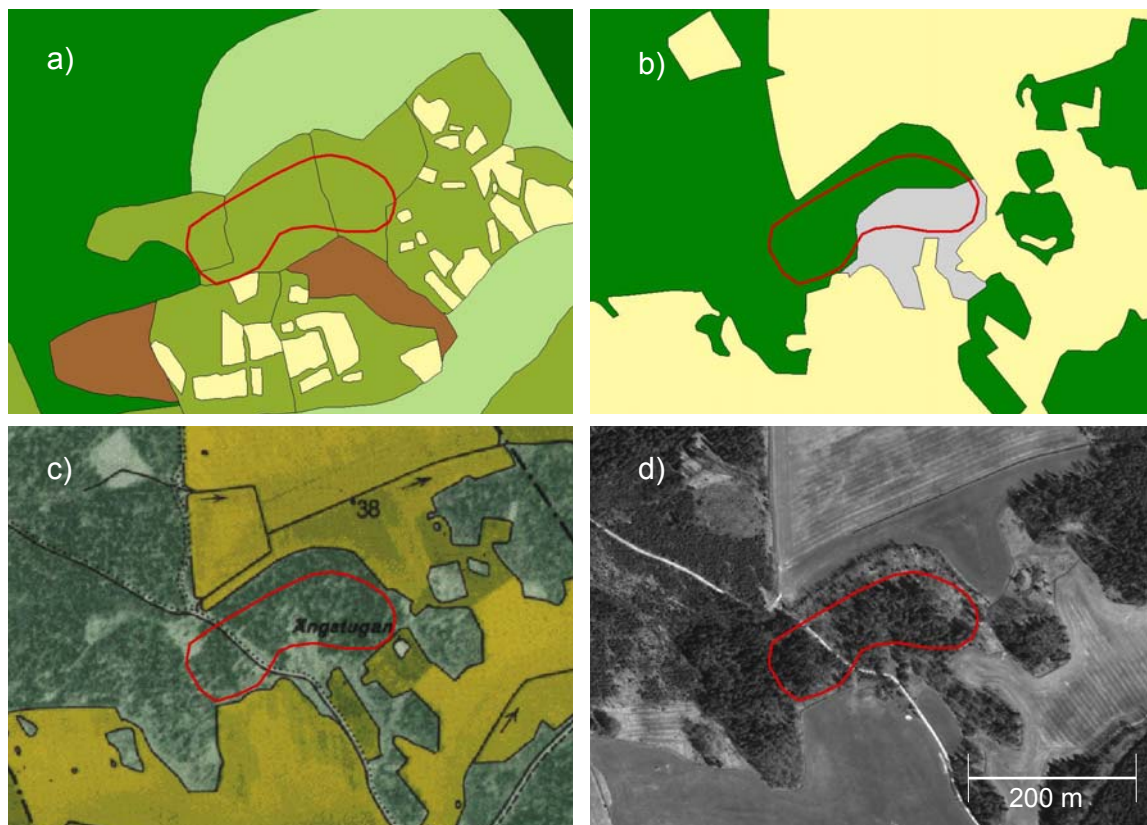


Figure 1. Example of an abandoned grassland site, Ängsstugan (marked with red; N 58° 55' 22.34", E 17° 0' 29.97"). The different time layers are represented by: a) cadastral map from 1750s, where the site consists of grazed pasture only and is mostly surrounded by meadows (light green), b) cadastral map from 1901 (häradskartan), where the site consists of grazed forest (dark green) and 'left-over' land (grey), mostly surrounded by arable fields (yellow), c) cadastral map from 1950s, and d) black and white orthophoto taken 2003.

Field survey and plant trait analysis

For each site, I inventoried ten 1 m² plots to obtain frequency data for the species. The plots were distributed over two transects per site. The first transect were placed across the longest section, including six m² plots and the remaining four m² plots were placed on the other

transect, perpendicular to the first. Plots were evenly distributed across the transects with the distance between them depending on the size of the site. Total inventories were performed at each site by walking through the area, noting additional species found. In total, 274 species were recorded. In addition to species richness of the two categories of sites, managed and abandoned semi-natural grassland (now forest), I calculated Jaccard index. The Jaccard index measures similarity between sample sets, and is defined as the ratio of the intersection to the union of the sample sets.

The different species recorded were assigned to four different categories, based on their response when the habitat was abandoned: increasing, constant, decreasing and disappearing. By performing χ^2 -tests on the frequencies of the recorded species in the abandoned and managed semi-natural grasslands, respectively, species could be assigned to the different response categories. This interpretation was based on a space-for-time substitution. I assume that managed sites represent the state of the now abandoned sites, as it was 50-100 years ago. A minimum criterion was used to sort out uncharacteristic and rare species. To be included in the analysis a species had to be recorded in at least five square meter plots of the managed semi-natural grasslands. This resulted in 67 species of which 2 increased, 17 stayed the same (no significant change), 44 decreased and 4 disappeared (table 1). The latter two categories are those of most interest when studying remnant populations and extinction debts. By analysing the response of these species and their relationship to different functional traits, it may be possible to characterize abilities contributing to the development of remnant populations.

Leaf properties, regenerative ability and life form traits were considered in these analyses, including: 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 characteristics. Information on SLA (m^2/kg) and seed mass (mg) was taken from the Swedish VISTA database (H. Quested and O. Eriksson, unpublished data). Information on LDMC (mg/g) was provided by B. Martéinsdóttir and M. Öster (unpublished data). The dispersal strategy was divided into two categories in the analyses. Those with an unassisted type of dispersal (but including myrmecochory) and those with dispersal attributes, e.g. pappus (including wind dispersal, exo-zoochory and endo-zoochory). Data on dispersal was taken from the Swedish VISTA database (Helene Quested and O. Eriksson, unpublished data).

Data on clonal ability was used in two ways: as a dichotomy, possessing or not possessing clonal abilities, and as a clonal index. The clonal index was created by adding estimates of the

amount of shoots produced per parent with an estimate of the capacity of lateral spread (m/year). Information on amount of offspring produced and lateral spread capacities was taken from the CLO-PLA 3 database (Klimeš and Klimešová 2006, Klimeš and Klimešová 2008). Ranging from 0-3 the first estimate was assigned to four different categories of offspring produced (0, 1, 2-10 and >10), where the largest amount of offspring produced per parent (>10) was represented with the highest estimate value (3) and vice versa. Three different categories of lateral spread (0-<0.01, 0.01-0.25, >0.25) was assigned in the same way, with values ranging from 0-2. 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 deserve a higher clonal index. If a species possessed more than one of these categories its final clonal index was the sum of estimates for all CGO's.

The information on the ability for each species to produce a perennial subterranean bud bank was also attained from CLO-PLA 3 database. If a species had been shown to produce buds below or at soil surface and if the bud bank for these soil-layers in some study had been found to be perennial instead of seasonal, the species was classified as having a perennial subterranean bud bank. Data on mean plant height (m) was taken from the Swedish VISTA database (Helene Quested and O. Eriksson, unpublished data). 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 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 the traits of the significantly declining species with species disappearing when the habitat is abandoned, and secondly, by correlating the amount of decrease in the declining species with the different functional traits. But since only four species were recorded as locally disappearing, the category of disappearing species was complemented by including species known to rapidly decrease in an early stage of succession (Ekstam and Forshed 1992). To be selected these species had to be present at a regional scale in the study area and be typical for the habitat (dry-mesic grasslands).

To examine the effect of SLA, LDMC, seed mass, and mean plant height on species declining or disappearing, logistic regressions were performed. Dispersal strategy, clonal ability,

perennial subterranean bud bank production, leaf distribution and life-cycle traits were analysed with Pearson's χ^2 -test.

For all the significantly decreasing species the extent of decrease was calculated using mean values from the different site categories. Regression analyses were performed to examine the relationships between decrease and SLA, LDMC, seed mass and plant height. Analyses of variance (ANOVA) were used to examine how the decreasing species respond to dispersal strategy, perennial subterranean bud bank production, leaf distribution and life-cycle traits. The effect of clonal ability was examined with Spearman rank correlation test using the clonal index.

Population dynamics of Primula veris

Study species and sample sites

Primula veris, Cowslip (Primulaceae), is an herbaceous perennial plant with a basal rosette of leaves. Individual plants may live for several decades (Inghe and Tamm 1988). *Primula veris* has one or a few inflorescences that emerge during spring. Each stalk usually has 5-10 yellow flowers, which open synchronously in May. Flowering continues for 2-3 weeks, and the seeds ripen in late July and August. Seeds are relatively small (mean seed mass \pm SE, 0.86 ± 0.044 mg) and lack adaptations for long-distance dispersal (Ehrlén et al. 2005). *Primula veris* is self-incompatible and the flowers are distylous, making them particularly sensitive to pollen limitation and genetic deterioration in small populations (Husband and Schemske 1996). Seed predation is common in some populations (Leimu et al. 2002). The main predators are larvae of the plume moth, *Amblyptilia punctidactyla* (Pterophoridae; Lehtilä et al. 2006), which lay their eggs in the inflorescence during flowering. After feeding from the developing seeds the full-grown larvae leave through characteristic exit holes in the fruit. The main distribution area of *P. veris* is the temperate zone of central and eastern Europe (Hultén and Fries 1986). The species was once a common grassland herb, but has become rare in many regions of its original distribution area as a consequence of changed land-use practices (Brys et al. 2003). It is however capable of persisting at many sites several decades after management has ceased (Ehrlén et al. 2005). Previous studies of *P. veris* have shown that plant demography varies with canopy cover (Lehtilä et al. 2006) and that population growth rates (λ) decreases with increased canopy cover (Kolb et al. 2007) and litter accumulation (Ehrlén et al. 2005). The study was conducted at two different locations during seed ripening in late August. Patches that were found suitable during the inventories in Aspa (n=7) were supplemented by previously known patches near Tullgarn, ca 60 km south of Stockholm, Sweden (N 58° 56', E

17° 34' ; n=23), used in present research (Kolb et al. 2007). Both areas have similar land use history (see above).

Field survey and data analysis

A total of 30 patches of *P.veris* were selected to represent a gradient in canopy cover from open grasslands to closed forests (see Appendix 1B for coordinates). A patch was defined as a group of plants located in an area that was homogenous in light environment and structure of the field layer vegetation (Kolb et al. 2007). For each patch, I recorded population structure in terms of total number of flowering individuals, proportion of flowering individuals and width and length of the largest leaf for 50 randomly selected individuals. In addition, data on the number of intact, preyed and aborted fruits were collected from at least 20 flowering individuals per patch. Supplementary flowering individuals were added beside the 50 randomly selected plants, if these did not include 20 flowering individuals. Length or width of leaves that had been exposed to herbivory or of other reasons were hard to measure, were estimated by dividing or multiplying the length or width, respectively, of a preyed leaf with the mean deviation of the length and width of all leaves within the same patch. This was possible since there is a significant positive relationship between length and width of leaves of *P. veris* ($r=0.93$, $p<0.001$). In some patches rosette leaves were sometimes dried and decomposed and instead new leaves had developed in some plants. To get more accurate measures of these leaves, I used the formula: $ol = nl * \overline{ol} / \overline{nl}$, where *ol* means old leaves and *nl*, new leaves (thereby assuming that the relationship between length and width is the same for older and newer leaves). These calculations were done separately for flowering and vegetative individuals.

