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Patch distribution and dispersal limitation of four plant species in Swedish semi-natural grasslands

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Abstract

This study examined whether the patch distribution of four plant species *Agrimonia eupatoria*, *Carlina vulgaris*, *Hypochoeris maculata* and *Plantago media* were affected by dispersal limitation. Analysis of the patch size/isolation relationship was combined with a seed sowing experiment examining the recruitment of the species. Patch size was negatively correlated to isolation in *Carlina*, *Hypochoeris* and indicating that dispersal processes might affect the distribution pattern. Patch size of *Agrimonia* was not correlated, or in one case positively correlated, to isolation. *Agrimonia* was also the only species among the four where the recruitment not was affected by disturbance treatment or locality. The recruitment of *Carlina*, *Hypochoeris* and *Plantago* was higher in disturbed plots compared to undisturbed, and the latter two species were also affected by locality. This suggests that *Agrimonia* is less sensitive to isolation (and the ongoing fragmentation of the landscape) compared to the other three species, probably due to better dispersal and recruitment ability. We conclude in a discussion how different management strategies could serve to maintain viable populations of these species.

Introduction

As in most of Europe, the traditional agrarian landscape in Sweden included large areas used for mowing or grazing. This management produced extensive areas of grasslands in a landscape naturally dominated by forests. During the last century the area of such "semi-natural grasslands" has declined dramatically, and it is now estimated that less than 10% of the area existing 100–150 years ago remains (Cousins 2001b). For plants with a main distribution in semi-natural grasslands, this means that in most regions their core habitat has become fragmented into smaller and more isolated areas. Even under conditions where there is plenty of suitable habitat, many plant species have a patchy distribution (Watt 1947; Whittaker and Levin 1977; Grubb 1986) and some degree of dispersal limitation is likely to occur (Eriksson 1996; Pulliam 2000). When habitats become more scarce, seed limitation is expected to be more pronounced, as dispersal routes cease to exist (Poschlod and Bonn 1998), target localities are less likely to be "found" by seeds (Primack and Miao 1992), and source populations may suffer from a reduced seed production (Jennersten 1988; Wolf and Harrison 2001). We have previously conducted studies indicating that seed limitation is common in our study area (Eriksson and Ehrlén 2001), and that dispersal processes influences local patterns of species richness even at a relatively small scale (Franzén and Eriksson 2001).

Few studies, however, have combined a spatially explicit documentation of patch distribution with experimental tests of seed limitation. The aim of this study was to examine seed limitation in the distribution of patches of four species characteristic of traditionally managed semi-natural grasslands, within a relatively small area (a few square-kilometers) in a landscape composed of a mixture of traditionally managed grasslands, arable fields and forests. We used two different approaches: experimental sowing of seeds at occupied and non-occupied localities, and an analysis of how patch size and changes in patch size were related to patch isolation within the study area. Moreover, by including a disturbance treatment in the sowing experiment we also aimed at quantifying the ability of the four target species to recruit in closed grass swards; species lacking such an ability are likely to experience a combination of seed and microsite limitation (Eriksson and Ehrlén 1992). The four target species, *Agrimonia eupatoria*, *Carlina vulgaris*, *Hypochoeris maculata* and *Plantago media* (hereafter denoted by their generic names), have been subjected to other studies in the same area in Sweden, *Agrimonia*, *Carlina* and *Plantago* concerning population dynamics (Eriksson and Eriksson 2000; Löfgren et al. 2000; Kiviniemi 2002 (in press)) and *Agrimonia*, *Hypochoeris* and *Plantago* concerning dispersal and distribution patterns (Eriksson 1997; Kiviniemi and Eriksson 1999). Thus, we conclude in a discussion how these grassland species respond to the ongoing fragmentation and which strategies should be considered for a future management of these grasslands.

Methods

The study area

The study area is located about 80 km south of Stockholm, Sweden. It is an agricultural area within the earlier domains of Nynäs castle, and contains arable land, grasslands and fragments of deciduous forests. The area is naturally surrounded by coniferous forests and by a lake (in the south). There are two hamlets Nyckelby and Litselby, within the area. The hamlets have a likely origin in the Iron age, and a pollen analysis from the area suggests that grazing has been apparent from at least 3200 years BP and mowing probably from 2500 BP (Cousins (2001a, 2001b)).