To estimate canopy cover, upwards-directed photos were taken at five random locations within each patch with a digital camera at 50 cm height above ground (Kolb et al. 2007). The percentage of canopy cover was calculated using the analysis tool Image J 1.40 (Rasband 2002) and was expressed as the mean cover of all photos taken in each patch. Vegetation samples were collected from four 0.25m² plots in each patch to get an estimate of the amount of litter in the coming year. No moss or tree leaves were included. The samples were dried in 60°C for 1-2 days, weighed and calculated as the mean desiccated litter per plot.

Observed population size structure

The size limit between 'small' and 'large plants' was defined as the threshold plant size (leaf length) for reproduction. By using the function for logistic regression,

$$\log it(pf) = \frac{pf}{1-pf} = a + bx$$

where a is the intercept, b the slope of the curve and pf the probability of flowering, threshold sizes (mm), x , could be calculated by setting the probability of flowering to 0.05. Threshold values were calculated separately for each patch, because plants of closed habitats had large shade leaves and plants of open habitats had smaller and thicker sun leaves (Lehtilä et al. 2006). For patches with a non-significant relationship, the value from a logistic regression of all patches combined was used. Individuals with a leaf longer than the threshold value were categorized as large.

Predicted population size structure

To create transition matrices it is necessary to conduct a survey for several, or at least two, years. Since this study only includes data collected during one year, I used data from Kolb et al. (2007), where vital rates of *P. veris* were expressed as linear functions of canopy cover (see Appendix 4), to construct stage-structured transition matrices for each patch based on the estimated values of canopy cover. Individuals were assigned to six life-cycle stages: (1) seeds in the seed bank; (2) seedlings; (3-5) small, intermediate and large vegetative individuals; and (6) flowering individuals. Matrix elements were calculated according to combinations of vital rates derived from Kolb et al. (2007; see Appendix 5). Vital rates significantly related to canopy cover ($p < 0.1$) were multiplied with the mean value canopy cover calculated for each patch, respectively. A constant mean fruit predation value ($=0.2$) was used in the calculations of the transitions from flowering to seeds and seedlings.

Stable stage size distributions and growth rates (λ) were calculated for each patch using Excel (macro created by K. Lehtilä). The proportion large individuals in the stable stage distribution was calculated as (large vegetative + flowering individuals) / (vegetative (3-5) + flowering individuals). To obtain the proportion flowering individuals, the stable stage value for flowering individuals were divided with the sum of large and flowering individuals. Seeds and seedlings were excluded from the study since no data was collected on these stages.

Regression analysis was performed to investigate the relationship between observed population size structure and the predicted stable stage structure obtained from the functions of canopy cover. Stage distributions were also tested against environmental variables.

Multiple regression analysis was performed to determine the most important environmental factor (canopy cover or amount of litter) for stage distribution patterns. All statistical analyses were conducted in freeware R 2.7.2 (R Development Core Team 2008).

Results

(i) Quantifying remnant populations at local sites

A total of 274 species were recorded in the study region. Of these species, 221 were found in the managed semi-natural grassland and 229 in the abandoned semi-natural grasslands all together, this leaving 45 species unique for managed semi-natural grasslands and 53 species unique for abandoned sites (see Appendix 2 for species list). The species densities of managed semi-natural grassland sites were larger than for abandoned grasslands, with a mean of 25 species per m² plot (S.D. = 6.2, range 12-40). Abandoned grassland sites had a mean of 14 species per plot (S.D. = 4.8, range 5 -28). The Jaccard index calculations resulted in managed semi-natural grassland sites having the largest mean percent of similarity between sample-sets (54%). The similarity among abandoned semi-natural grassland sites was lower, 44% and comparing abandoned with managed semi-natural grasslands resulted in a mean similarity of 40 % (see Appendix 3 for details).

The 67 species that fulfilled the criterion to be selected for further analysis (present in at least five square meter plots in managed sites) are listed in table 1A. Species marked as significantly declining (-) or locally disappearing (†) are used in the analyses and are hence the ones that are most likely to develop remnant populations. The rapidly decreasing species selected from Ekstam and Forshed (1992) are listed in table 1B.

(ii) Functional plant trait analysis

Comparison between declining and disappearing species

The results indicated that regenerative- and life form traits, rather than leaf traits, were associated to whether a species decline in frequency or disappear locally when the grassland habitat is abandoned (overview in table 2). Logistic regression analyses examining the effect of SLA and LDMC gave no significant results. The analysis of different life cycle traits suggested that a much larger fraction of species with annual or biennial life cycle disappear (Fig. 2a). Most perennial species (ca 70%) are declining instead of disappearing. Results for other life form traits showed that species with larger plant mean heights are less likely to disappear (Fig. 2b). This is however more likely an effect of life cycle, since perennial species more often have larger plants (Fig. 3). The distribution of leafs was not associated with species response.

Table 1 A. List of species analysed with regard to their response to abandonment of management semi-natural grasslands: ‘-‘ declined in frequency, ‘+’ increased in frequency, ‘n.s.’ no significant change, ‘†’ disappeared. The percentage of decrease for the declining species, calculated from frequency data. P-values are calculated by χ^2 -analyses.

Species	Response to habitat change	Decrease (%)	P-value
<i>Achillea millefolium</i>	-	60.4	<0.001
<i>Agrostis capillaris</i>	-	56.7	<0.001
<i>Ajuga pyramidalis</i>	n.s.		0.111
<i>Alchemilla glaucescens</i>	-	98.0	<0.001
<i>Anthoxanthum odoratum</i>	-	73.1	<0.001
<i>Anthriscus sylvestris</i>	n.s.		0.0735
<i>Briza media</i>	†		<0.001
<i>Campanula persicifolia</i>	n.s.		0.358
<i>Campanula rotundifolia</i>	-	43.3	0.0430
<i>Carex caryophylla</i>	n.s.		0.256
<i>Carex leporina</i>	-	87.1	0.00133
<i>Carex pallescens</i>	-	95.0	<0.001
<i>Carex panicea</i>	†		<0.001
<i>Carex spicata</i>	-	77.5	0.00537
<i>Centaurea jacea</i>	-	94.0	<0.001
<i>Cerastium fontanum</i>	-	87.1	<0.001
<i>Dactylis glomerata</i>	+		0.0109
<i>Danthonia decumbens</i>	-	96.5	<0.001
<i>Deschampsia cespitosa</i>	-	63.0	<0.001
<i>Deschampsia flexuosa</i>	+		<0.001
<i>Festuca ovina</i>	-	38.6	<0.001
<i>Festuca pratensis</i>	-	78.3	<0.001
<i>Festuca rubra</i>	-	88.9	<0.001
<i>Filipendula vulgaris</i>	-	72.7	<0.001
<i>Fragaria vesca</i>	n.s.		0.395
<i>Galium boreale</i>	n.s.		0.880
<i>Galium uliginosum</i>	-	98.0	<0.001
<i>Galium verum</i>	-	57.6	<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 sect. 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>	-	81.7	<0.001
<i>Leontodon autumnalis</i>	†		<0.001
<i>Leucanthemum vulgare</i>	-	67.5	0.00422
<i>Lotus corniculatus</i>	-	97.9	<0.001
<i>Luzula campestris</i>	-	97.6	<0.001
<i>Melampyrum pratense</i>	n.s.		0.706
<i>Phleum pratense</i>	-	65.9	<0.001
<i>Pilosella officinarum</i>	-	92.9	<0.001
<i>Pimpinella saxifraga</i>	-	57.0	<0.001
<i>Plantago lanceolata</i>	-	99.2	<0.001
<i>Poa pratensis</i>	n.s.		0.185
<i>Polygala vulgaris</i>	-	94.5	<0.001
<i>Potentilla erecta</i>	-	93.3	<0.001
<i>Primula veris</i>	n.s.		0.372
<i>Prunella vulgaris</i>	-	85.0	<0.001
<i>Ranunculus acris</i>	-	54.7	<0.001
<i>Ranunculus auricomus</i>	-	90.0	<0.001
<i>Ranunculus polyanthemus</i>	n.s.		0.131
<i>Rhinanthus minor</i>	-	97.7	<0.001
<i>Rumex acetosa</i>	-	83.3	<0.001
<i>Saxifraga granulata</i>	†		<0.001
<i>Stellaria graminea</i>	-	74.4	<0.001
<i>Succisa pratensis</i>	-	95.0	<0.001
<i>Taraxacum sect. Ruderalia</i>	-	58.0	0.00140
<i>Trifolium medium</i>	-	36.3	0.0108
<i>Trifolium pratense</i>	-	92.9	<0.001
<i>Trifolium repens</i>	-	84.6	<0.001
<i>Veronica chamaedrys</i>	-	57.1	<0.001
<i>Veronica officinalis</i>	-	70.0	<0.001
<i>Veronica serpyllifolia</i>	-	91.4	<0.001
<i>Vicia cracca</i>	-	82.0	<0.001
<i>Viola canina</i>	-	85.0	<0.001

Significance codes: *** 0.001, ** 0.01, * 0.05, (*) 0.1

Table 1 B. Species added to the category “disappearing”, as they are known to rapidly decrease in an early stage of succession after abandonment of grassland management (Ekstam and Forshed 1992). ‘*’ recorded during site inventory.

Species	
<i>Antennaria dioica</i> *	<i>Matricaria matricarioides</i>
<i>Arabis thaliana</i> *	<i>Myosotis discolor</i>
<i>Arenaria serpyllifolia</i> *	<i>Myosotis ramosissima</i>
<i>Bellis perennis</i>	<i>Myosotis stricta</i>
<i>Botrychium lunaria</i>	<i>Pilosella lactucella</i> *
<i>Bromus hordeaceus</i> *	<i>Plantago major</i> *
<i>Capsella bursa-pastoris</i> *	<i>Poa annua</i> *
<i>Carex pilulifera</i> *	<i>Poa supina</i> *
<i>Carlina vulgaris</i>	<i>Polygonum aviculare</i> *
<i>Cerastium semidecandrum</i>	<i>Potentilla cranzii</i>
<i>Cynosurus cristatus</i>	<i>Potentilla tabernaemontani</i> *
<i>Erophila verna</i> *	<i>Rhinanthus serotinus</i>
<i>Euphrasia rostkoviana ssp. Fennica</i>	<i>Satureja acinos</i>
<i>Euphrasia stricta</i>	<i>Scleranthus annuus</i> *
<i>Gagea minima</i>	<i>Taraxacum sect. Hamatum</i>
<i>Gentianella campestris</i>	<i>Taraxacum sect. Erythrosperma</i>
<i>Geranium pusillum</i> *	<i>Trifolium arvense</i> *
<i>Hypochoeris maculata</i> *	<i>Trifolium campestre</i>
<i>Jasione montana</i>	<i>Veronica verna</i>
<i>Linum catharticum</i>	<i>Vicia tetrasperma</i> *
<i>Lolium perenne</i> *	

Table 2. Effects of different functional traits on plant species, responding as either declining or disappearing after abandonment of grazing in semi-natural grasslands. Functional trait (x), probability value (P) and single predictor tests used for analyses.

Functional trait (x)	P-value	Statistical test
Leaf traits:		
SLA	0.310	Logistic regression
LDMC	0.856	Logistic regression
Life form/cycle traits:		
Plant height mean	0.00107	Logistic regression
Leaf distribution	0.195	Pearson χ^2 -test
Life cycle	<0.001	Pearson χ^2 -test
Regenerative traits:		
Seed mass	0.0658	Logistic regression
Dispersal strategy	0.0258	Pearson χ^2 -test
Clonal ability (yes/no)	0.00787	Pearson χ^2 -test
Perennial subterranean bud bank (yes/no)	<0.001	Pearson χ^2 -test
Significance codes: *** 0.001, ** 0.01, * 0.05, (*) 0.1		

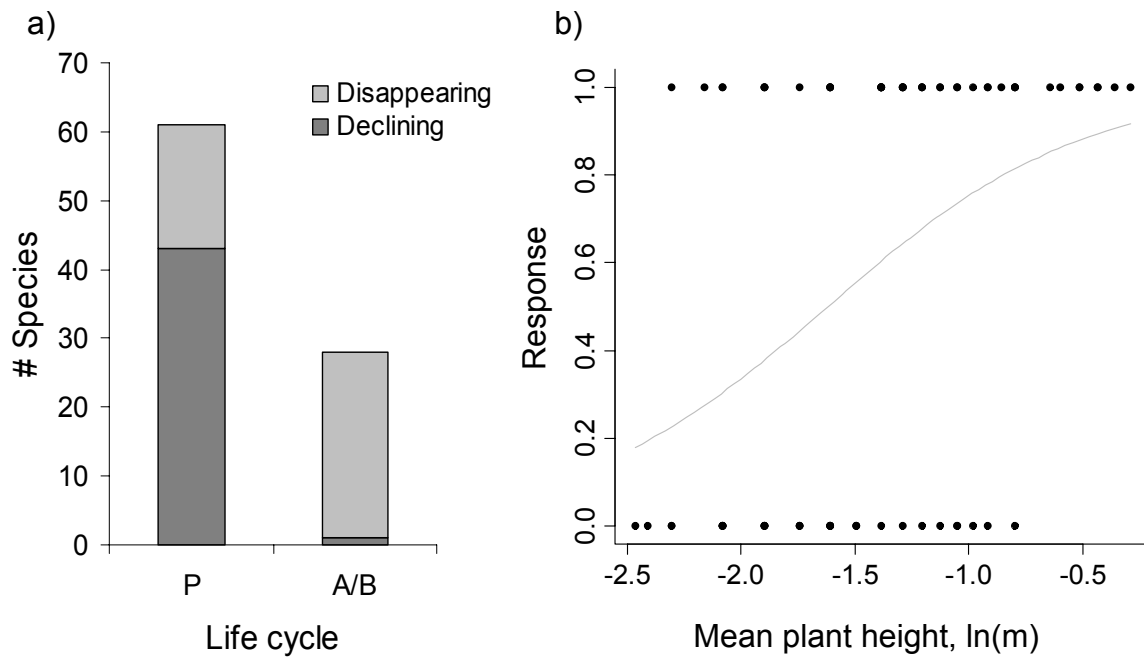


Figure 2. The relationship between plant species response (declining but still occurring vs. disappearing) to 50-100 years of abandonment of management in semi-natural grasslands in Sweden, and species traits: a) perennial vs. annual/biennial life cycle ($\chi^2 = 31.76$, $P < 0.001$), b) effect of plant height on the probability of decline but still occur (0=disappearing, 1= declining; logistic regression, $P = 0.00107$).

Table 3. Analysis of variance table: mean plant height (m) responding to (x), degrees of freedom (Df), (Sum Sq), (Mean Sq), F value and probability value (P).

Explanation (x)	Df	Sum Sq	Mean Sq	F value	P (>F)
Life cycle	1	0.23823	0.23823	11.204	0.00129

Significance codes: *** 0.001, ** 0.01, * 0.05, (*) 0.1

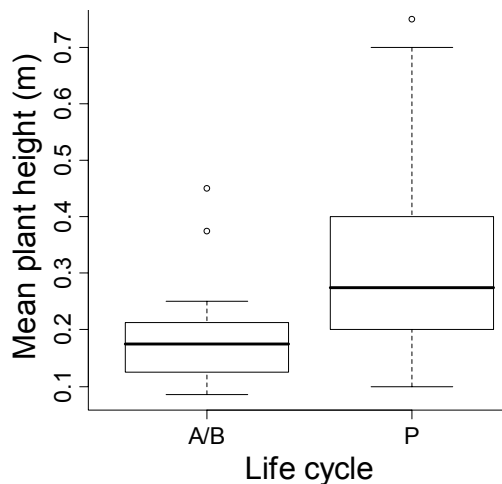


Figure 3. Relationship between annual/biennial or perennial life cycle and mean plant height (ANOVA, $P = 0.00129$).

Possessing clonal abilities or a perennial subterranean bud bank was significantly more common among declining species than among those rapidly disappearing (Fig. 4a & b). Species responses to seed mass were marginally significant, which might indicate a trend benefiting species with larger seeds. Results also showed that disappearing species more frequently possessed attributes for seed dispersal facilitating long distance dispersal (Fig. 4c).

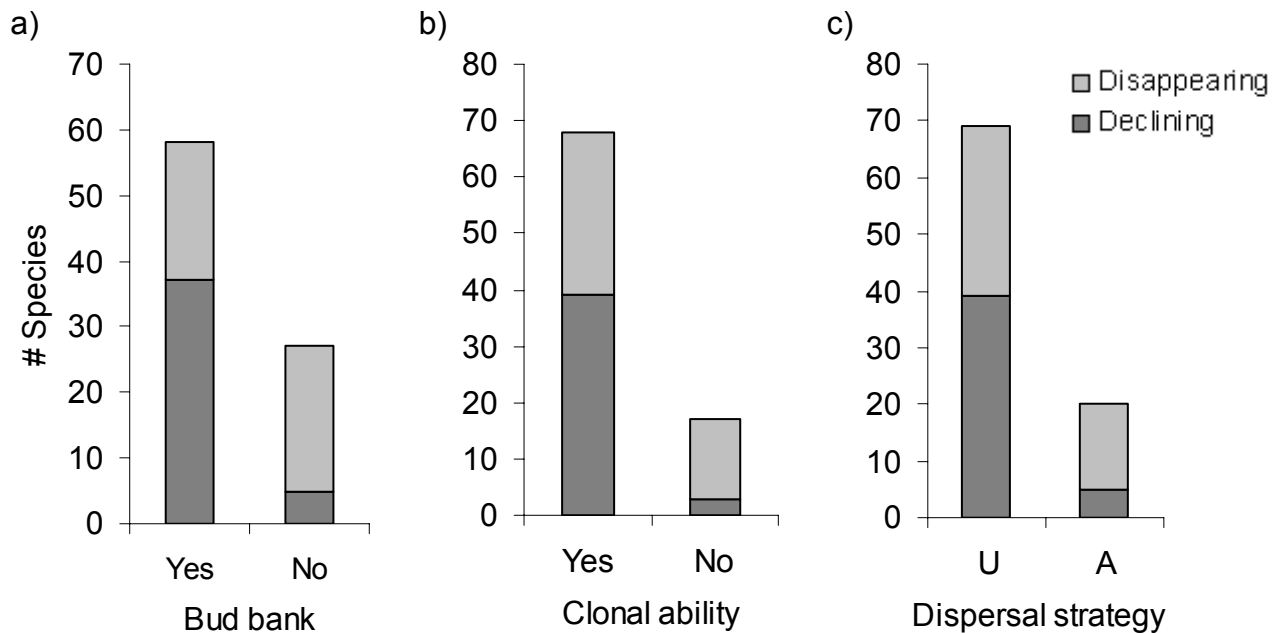


Figure 4. The relationship between plant species response (declining but still occurring vs. disappearing) to 50-100 years of abandonment of management in semi-natural grasslands in Sweden, and species traits: a) Possession of a perennial subterranean bud bank ($\chi^2=13.35$, $P<0.001$), b) Possession of clonal ability ($\chi^2=7.06$, $P<0.01$), c) Possession of attributes promoting long-distance seed dispersal (unassisted, U, including myrmecochory or with attributes, A, including wind dispersal, exo-zoochory and endo-zoochory), ($\chi^2=4.97$, $P=0.0258$).

Functional traits and declining species

The results of the analyses examining the relationship between different functional traits and the decrease in frequency (%) of species after grassland abandonment showed significant effects only for clonal ability (overview in table 4). Spearman rank correlation test showed that species with a greater ability to produce clonal offspring were decreasing less in frequency than species with a more limited clonal ability (Fig. 4). The correlation between mean plant height and amount of decrease was marginally significant, where larger plants decreased less in frequency. The other traits, SLA, LDMC, leaf distribution, life cycle, seed

mass, dispersal strategy and bud bank production, were not related to the extent of decrease in species frequency after grassland abandonment.

Analysis of variance between the percentage of decrease and life cycle characteristics was not applicable since only one of the decreasing species had an annual/biennial life cycle.

Table 4. Overview of results and analyses used for examining the relationship between the extent of decrease in frequency and different functional traits. Functional trait (x), probability value (P), least squares estimates (r^2) and single predictor tests used for analyses. Note: the amount of decrease has been arcsine square root transformed in the analyses.

Functional trait (x)	P-value	r^2	Statistical test
Leaf traits:			
SLA	0.759		Linear regression
LDMC	0.294		Linear regression
Life form/cycle traits:			
Plant height mean	0.0685	0.0768	Linear regression
Leaf distribution	0.677		ANOVA
Life cycle	n.a.		ANOVA
Regenerative traits:			
Seed mass	0.18		Linear regression
Dispersal strategy	0.492		ANOVA
Clonal ability	0.0487		Spearman rank correlation test
Perennial subterranean bud bank	0.112		ANOVA

Significance codes: *** 0.001, ** 0.01, * 0.05, (*) 0.1, n.a: not applicable

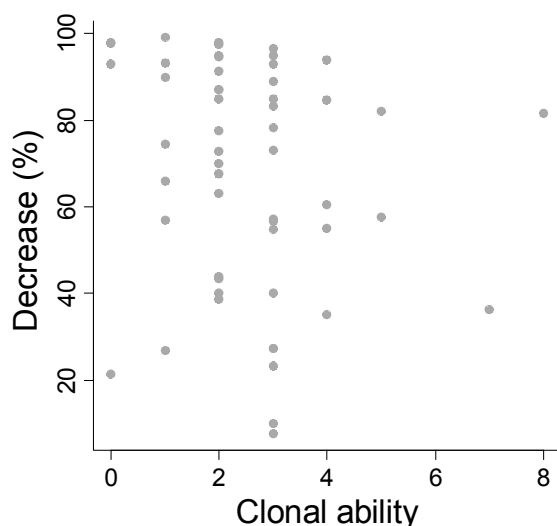


Figure 4. The relationship between plant species decline after 50-100 years of abandonment of management in semi-natural grasslands in Sweden, and clonal ability measured as an index based on number of clonal propagules produces per year and lateral spread (see text for an explanation; $\rho=-0.306$, $P=0.0487$).