The field survey

A survey of the patch distributions of four plant species *Agrimonia, Carlina, Hypochoeris* and *Plantago* was conducted during the summers 1996 and 1997 within a 3.6-km^2-large area (Figure 1). These four species were chosen because they are traditionally categorized as semi-natural grassland species and their abundances are intermediate between common and rare, and the patch distribution could easily be recorded. The survey was carried out by a systematically inventory throughout the area, and every patch was recorded with GPS-position. The size of patches was estimated by counting the number of individuals (ramets). The minimum distance between patches was delimitated was of 20 meters made by a. The main inventory of species was carried out 1996, but during the summer 1997 the inventory was complemented to check for patches overlooked in the first year. The area was reinventoried during the summer of 2000. The size of all patches was estimated again and new patches were recorded.

Analyses of isolation and population changes

A first analysis examined whether there were any overall changes in patch size for the species between the surveys of 1996–97 and 2000. This was done by comparing the number of individuals per patch between the two surveys. This was analyzed statistically with a Wilcoxon matched pairs test. A second analysis examined whether isolation was related to the patch size. Isolation was measured as a negative form of connectivity measurement suggested by Hanski (1994):

$$S_i = -\sum_{i \neq j} \exp(-\alpha d_{ij}) N_j$$

S_i denotes the isolation of patch i. N_j denotes size of patch j and d_{ij} describes the distance between patch i and patch j. The constant α describes how fast the number of migrants from patch j declines with increasing distance (Hanski 2000). This constant is difficult to estimate for plants, but values between 1 and 5 have been suggested as reasonable to check for patterns (Bastin and Thomas 1999). We used isolation measurements based on α-values 1, 3 and 5 (ISOL 1, 3 and 5). Low α-values indicates good dispersal ability while high α-values indicates weak dispersal ability. Large values of S_i correspond to large isolation. The isolation measure was based on the 1996–97 years survey. The relationship between isolation and the size of the individual patches was analyzed with a Spearman Rank Correlation (patch size data was not normal distributed according to a Liljefors test).

A third analysis was made on the relationship between the relative patch size changes and patch size and isolation. This was analyzed with a multiple regression including patch size, patch isolation and the interaction-term between the two (patch size change