(iii) *Primula veris*

Linear regression showed a positive correlation between the proportions of large individuals, recorded during the field survey, and the proportion of large individuals predicted (Fig. 5a). Analysing flowering individuals separately, gave no significant relationship (Fig. 5b). The predicted proportion large individuals were negatively correlated with growth rate (Fig. 6a). This relationship and the correlation between predicted and observed proportion large individuals leads to the expectation that there is a similar negative relationship between the observed proportion large individuals and growth rate. Larger proportion of observed large individuals was in turn correlated with lower population growth rates (Fig. 6b), which may indicate the presence of remnant populations.

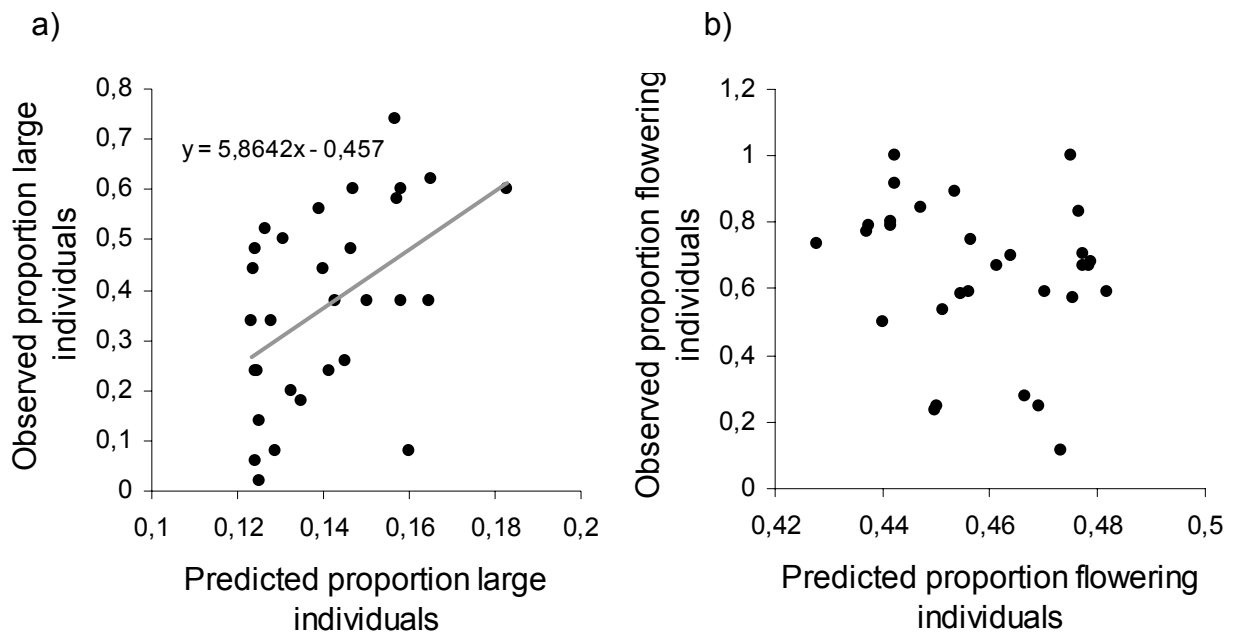


Figure 5. a) The linear relationship between the proportions of large individuals (flowering included) and the proportions of large individuals at stable stage in *Primula veris* ($P=0.00632$, $r^2=0.2101$), b) the relationship between the proportions of flowering individuals extracted from stable stage matrices and the proportion flowering individuals observed during the field survey ($P= 0.254$).

Amount of litter and canopy cover, both had an effect on the observed proportion of large individuals. The correlation between proportions of large individuals and mean dry weight litter show that the more litter that is produced, the fewer larger individuals was found (Fig 7a). There was a larger proportion of large individuals at higher canopy cover (Fig. 7b). These results indicate that the stage structure distribution of *P. veris* is either determined by canopy cover directly, or by canopy cover acting via the amount of litter.

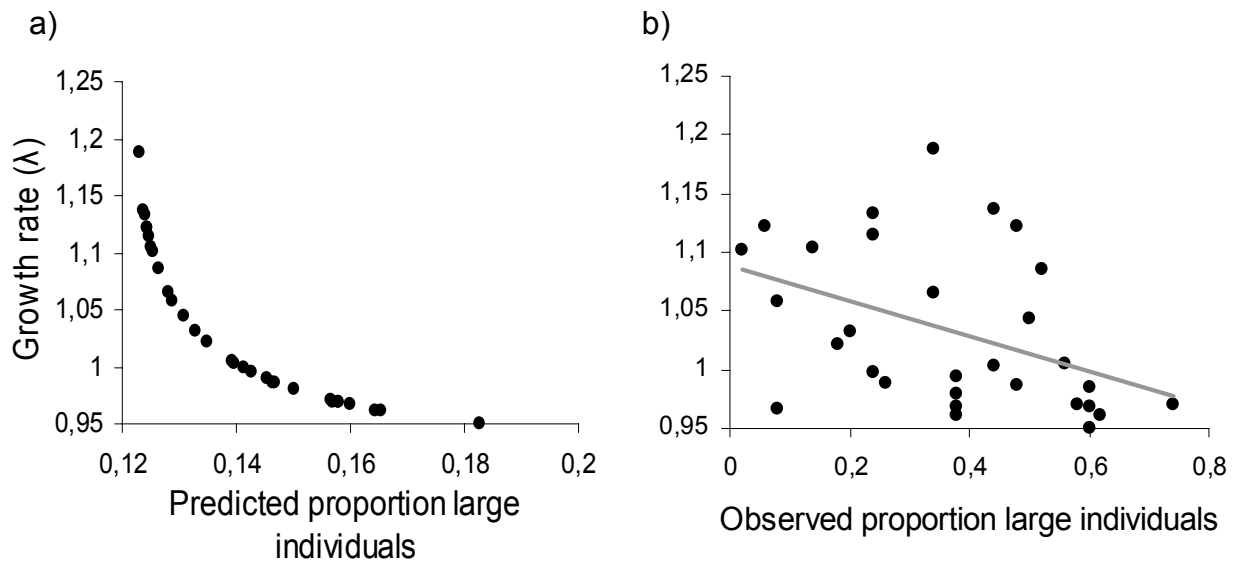


Figure 6. The linear relationship between a) predicted proportion large individuals and growth rate (λ) in *Primula veris* ($P < 0.001$, $r^2 = 0.77$), b) observed proportion large individuals and growth rate (λ) in *Primula veris* ($P = 0.0198$, $r^2 = 0.179$).

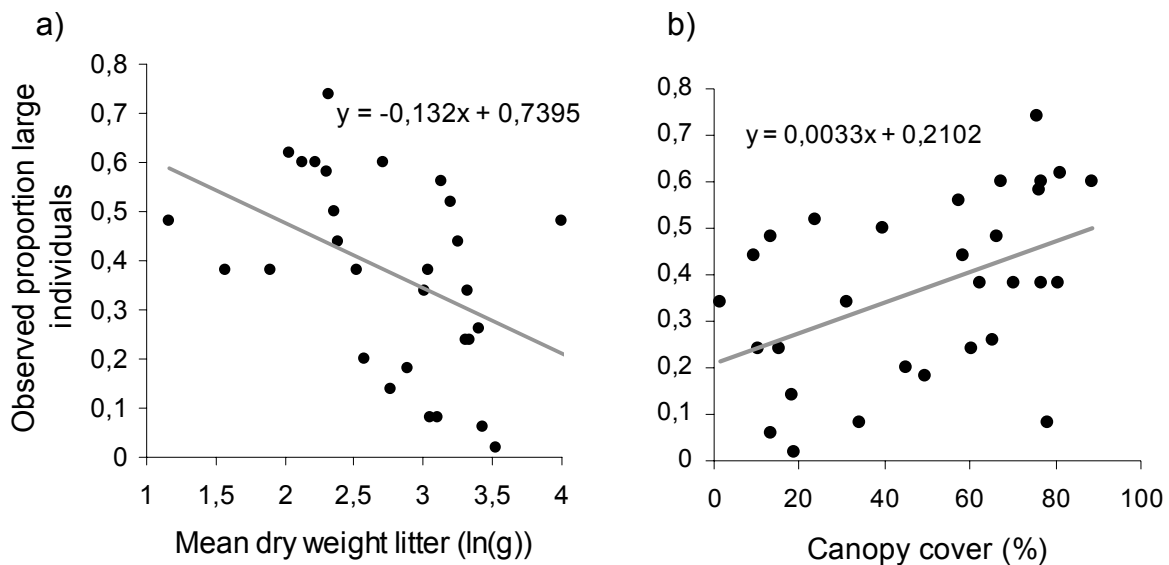


Figure 7. The linear relationship between the proportions of large individuals in *Primula veris* and: a) the mean dry weight litter (ground vegetation; $P = 0.0101$, $r^2 = 0.214$), and b) the canopy cover (%), calculated as mean values for each patch ($P = 0.0138$, $r^2 = 0.198$).

The attempt to determine which environmental factor that was most important for stage distribution gave no significant results. Multiple regression analysis was incapable of separating the effects of canopy cover from the effects of the amount of litter. The strong

correlation between canopy cover and mean dry weight litter causes a collinear relationship because there is too little independent variation in the data (Fig. 8). This interaction-effect causes the model to get a significant value, while the separate variables are non-significant (table 5).

Table 5. Multiple regression model: the proportions of large individuals responding to (x), intercept (b), standard error (SE), (t) and probability values (P). Note: Canopy cover has been arcsine square root transformed. (P= 0.0220, $r^2= 0.246$).

Explanation (x)	b	SE	t	P
Mean dry weight litter, log(g)	-0.0852	0.06	-1.32	0.198
Canopy cover (%)	0.154	0.14	1.08	0.291

Significance codes: *** 0.001, ** 0.01, * 0.05, (*)

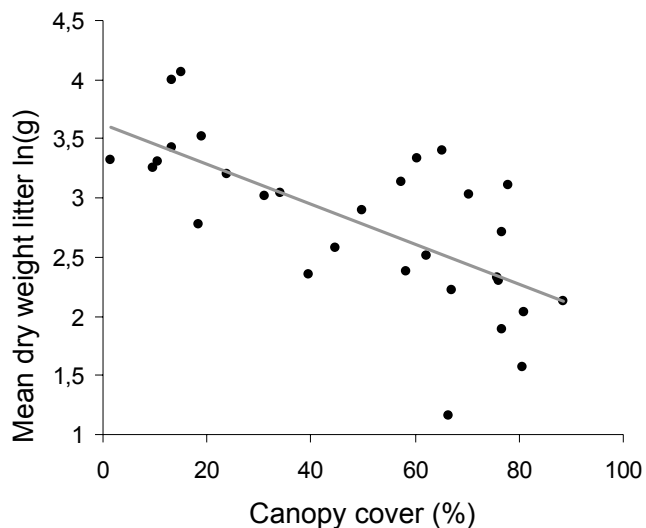


Figure 8. The linear relationship between canopy cover (%) and mean dry weight litter per patch in *Primula veris*, where a larger canopy coverage correlates with lesser amount of litter (ground vegetation; $P < 0.001$, $r^2 = 0.4539$).

Discussion

The abundance of remnant populations

The species diversity in the study area might be an effect of previous site area and connectivity to similar habitats. Lindborg (2007) showed in a study 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. 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 as well as the importance to study them. The first objective of this study was to investigate and quantify the presence of remnant populations in semi-natural grasslands. About 20 % (44 of 221) of the species found in the managed semi-natural grassland sites were significantly declining in frequency, but still occurred in the abandoned sites after 50-100 years without grazing management. It is however hard to determine whether species found decreasing in fact are remnant populations. A decrease in frequency does not necessarily imply a species having a negative growth rate, although it might indicate it. Demographic studies of each species would be necessary to be certain of this pattern. It is however reasonable to assume that species, typical for managed semi-natural grasslands, which are decreasing in frequency as a response to ceased grazing, but still present more than 50 years after abandonment of grazing, are those that develop remnant populations. There is also the possibility that species which show no signs of decreasing in frequency may develop remnant populations. Species like *Primula veris* and *Ajuga pyramidalis* might be examples of this. They show no significant decrease in frequency in response to changing habitats in this study, although they are suspected of developing remnant populations.

The results showed that abandoned sites had more ‘unique’ species. This can however be explained by managed sites being more similar than abandoned sites, as the Jaccard indices indicate. During a successional development it is common that at some period of change, species of the previous habitat coexist with successional species. Managed sites were more diverse at smaller scales, although it varied. Some managed sites might not have been of the highest quality. Another explanation could be that managed sites with lesser species diversity may be dispersal limited caused by isolation from other fragments, leading to lesser new colonisations.

Functional traits contribute to develop remnant populations

Plant life history traits have been recognized as important for structuring grassland plant communities. Different plants species are successful in different parts of the landscape, and respond differently to changes in habitat, because of a diversity of functional traits (Westoby et al. 2002). The second objective of this study was to examine if functional traits of grassland plants, associated with long term persistence, contribute to the development of remnant populations. For this analysis, the assumptions were that the 44 species identified as declining actually exist as remnant populations in the former, presently abandoned grasslands.

The overall conclusion is that regenerative and life-form traits are of larger importance than leaf traits.

Leaf traits 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 (Wetsoby et al 2002). In particular, the expectation was that they would respond to the changing light environment which accompanies abandonment of semi-natural grasslands. Both SLA and LDMC was included, 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). No patterns were however found in the analysis comparing leaf traits in declining and disappearing species, or in the analysis of declining species only. The measurements of SLA used in this study were performed on plants from managed semi-natural grasslands. Since SLA can be very variable between samples (Wilson et al. 1999) it would have been interesting to have measurements taken from plants in abandoned sites as well. Such data might be better estimates of the different species capacity to adjust to light environment. Data on both LDMC and SLA were deficient in some ways. Measurements of rarer species and some annual/biennial species were missing from the data set which may have affected the outcome of the analyses. 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 having higher SLA (lower LDMC) in competition of 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.

The capacity to develop remnant populations depends to a large extent on the occurrence of persistent life-cycle stages. The analyses show that perennial species more often decline in frequency in response to habitat change instead of disappearing completely, while most of the annual/biennial species disappear more rapidly. This is supported by a lot of studies showing that perennial species are those capable of developing remnant populations (e.g. Picó and

Riba 2002; Brys et al. 2003). The comparison between declining with disappearing species also showed that species with higher mean plant height were less likely of disappearing. This is possibly a result of benefits related to competition for light or an effect of life cycle, since there is a significant difference between being perennial or annual/biennial and mean plant height. Perennial plants are in general larger than annual/biennial species, which benefits perennial species when competing for light. The effect of plant height was marginally significant in the analysis of declining species only. This is however not an effect of life cycle since only one of the included species had an annual lifecycle. Instead it might suggest a trend towards perennial species with larger mean plant heights being less likely of decreasing in frequency in response to habitat change.

Regenerative traits including seed mass, dispersal strategy, clonal ability and bud bank properties, was the category of functional traits showing most significant differences in species responding as either disappearing or declining after grassland abandonment. The hypothesis was that for a species to sustain better in a changing landscape it would have larger seed size, unassisted dispersal, high clonal ability and a perennial subterranean bud bank. Studies have shown that woodland species often have larger seeds than species typical for grasslands (Salisbury 1942). Larger seeds have more available resources, making recruitment easier in suboptimal habitats. It is however often a trade-off between seed size and number of seeds produced (Jakobsson and Eriksson 2000). The analyses of the effect of seed size showed a marginal significance. This indicates that declining species may have larger seeds than those disappearing. When analysing declining species separately no relationship could however be found.

Furthermore, persistent species were more commonly lacking attributes favouring long distance dispersal, as compared to species which disappeared. Producing seeds with attributes requires a lot of resources which might not be well spent in a suboptimal habitat. On the other hand, possessing attributes benefiting long distance dispersal may be a way for species to colonize better suited habitats, although the chance is smaller in a fragmented landscape. Both exo and endo-zoochory is less likely to occur in un-grazed areas, and wind dispersal might be disadvantageous as the course of succession continues. The results showing a larger proportion of disappearing species having dispersal attributes was consequently expected. No difference was however found when analysing the declining species separately.

Clonal reproduction is often overlooked when considering dispersal in plants. It may be important for both survival and dispersal at larger regional scales in the long term (Eriksson and Ehrlén 2001) and hence important when studying remnant populations (Eriksson 2000). The results clearly show that clonal ability is most important for species to be able to sustain in response to grassland abandonment. This is reasonable since reproduction and recruitment decrease in most species in an unfavourable habitat. But even though clonality seems to be widespread amongst plants in semi-natural grasslands (ca 80 % of decreasing and disappearing species together), the overall clonal ability remains low (maximum index= 8 out of 15). The fact that a plant has a high clonal ability index does not necessarily imply that the plant grows clonally, but rather indicates the possibility of the species to do so. Some examples of perennial species that were found to possess high clonal ability and lower extents of decrease in frequency despite habitat alteration are *Trifolium medium*, *Ranunculus acris*, *Veronica chamaedrys*, *Galium verum* and *Achillea millefolium*. These species are all relatively common which supports the conclusion that they are developing remnant populations.

A large proportion of semi-natural grassland species would be expected to have a subterranean bud bank since this is a mean by which a species can survive disturbances like mowing or grazing. Having this trait may lead to a better persistence in a changing habitat, and thus a capability of developing remnant populations. Most perennial species possess a perennial subterranean bud bank, while annual and biennial species have seasonal bud banks, but there are exceptions. The results showed that a larger proportion of species disappear when lacking a perennial subterranean bud bank. There is no data on the possible time-period a perennial bud can lay dormant below ground. This would however be interesting to know since a longer dormancy would suggest a larger possibility for a species to overlap unfavourable environmental conditions. A 'short-lived' perennial subterranean bud bank could explain the relatively large proportion of species (ca 36 %) disappearing despite having a perennial subterranean bud bank.

Persistence in the seed bank also contributes to long-term survival, and would be interesting to include as a functional trait in this study. Persistence in the seed bank may be more important for annuals and biennials which lack the capacity of developing remnant populations. The data available concerning seed banks are however scarce and unreliable. Studies have shown that rare species are often under-represented in the seed bank compared

with their abundance in the vegetation (Bakker and Berendse 2001). Seed bank traits were therefore excluded from analysis.

Remnant populations of Primula veris and environmental factors

An alternative way to study remnant populations and estimate extinction rates of local populations is to use stochastic population modelling, based on short-term demographic data. This kind of analysis must however be viewed with caution, because the short-term variability in demographic parameters does not necessarily represent the variation that is relevant for longer time periods (Eriksson and Ehrlén 2001). But populations of *P. veris* situated in habitats with a higher canopy cover can be assumed to be remnants from earlier successional stages where recruitment was possible.

When studying the environmental variables, analysis showed that both canopy cover and the amount of litter accumulated on the ground, had an effect on the population size structure of *P. veris*. Survival of seedlings is favoured by litter and ground vegetation as well as a favourable light environment. Consequently, habitats with lower amounts of ground vegetation, and higher canopy cover, could be counted for as less suitable and more likely of showing remnant populations. These expectations correspond to the results obtained.

However, due to the strong co-linearity between canopy cover and amount of litter biomass, it was impossible to determine the impact of both factors separately on the proportion of large individuals. It is however reasonable to believe that the stage structure distribution of *P. veris* is determined by either canopy cover as the main direct effect, or by canopy cover acting on the amount of litter, which then in turn affects *P. veris*. A reverse pattern where the amounts of litter act on canopy cover is not likely.

Other environmental variables, e.g. pH and available nutrients in the ground that changes during the course of succession, might be interesting to include in future studies.

The results show that a larger proportion of adult individuals was observed in suboptimal habitats. Demographic models suggest that this might be due to a lack of new recruitment, leaving the already established individuals. This supports the idea that *P. veris* is capable of developing remnant populations, since a high number of adult individuals was associated with lower growth rates in population models.

In the analyses studying functional traits that contribute to the development of remnant populations, *P. veris* was, contrary to expectations, not found to be significantly decreasing in frequency as the habitat is abandoned. This could imply that *P. veris* does not develop

remnant populations, or it could be an effect of the wide range of habitats that *P. veris* can occupy. The optimal habitat for *P. veris* is early-middle successional patches. During the inventory of abandoned grasslands, most of the study sites were of this kind since older forests were excluded because of the likelihood of them not having the same history of management. Hence, selected patches used for the model species study better describe remnant populations of *P. veris* since these include forest-patches with high canopy cover. Populations can most likely persist for a long time because *P. veris* is a long lived species. Populations of *P. veris* may even be able to maintain themselves until environmental conditions improve (e.g., forest thinning, or occasional good years for recruitment).

Final remarks

Population extinction due to habitat deterioration 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, common perennials (Brys et al. 2005). The population dynamics of annual/biennial species, compared with perennial species, is often characterized by higher turnover rates, and the persistence of populations depends on frequent recruitment (Lindborg 2007). Annual and biennial species are therefore more vulnerable and respond more quickly to habitat fragmentation than perennial species. The 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. These results support the suggestion 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.