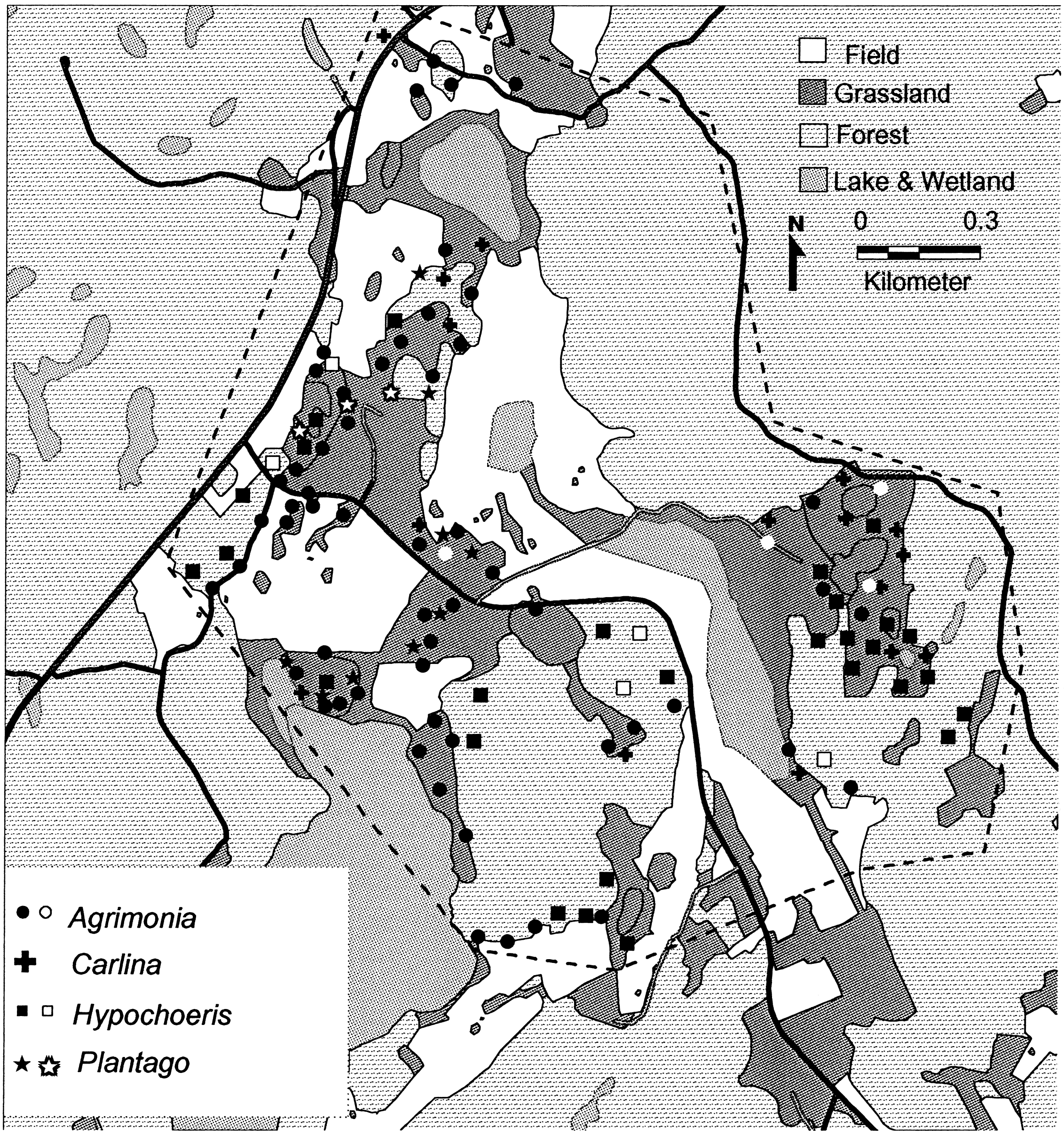

Figure 1. Patch distribution of *Agrimonia eupatoria*, *Carlina vulgaris*, *Hypochoeris maculata* and *Plantago media* in the Nynäs study area (dashed line) in Sörmland, Sweden according to the 1996–97 years survey. Black symbols denote persistent patches and white symbols extinct patches during the study period.

data was found normal distributed, or had normal disribuded residuals according to a Liljefors test).

Relative patch size changes was measured as:

$$\mathrm{Log}(N_{2000} + 1) - \mathrm{Log}(\mathrm{N}_{1996\text{–}97} + 1)$$

Where N = Number of individuals within a patch.

Two new large patches were found during the 2000 years inventory, one for *Plantago* and one for *Carlina*. These were treated as patches overlooked from the 1996–97 survey, as they were unlikely to be newly colonized patches (the number of individuals in the overlooked patches in the 1996–97 survey was approximated to the same as the number of individuals found in year 2000 concerning isolation measures).

The seed sowing experiment

The sowing experiment was initiated in the summer 1997. The experiment was conducted in two types of localities in semi-natural grasslands within the survey area, one where the species were occurring naturally at least within 100 m of the sowing site ("occupied localities") and the other type where the species were not occurring ("unoccupied localities") within 100 m of the sowing site (except for *Agrimonia*, which was the most widely distributed among the four species and therefore got the occupancy limit of 50 m). The species were sown at two occupied localities and two unoccupied localities. At each locality four pairs of 1 dm^2-quadrates were randomly set out, for each species within a 20 by 20 m large area of semi-natural grassland. The two quadrates in each pair were distributed 3 dm apart. In one of the quadrates in each pair the above ground biomass (green tissue) was removed ("disturbed"), and in the other quadrate vegetation was left "undisturbed". In addition there was a control quadrate between the two treatment quadrates, which was "undisturbed" and not subjected to any seed sowing. For *Agrimonia* and *Plantago* 50 seeds were sown per quadrate, while for *Hypochoeris* and *Carlina* were 100 seeds were sown per quadrate. Recruitment was recorded in august 1999. There were no germinating seedlings of the four examined species in the control quadrates during the experiment (1998–1999). The effects of three treatments were analyzed from the experiment: disturbance, occupied vs. unoccupied localities, and differences among localities. The effects of the treatments on recruitment for each species were analyzed with a general linear model with the paired quadrates as repeated subjects, and localities nested within locality type (occupied or not).