The results also provide a trait-based mechanism for the delayed response of plant species distribution to ongoing landscape change. They also suggest that a considerable fraction of the species inhabiting semi-natural grasslands maintain what are most likely remnant populations after more than 50 years of spontaneous succession from managed semi-natural grasslands to forests. 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, although slowly.

To examine extinction debts further it would however be necessary to study multiple regions with different land-use history. The fact that it takes so long for the extinction debt to be paid off, leaves an opportunity to prevent further local extinctions. Remnant populations may

contribute to avoidance of extinctions for some species, provided that further habitat deterioration does not take place. Nature conservation projects as well as land-owners work a lot with reopening abandoned and overgrown grasslands. Some recently cleared areas were found during the field survey. There was evident that new recruitments had taken place in these areas, amongst them of *P. veris*. The state of the habitats before cutting is however not known.

Some believe that present-day surveys may provide an overly optimistic assessment of landscapes ability to support biodiversity. This may be true and it might be better to relate to conservation issues in a more reserved way. But when it comes to perennial plant species, capable of developing remnant populations, there might be possible to have a more positive approach towards preservation. Especially if these remnant species possess functional traits contributing to plant population inertia, like high clonal ability.

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Appendix 1A. GPS coordinates (Swedish Grid) of sites used for quantifying and identifying remnant populations in abandoned semi-natural grasslands. Sites 1-6 are managed grasslands while sites 7-26 are abandoned grasslands.

Site	Site code	Y	X
Davik	1	1575600	6534564
Ekbacken	2	1574057	6535211
Stene fornborg	3	1572221	6534511
Davik/Kojstugan	4	1576259	6534689
Värnlund/Ryssinge	5	1573235	6534350
Edeby	6	1571397	6534309
Edeby 2	7	1571558	6533744
Jursta	8	1572268	6534292
Lilla Lundby/Sandbrink	9	1570065	6533650
Lillgården	10	1572085	6533776
Långbro	11	1576208	6536020
North of Sanda	12	1570472	6533673
North of Davik	13	1575727	6535132
North of Edeby	14	1571652	6534394
Näset	15	1570910	6533159
Ryssinge	16	1573312	6534715
Ryssingestugan	17	1573464	6535116
Skinnartorp/Höjden	18	1576463	6534737
Svista	19	1567983	6532638
Väderkvarnsbacken	20	1569604	6532177
West of Stenhagen	21	1567396	6530657
Vällkärrsviken	22	1572760	6532257
Ängstugan	23	1569306	6534063
East of Risbacken	24	1573621	6532264
East of Gröna lund	25	1576104	6534349
Över-Aspa	26	1574222	6534250

Appendix 1B. GPS coordinates (Swedish Grid) of patches used for studying population dynamics of model species *Primula veris*. Patches 1-55 refers to Kolb et al. (2007).

Patch	Y	X	Patch	Y	X
1	1600003	6540690	28	1603837	6539479
2	1600138	6540463	29	1603996	6539391
3	1600139	6540390	30	1603967	6539484
4	1600210	6540145	33	1603983	6539770
5	1600270	6540166	40	1603819	6538413
6	1600337	6540076	41	1603807	6538360
8	1600048	6539905	55	1600131	6540294
9	1600027	6539862	Juresta	1572204	6534497
11	1599931	6539684	North of Sanda	1572244	6534308
12	1599837	6539627	Skinnartorp/höjden	1576463	6534737
13	1600891	6539484	Stene fornborg	1567398	6530655
18	1600358	6537800	Sörtrössla	1600369	6537703
20	1600384	6537665	Ängsstugan	1569315	6534065
23	1601550	6537650	Över-Aspa 1	1574148	6534227
25	1602431	6539807	Över-Aspa 2	1570504	6533676

Appendix 2. Species list containing frequencies (1-10) for each species and site. If a species is marked with x it has been recorded during the total site inventory, but was not found in any square meter plots. Sites 1-6 are managed semi-natural grasslands while sites 7-26 are abandoned semi-natural grasslands.

Species	Managed -						Abandoned semi-natural grassland sites																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
<i>Acer platanoides</i>	0	0	0	x	0	0	x	x	x	x	x	0	2	0	0	0	0	9	3	0	0	1	1	0	0	x
<i>Achillea millefolium</i>	9	10	10	7	10	7	7	3	8	3	x	4	6	x	x	7	1	4	2	5	3	3	2	5	5	2
<i>Achillea ptarmica</i>	x	2	0	x	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	x	0	0
<i>Agrimonia eupatoria</i>																										x
<i>Agrostis canina</i>	0	0	0	0	0	0	0	0	0	0	x	6	0	0	0	1	0	0	0	4	0	0	0	0	0	0
<i>Agrostis capillaris</i>	6	8	9	8	7	5	5	x	9	9	1	1	0	5	2	4	1	0	1	2	6	6	3	1	1	5
<i>Agrostis gigantea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
<i>Agrostis gigantea</i>																								x	x	
<i>Agrostis stolonifera</i>	x	0	0	0	0	0	3	0	2	0	0	1	0	1	0	2	0	0	0	4	x	0	0	2	0	6
<i>Agrostis vinealis</i>	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0
<i>Ajuga pyramidalis</i>	1	1	x	4	1	1	0	0	3	0	2	x	0	0	0	x	x	2	0	0	0	2	1	2	0	0
<i>Alchemilla glaucescens</i>	2	x	4	7	x	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Alchemilla spp.</i>	x	x	0	0	x	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Allium oleraceum</i>	0	0	0	0	0	0	0	x	0	0	0	0	0	0	x	0	x	0	1	0	0	0	0	1	0	0
<i>Alnus glutinosa</i>	x			x						x	x								x							
<i>Alopecurus geniculatus</i>	x			x								x												x		
<i>Alopecurus pratensis</i>	x	4	3	x	3	4	1	2	2	2	0	2	0	x	0	5	1	x	4	5	9	0	0	5	1	3
<i>Amelanchier confusa</i>												x							x							
<i>Amelanchier spicata</i>									x						x											
<i>Anemone nemorosa</i>	x	x	1	1	x	1	0	1	x	0	5	x	7	x	10	x	6	8	4	6	1	3	6	x	9	0
<i>Angelica sylvestris</i>	0	0	0	0	0	0	0	0	0	x	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	0
<i>Antennaria dioica</i>	x																									
<i>Anthoxanthum odoratum</i>	9	4	6	10	4	6	1	x	3	1	1	5	0	1	4	2	2	1	2	2	1	1	3	3	1	1
<i>Anthriscus sylvestris</i>	1	7	3	2	3	4	3	2	6	4	x	3	5	2	2	8	1	8	10	7	7	5	4	6	8	4
<i>Arabidopsis thaliana</i>	x																									
<i>Arabis glabra</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Arabis hirsuta</i>	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	x	0	0	0	4
<i>Arctium tomentosum</i>	0	0	0	0	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Arenaria serpyllifolia</i>	0	1	0	x	0	x	0	0	0	0	0	0	0	0	0	0	0	0	x	1	0	0	0	x	0	2
<i>Artemisia vulgaris</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	x	0	1	1	0	0	0	0	0	0	0	0	x
<i>Asplenium septentrionale</i>			x															x								

<i>Athyrium filix-femina</i>	x	x	0	0	0	0	0	0	0	0	0	x	0	0	0	0	0	0	x	x	x	0	x	1	0	0	0	0		
<i>Atriplex patula</i>	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	x	
<i>Berberis vulgaris</i>																														
<i>Betula pendula</i>	x	x	x	x	x	x	x	3	x	1	2	x	3	6	0	x	1	4	5	1	1	x	2	1	x	x				
<i>Bidens tripartita</i>	x			x																										
<i>Briza media</i>	2	1	3	4	3	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Bromus hordeaceus</i>	x																													
<i>Calamagrostis arundinacea</i>	0	0	0	0	0	0	0	0	0	5	0	3	0	0	0	5	0	0	x	0	0	3	0	0	0	0	0	0	0	
<i>Calluna vulgaris</i>	2	x	x	0	0	x	0	x	x	1	3	3	0	x	0	0	0	0	0	0	0	0	0	x	0	0	0	0	0	
<i>Caltha palustris</i>	x																													
<i>Campanula patula</i>	0	1	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Campanula persicifolia</i>	2	2	1	3	4	2	4	1	3	x	1	1	4	2	1	1	4	3	1	1	0	3	2	0	1	1				
<i>Campanula rotundifolia</i>	2	4	4	3	3	2	3	0	3	5	x	3	1	2	3	3	1	0	4	x	1	x	2	1	2	x				
<i>Capsella bursa-pastoris</i>	x	x	x	x	x	x	x																						x	
<i>Carex acuta</i>				x																										
<i>Carex caryophyllea</i>	2	x	x	0	4	2	0	5	1	0	1	0	0	0	2	0	3	0	0	1	1	0	1	0	0	0	0	0	0	
<i>Carex hirta</i>	x	2	x	1	0	x	0	0	0	x	0	0	0	0	0	x	0	0	x	0	0	0	0	0	x	0	0	0	0	
<i>Carex leporina</i>	1	x	2	4	0	x	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	x	0
<i>Carex pallescens</i>	4	4	x	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	
<i>Carex panicea</i>	4	1	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carex pilulifera</i>	x	0	1	0	x	x	0	0	x	0	0	2	0	x	0	1	0	0	0	0	0	0	x	0	0	0	2	0	0	
<i>Carex spicata</i>	x	x	6	2	x	x	1	0	1	0	0	2	0	0	0	0	x	0	0	1	0	0	x	0	0	x	1			
<i>Carex vesicaria</i>	x			x																										
<i>Carum carvi</i>	0	1	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Centaurea jacea</i>	5	1	1	1	2	5	0	0	x	1	0	x	0	0	0	x	0	0	0	0	0	1	0	0	0	0	1	0	0	
<i>Centaurea scabiosa</i>	0	1	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cerastium fontanum</i>	3	2	9	6	x	1	2	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	x	0	x	x	4			
<i>Chelidonium majus</i>																														x
<i>Chenopodium album</i>	0	0	0	0	0	0	1	x	0	1	0	0	0	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cirsium arvense</i>	x	x	x	1	x	0	x	1	0	x	0	0	0	x	0	x	0	x	x	1	2	x	0	0	1	1				
<i>Cirsium palustre</i>	1	2	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	x	0	0	x	0	0	0	0	0	0	0
<i>Cirsium vulgare</i>		x	x		x	x	x			x												x	x		x	x	x			
<i>Convallaria majalis</i>	x	0	0	0	0	0	x	1	0	1	3	1	4	x	7	1	10	0	x	0	0	0	1	0	0	x				
<i>Convolvulus arvensis</i>		x						x		x																				
<i>Corylus avellana</i>	x	x	0	0	0	0	0	0	0	x	0	x	0	x	0	x	x	x	0	0	0	0	x	0	2	0				

<i>Crataegus rhipidophylla</i>	0	0	0	x	0	x	0	0	x	0	0	0	0	0	0	0	1	0	0	0	0	x	1	0	0	0	0	2
<i>Crepis sp.</i>																												
<i>Dactylis glomerata</i>	2	5	2	2	x	x	10	x	4	1	0	6	1	x	x	2	x	5	4	7	1	7	5	7	5	9		
<i>Dactylorhiza maculata</i>	2	0	0	x	x	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Danthonia decumbens</i>	6	3	1	1	4	2	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Deschampsia cespitosa</i>	5	5	5	7	1	7	x	0	0	1	1	0	0	0	1	0	0	9	1	5	3	3	3	x	8	2		
<i>Deschampsia flexuosa</i>	3	1	x	x	4	x	2	8	7	7	7	6	4	10	9	6	7	x	8	2	2	3	6	6	1	5		
<i>Dianthus deltoides</i>	0	0	1	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dryopteris expansa</i>																												
<i>Dryopteris filix-mas</i>	0	0	x	0	0	x	x	0	0	x	0	x	x	x	x	x	0	0	1	x	x	x	x	x	0	x		
<i>Elytrigia repens</i>	0	0	0	x	0	0	1	x	x	0	0	3	0	x	0	x	0	0	1	2	2	1	0	x	3	1		
<i>Epilobium angustifolium</i>																												
<i>Epilobium montanum</i>							x																					
<i>Epilobium sp.</i>	x	x		x		x																						
<i>Epilobium sp.2</i>	x																											
<i>Equisetum arvense</i>	x	0	x	x	0	0	0	0	0	x	0	0	x	0	0	x	0	1	0	2	0	0	0	0	0	0	0	
<i>Equisetum palustre</i>																												
<i>Equisetum sylvaticum</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	x	0	0	0	0		
<i>Erophila verna</i>	x	1	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Erysimum cheiranthoides</i>																												
<i>Fallopia convolvulus</i>	0	0	0	0	0	0	x	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	x	0	0	0	0	
<i>Festuca ovina</i>	9	5	5	8	10	6	2	8	7	6	4	7	4	6	2	4	6	2	7	4	4	2	4	3	4	2		
<i>Festuca pratensis</i>	x	3	7	x	3	5	0	0	4	0	0	0	0	0	3	0	0	0	3	1	2	0	0	0	0	0	0	
<i>Festuca rubra</i>	1	5	3	4	x	6	0	0	7	0	0	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Filipendula ulmaria</i>	1	1	0	1	0	0	0	0	0	x	0	0	0	0	0	0	2	0	1	0	0	x	0	1	0			
<i>Filipendula vulgaris</i>	8	x	1	2	6	5	x	2	1	x	0	x	4	0	1	2	x	x	1	0	1	1	x	x	6	1		
<i>Fragaria vesca</i>	3	1	x	4	3	1	1	2	4	x	x	3	4	2	x	2	4	8	0	2	1	6	7	1	6	x		
<i>Frangula alnus</i>	x		x																									
<i>Fraxinus excelsior</i>	0	0	0	0	0	0	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	
<i>Galeopsis bifida</i>																												
<i>Galeopsis sp.</i>	x	1	0	x	0	0	0	0	1	1	1	0	x	x	0	4	x	0	x	0	0	x	0	0	0	0		
<i>Galeopsis speciosa</i>			x		x																							
<i>Galeopsis tetrahit</i>							x		x																			
<i>Galium album</i>	0	0	0	0	0	x	0	0	0	0	0	1	0	1	0	x	0	0	1	0	4	0	x	1	x	0		
<i>Galium aparine</i>	0	0	0	x	0	x	1	0	0	x	0	0	0	0	0	0	x	0	0	x	x	0	0	0	0	0	2	

<i>Galium boreale</i>	x	x	1	4	x	2	x	3	x	2	0	x	5	x	1	x	x	1	2	2	x	2	3	x	4	2
<i>Galium uliginosum</i>	3	4	x	1	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Galium verum</i>	7	7	8	6	8	10	6	5	9	4	0	2	2	2	0	7	1	1	1	0	5	5	2	9	3	1
<i>Geranium pusillum</i>	0	1	0	x	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	x	0	1
<i>Geranium robertianum</i>	0	x	0	0	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	x	0	1	0	x	0
<i>Geranium sylvaticum</i>	1	x	x	x	0	0	0	1	0	0	x	0	7	0	x	0	1	3	2	0	0	2	0	x	5	0
<i>Geum rivale</i>	2	1	x	5	x	1	0	0	x	0	1	x	0	0	0	3	x	0	2	0	0	8	1	0	7	0
<i>Geum urbanum</i>	0	0	x	0	0	0	7	1	x	x	0	0	x	0	0	0	0	0	8	0	1	0	x	0	0	3
<i>Glechoma hederacea</i>		x		x																						
<i>Glyceria fluitans</i>					x																					
<i>Gymnocarpium dryopteris</i>		x																								
<i>Helianthemum nummularium</i>	0	0	x	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Helictotrichon pratense</i>	1	3	x	x	4	3	2	3	4	2	0	0	0	2	0	x	0	0	0	2	0	2	0	4	0	1
<i>Helictotrichon pubescens</i>	x	4	x	1	2	2	0	0	x	2	0	x	4	0	1	2	0	0	1	2	3	2	1	6	3	0
<i>Hepatica nobilis</i>		x													x											
<i>Hesperis matronalis</i>																					x					
<i>Hieracium sect. Vulgata</i>	2	2	x	x	1	x	0	3	x	1	4	2	2	1	4	1	6	4	0	x	2	0	x	x	0	2
<i>Hieracium umbellatum</i>	x	4	x	x	4	4	2	8	2	3	0	1	5	x	x	4	x	3	2	0	4	x	1	1	0	1
<i>Holcus lanatus</i>	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hypericum maculatum</i>	7	7	x	2	1	1	x	3	x	3	0	x	6	x	x	3	x	8	2	3	0	x	1	6	2	2
<i>Hypericum perforatum</i>	x	1	x	x	x	0	1	x	3	2	0	0	0	3	x	1	x	0	0	0	1	0	0	0	x	x
<i>Hypochoeris maculata</i>	x													x												
<i>Juncus articulatus</i>		x																								
<i>Juncus conglomeratus</i>		x		x																						
<i>Juncus effusus</i>	x	x		x	x	x																	x	x		
<i>Juniperus communis</i>	x	x	x	x	x	x	x	x	x	x	1	x	x	x	x	x	x	0	x	x	x	x	x	x	x	x
<i>Knautia arvensis</i>					x	x																				
<i>Lapsana communis</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	x	1	0	0	0	2	x	0	0	0	0	0	0
<i>Lathyrus linifolius</i>	7	4	x	5	7	3	1	3	4	2	5	6	1	4	6	3	8	0	3	x	0	7	6	0	3	1
<i>Lathyrus pratensis</i>	4	6	6	7	5	8	1	1	4	0	0	0	x	0	0	1	x	2	1	0	5	2	0	2	3	x
<i>Leontodon autumnalis</i>	2	2	7	3	x	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Leucanthemum vulgare</i>	4	1	1	2	3	1	1	2	x	1	x	x	0	1	0	1	0	x	0	0	2	0	2	0	3	x
<i>Listera ovata</i>							x																			
<i>Lolium perenne</i>	x	x		x																						
<i>Lonicera caprifolium</i>			x																							

<i>Lotus corniculatus</i>	7	x	4	6	4	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	x	1	0	1	x		
<i>Luzula campestris</i>	10	5	10	10	7	7	1	0	2	0	0	x	0	0	x	x	0	1	0	0	0	x	0	0	0	x	
<i>Luzula multiflora</i>	0	1	1	x	0	x	0	2	0	0	0	1	0	1	0	x	0	x	x	0	0	0	1	0	1	1	
<i>Luzula pilosa</i>	1	x	x	0	3	x	0	4	2	0	3	3	2	2	2	1	2	6	0	0	0	3	8	x	1	1	
<i>Lychnis viscaria</i>	1	x	x	1	x	x	1	x	0	2	x	x	x	x	0	1	x	x	x	0	x	0	x	x	x	3	
<i>Maianthemum bifolium</i>				x																							
<i>Malus sylvestris</i>				x							x															x	
<i>Matteuccia struthiopteris</i>																										x	
<i>Melampyrum cristatum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	
<i>Melampyrum pratense</i>	x	0	x	0	8	x	0	0	5	0	3	2	2	x	0	0	3	1	0	0	0	1	2	2	0	0	
<i>Melica nutans</i>	0	0	x	x	0	0	0	0	0	1	x	x	4	x	0	0	x	0	0	0	0	0	x	0	0	0	
<i>Mentha arvensis</i>	x			x																							
<i>Milium effusum</i>	0	1	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Moehringia trinervia</i>	0	x	0	0	0	0	x	2	0	0	0	0	0	x	0	x	0	4	1	x	x	0	1	1	x	1	5
<i>Molinia caerulea</i>	x																										
<i>Monotropa hypopitys</i>																											x
<i>Mycelis muralis</i>	0	x	0	0	0	0	1	0	0	0	1	0	x	x	2	0	1	2	1	1	x	x	2	x	0	0	
<i>Myosotis arvensis</i>	0	0	0	0	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	x	0	1	x	0	1
<i>Myosotis laxa</i>	x	x		x		x																					
<i>Oxalis acetosella</i>	1	x	0	0	0	x	0	0	0	0	2	0	2	0	0	0	0	9	0	3	0	0	1	0	0	0	
<i>Paris quadrifolia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	x	0	0	0	0	0	0	
<i>Persicaria hydropiper</i>	x	x		x		x																					x
<i>Phleum pratense</i>	1	4	6	x	6	5	0	1	1	x	0	x	1	0	x	3	1	2	2	5	0	2	x	x	5	2	
<i>Picea abies</i>	x	0	x	x	x	x	x	x	0	x	2	1	x	x	x	0	x	1	x	1	x	x	x	x	x	x	0
<i>Pilosella lactucella</i>	0	x	0	1	x	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pilosella officinarum</i>	5	3	2	2	5	x	1	x	x	2	x	1	0	x	x	x	x	0	0	0	x	0	0	x	x	x	
<i>Pilosella peleteriana</i>	x	1	0	x	0	0	0	0	0	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pimpinella saxifraga</i>	5	6	7	6	6	7	8	6	5	3	0	5	3	2	1	5	0	1	1	0	2	1	2	2	2	4	
<i>Pinus sylvestris</i>	1	x	x	x	1	x	x	x	x	x	x	x	0	x	0	0	x	x	0	0	1	x	x	x	x	x	
<i>Plantago lanceolata</i>	7	7	6	5	8	5	x	0	x	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Plantago major</i>	x	x	0	1	x	x	2	0	0	0	x	0	0	0	0	0	x	0	0	0	0	1	0	0	0	0	0
<i>Platanthera bifolia</i>	2	0	0	0	0	0	0	0	0	0	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Poa annua</i>	x	x	x	x																							
<i>Poa nemoralis</i>	0	0	x	x	0	0	1	3	0	2	1	x	10	0	7	5	7	8	10	1	2	3	4	0	5	5	
<i>Poa palustris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0