Results

In the survey during 1996–97 the number of recorded patches ranged from 12 to 60 for the different species. *Plantago*, was the least abundant species among the four and was only found in 12 patches, *Carlina* occurred in 16 patches, *Hypochoeris* in 33 patches and *Agrimonia* in 60 patches. The reinventory of the four species during the summer 2000 showed a very similar patch distribution as in 1996–97. Some patches went extinct between the two surveys; five for *Hypochoeris* (or 14.7% extinct patches), four for

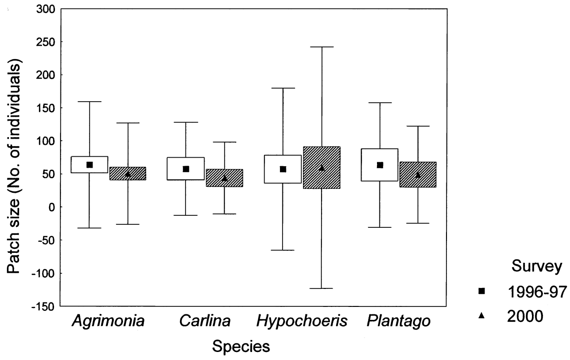

Figure 2. Mean patch size error of the examined species 1996–97 and 2000. Boxes denote standard error and whiskers denote the standard deviation.

Agrimonia (6.7%) and three for *Plantago* (25.0%) but no *Carlina* patch went extinct. Few new patches were found in the 2000 survey (one for *Agrimonia* and one for *Carlina* and two for *Plantago*). The patch size of *Agrimonia* and *Hypochoeris* tended to decrease the area between the 1996–97 and 2000 years surveys according to a Wilcoxon matched pairs test) (*Agrimonia* N = 61, Z = 1.86, p = 0.062, *Hypochoeris* N = 33 (two patches were combined to one patch), Z = 1.76, p = 0.0769) while there was no significant difference in patch size for *Carlina* (N = 17, Z = 0.805, p = 0.421) or *Plantago* (N = 15, Z = 1.22, p = 0,221). (Figure 2).

Depending on the chosen α-value all four species showed, at least in some cases, a significant correlation between patch size (from 1996–97) and isolation (Figure 3, Table 1). For *Agrimonia* there was a positive relationship between patch size and isolation (only for α-value 1), while for *Carlina*, *Hypochoeris* and *Plantago* there was a negative relationship between patch size and isolation (when α was 3 or 5).

Relative patch size changes in *Agrimonia* were negatively related to patch size when the interaction-term between isolation and patch size was removed from the model (F = 4.11, p = 0.047), but relative patch changes were not related to isolation. There were no significant relationships between patch size changes and patch size or isolation for the other three species.

All species recruited in the sown plots. However there were large differences among species regarding the effects of disturbance and locality (Figure 4). *Agrimonia* had the most successful recruitment of the four species, on average 15.0% of the seeds germinated and survived two years after sowing. Recruit-