<i>Poa pratensis</i>	4	4	2	4	7	6	9	3	4	2	1	2	2	6	1	4	3	x	6	3	1	3	4	5	1	9
<i>Poa supina</i>	0	x	0	2	0	0	0	0	0	0	0	0	0	0	0	0	x	0	0	0	0	0	0	0	0	0
<i>Polygala vulgaris</i>	5	3	x	x	2	1	0	0	0	0	0	x	0	0	x	1	0	0	0	0	0	0	1	0	0	0
<i>Polygonatum odoratum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
<i>Polygonum aviculare</i>	0	0	0	0	0	x	1	0	0	0	0	0	0	0	0	x	0	0	0	0	0	0	0	0	0	2
<i>Polypodium vulgare</i>	x	x	x	0	0	x	x	x	x	x	x	x	x	x	0	x	1	x	x	x	0	0	x	x	0	x
<i>Populus tremula</i>	x	x	x	0	0	x	x	x	x	x	x	x	2	x	x	1	1	x	x	x	x	x	x	x	x	x
<i>Potentilla anserina</i>	x						x																			
<i>Potentilla argentea</i>	x	x	x	x	0	x	x	0	x	0	0	0	0	0	0	0	0	0	0	0	x	0	0	1	0	0
<i>Potentilla erecta</i>	10	4	2	7	1	3	0	0	x	x	1	1	x	x	x	0	0	1	0	0	0	x	1	0	2	0
<i>Potentilla reptans</i>	0	0	x	x	x	3	x	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	x	0	0	0
<i>Potentilla tabernaemontani</i>																										
<i>Primula veris</i>	x	x	1	2	4	x	0	2	0	0	0	x	x	0	0	0	0	4	1	0	0	0	1	0	3	3
<i>Prunella vulgaris</i>	3	3	3	3	0	x	0	0	0	0	1	x	x	0	0	0	0	5	0	0	0	0	0	0	0	0
<i>Prunus avium</i>	0	0	x	0	0	0	0	x	0	0	0	0	0	0	0	0	0	x	1	0	1	0	x	0	0	x
<i>Prunus padus</i>																										
<i>Prunus spinosa</i>			x		x																					
<i>Pteridium aquilinum</i>	2	1	x	1	x	x	x	0	4	x	3	1	3	2	0	0	0	2	0	0	x	0	3	x	0	x
<i>Pyrola minor</i>	x			x																						
<i>Quercus robur</i>	x	x	x	x	x	x	x	x	x	x	2	x	x	x	3	x	4	2	3	0	1	3	x	x	2	x
<i>Ranunculus acris</i>	7	10	10	10	3	9	3	2	5	1	x	4	2	1	3	5	1	6	9	5	4	6	4	1	7	5
<i>Ranunculus auricomus</i>	3	0	4	0	x	2	0	0	x	0	0	0	0	0	1	x	x	1	0	0	0	0	0	0	1	0
<i>Ranunculus bulbosus</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Ranunculus flammula</i>	x	x		x																						
<i>Ranunculus polyanthemos</i>	0	0	4	0	x	3	2	5	5	0	0	6	0	2	5	0	0	x	4	0	6	2	4	0	1	1
<i>Ranunculus repens</i>	x	1	0	x	x	1	0	0	0	0	1	0	0	0	0	1	0	2	1	7	0	0	0	0	1	0
<i>Ranunculus sceleratus</i>	x																									
<i>Rhinanthus minor</i>	9	1	x	x	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ribes alpinum</i>	x	x																								
<i>Ribes uva-crispa</i>			x	x	x	x	x																			
<i>Rosa dumalis</i>	x	x	x	x	x	x	x	x	x	0	x	0	0	1	x	x	2	0	x	x	x	0	x	0	x	
<i>Rubus idaeus</i>	x	x	x	x	x	x	1	1	1	3	1	0	3	2	0	1	2	1	1	2	3	3	4	2	1	0
<i>Rubus saxatilis</i>	0	0	0	0	0	0	0	0	0	x	0	0	0	3	2	x	x	0	x	0	0	x	0	0	1	1
<i>Rumex acetosa</i>	8	9	9	10	4	5	1	1	5	0	0	1	1	1	0	3	0	1	x	0	0	4	1	2	3	1
<i>Rumex acetosella</i>	x	0	x	x	x	x	x	x	x	1	x	x	0	x	0	x	x	0	0	0	0	0	0	1	0	0

Appendix 3. Jaccard index calculations showing the similarity (%) between sample sets of ten square meter plots per site. Sites 1-6 are managed semi-natural grasslands while sites 7-26 are abandoned grasslands. Total number of species per site is shown at the bottom of the table.

Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	
1																											
2	59																										
3	53	54																									
4	61	55	50																								
5	50	48	59	48																							
6	54	62	57	53	56																						
7	36	38	44	38	43	46																					
8	35	38	47	31	41	38	48																				
9	46	42	58	41	50	52	45	50																			
10	38	38	48	39	44	42	48	56	44																		
11	35	37	37	29	30	39	33	42	38	42																	
12	43	42	50	40	43	50	45	49	53	44	44																
13	33	35	43	31	30	35	34	46	39	42	46	46															
14	37	34	47	33	40	43	48	51	54	52	46	60	46														
15	30	32	39	27	32	30	34	44	40	38	38	41	47	44													
16	41	38	48	40	45	48	50	45	47	46	34	50	33	46	33												
17	35	37	40	31	36	38	43	54	43	45	52	45	47	49	48	45											
18	42	44	46	39	38	43	38	49	40	41	42	47	57	42	39	37	42										
19	34	37	40	33	34	36	43	50	36	44	35	45	46	46	43	45	45	46									
20	33	36	35	34	29	37	39	37	34	43	40	36	39	38	35	38	38	41	44								
21	33	35	43	34	40	42	53	45	42	45	34	46	34	50	37	46	42	37	45	38							
22	37	43	49	38	47	45	48	46	52	45	38	49	49	49	43	48	46	51	53	46	42						
23	41	44	48	37	40	46	38	49	43	44	48	55	50	50	43	36	45	55	47	41	39	47					
24	39	42	47	40	40	46	51	44	46	43	33	47	42	47	39	42	44	41	43	36	48	47	41				
25	38	45	45	36	49	45	40	51	43	45	38	49	45	49	44	46	47	53	53	37	43	59	49	38			
26	33	38	43	38	39	47	61	49	45	46	27	44	36	44	33	50	39	41	43	33	49	48	40	44	43		
Total # Species:	149	121	113	134	95	114	101	81	91	83	65	90	68	78	66	108	78	81	84	74	78	84	90	92	78	99	

Appendix 4. Vital rates of *Primula veris* expressed as linear functions of canopy cover (**p<0. 01, *p<0. 05 and (*) p<0.1 and as means across the 13 patches for which demographic data was available. Note: The percentage of canopy cover and all vital rates were arcsine-square root transformed prior to analysis, except seed production, which was log-transformed (Kolb et al. 2007).

Vital rate (y)	Function of canopy cover (x)	Mean across 13 patches
Survival of seeds	$y= 0.606-0.208x$	0.247
Germination	$y= 0.857-0.003x$	0.569
Survival of seedlings	$y=0.813-0.327x$ *	0.344
Survival of established individuals		
small	$y= 0.944-0.120x$	0.571
intermediate	$y= 1.300-0.171x$	0.824
large	$y= 1.329+0.094x$	0.956
flowering	$y= 1.489-0.004x$	0.979
Probability of growing intermediate once surviving. but not growing large		
small	$y= 1.571-(1.121+0.274x)^*$	0.098
intermediate	$y= 1.571-(0.308-0.153x)$	0.912
large	$y= 1.571-(0.240-0.190x)$	0.944
flowering	$y= 1.571-(0.210-0.011x)$	0.901
Probability of growing large once surviving		
small for $0 \geq x \leq 0.90$:	$y= 0.125-0.139x$ (*)	0.012
intermediate	$y= 0.616+0.021x$	0.358
large	$y= 1.226+0.067x$	0.889
flowering	$y= 1.277+0.064x$	0.915
Probability of flowering once surviving and growing large		
small	$y= 0.133-0.157x$	0.016
intermediate	$y= 0.434-0.021x$	0.203
large	$y= 0.794-0.089x$	0.454
flowering	$y= 1.060-0.270x$ (*)	0.599
Seed production	$y= 1.638+0.775x$ **	190.100

Appendix 5. Matrix elements of *Primula veris* expressed as combinations of vital rates (Kolb et al. 2007).

	Seed	Seedling	Small	Intermediate	Large	Flowering
Seed	$P_{ssu}(1-P_{sdl})$					$S P_{ssu}(1-P_{sdl}) Pred$
Seedling	$P_{ssu} P_{sdl}$					$S P_{ssu} P_{sdl} Pred$
Small		P_{slsu}	$P_{su,j}(1-P_{int,j})(1-P_{large,j})$	$P_{su,j}(1-P_{int,j})(1-P_{large,j})$	$P_{su,j}(1-P_{int,j})(1-P_{large,j})$	$P_{su,j}(1-P_{int,j})(1-P_{large,j})$
Intermediate			$P_{su,j} P_{int,j}(1-P_{large,j})$	$P_{su,j} P_{int,j}(1-P_{large,j})$	$P_{su,j} P_{int,j}(1-P_{large,j})$	$P_{su,j} P_{int,j}(1-P_{large,j})$
Large			$P_{su,j} P_{large,j}(1-P_{fl,j})$	$P_{su,j} P_{large,j}(1-P_{fl,j})$	$P_{su,j} P_{large,j}(1-P_{fl,j})$	$P_{su,j} P_{large,j}(1-P_{fl,j})$
Flowering			$P_{su,j} P_{large,j} P_{fl,j}$	$P_{su,j} P_{large,j} P_{fl,j}$	$P_{su,j} P_{large,j} P_{fl,j}$	$P_{su,j} P_{large,j} P_{fl,j}$

Note: $P_{su,j}$ =probability that an established individual in stage class j will survive; $P_{int,j}$ =probability that a surviving individual in stage class j, not growing large, will grow to intermediate; $P_{large,j}$ =probability that a surviving individual in stage class j will grow to large; $P_{fl,j}$ =probability that an individual in one of the two largest stage classes will flower; S=average number of seeds produced by a flowering individual; P_{ssu} =probability that a seed will survive to the next season and appear as a seed in the seed bank or as a seedling; P_{sdl} =probability that a surviving seed will germinate and appear as a seedling; P_{slsu} =seedling survival

^aWhen population growth rates were modeled in the presence of seed predation (see Data analysis), this term was multiplied by $(1 - \text{seed predation rate})$, with the predation rate being calculated as a function of canopy cover ($y=0,19-0,19x+0,58x^2$)

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