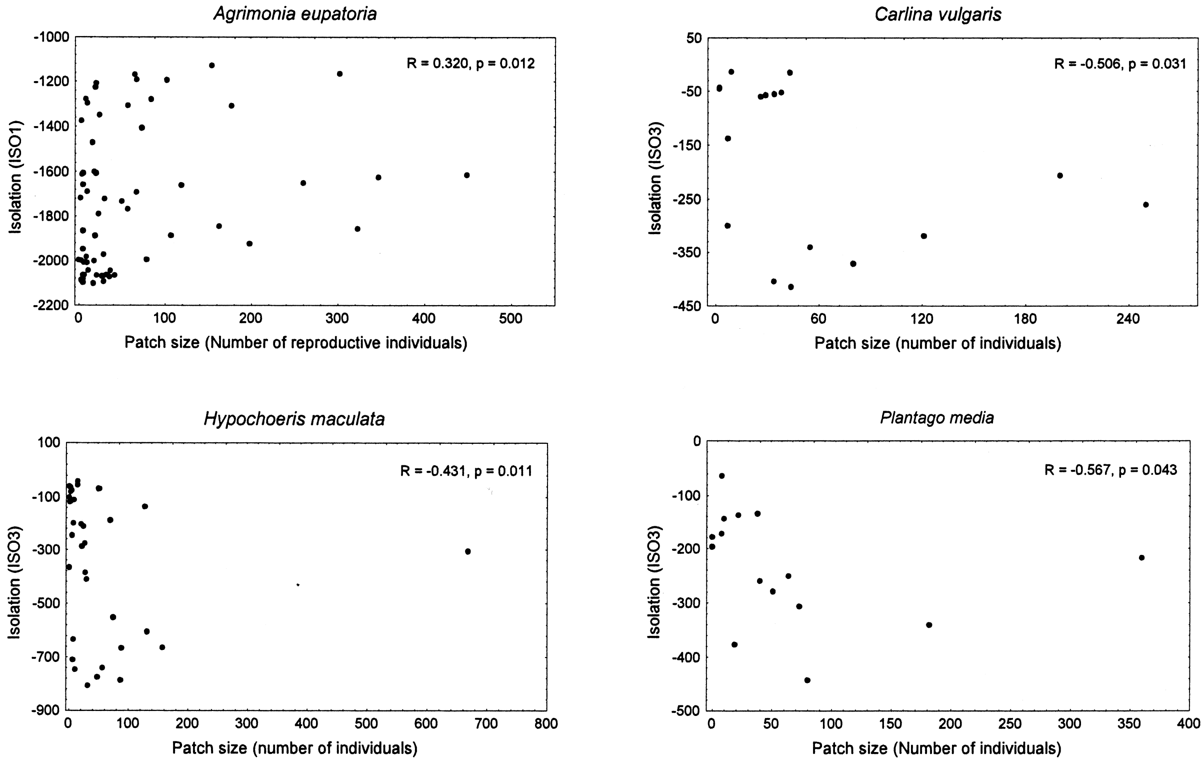

Figure 3. A-D. The relationship between patch size and isolation of the four examined species (ISO 1 is used for *Agrimonia* and ISO 3 for the other species, see text for explanation). Results from Spearman rank correlations are presented in the figures.

Table 1. Results from Spearman rank correlations between patch size (1996–97) and isolation (ISO 1, 3 and 5) for *Agrimonia eupatoria*, *Carlina vulgaris*, *Hypochoeris maculata* and *Plantago media*.

	ISO1	ISO3	ISO5
Agrimonia	p = 0.012, R = 0.320	n.s	n.s
Carlina	n.s	p = 0.031, R = −0.506	p = 0.049, R = −0.484
Hypochoeris	n.s	p = 0.011, R = −0.431	p = 0.004, R = −0.477
Plantago	n.s	p = 0.043, R = −0.567	p = 0.024, R = −0.619

ment of *Agrimonia* did not differ between disturbed and undisturbed quadrates or between different localities (Figure 4a). *Carlina* had an average recruitment of 5.8% and the recruitment was higher in disturbed than in undisturbed quadrates (F = 21.2, p = 0.001), but was not affected by locality (Figure 4b). *Hypochoeris* (on average 4.2% recruitment) had a more complex association with the treatments. Disturbance treatment had a positive effect on recruitment (F = 22.6, p < 0.001) and the recruitment was higher in occupied than unoccupied localities (F = 5.89, p = 0.032). However, there was also a general effect of locality (independent of occupancy, F = 10.77, p = 0.02) and there was a significant interaction between disturbance treatment and locality (F = 4.53, p = 0.034) (Figure 4c). *Plantago* had a low average recruitment (1.8%) that was positively affected by disturbance (F = 8.38, p = 0.013) and also influenced by locality (F = 5.77, p = 0.018) (Figure 4d).

Discussion

Patch size was negatively related to isolation (when isolation were based on α-values 3 or 5) in three of four species: *Carlina*, *Hypochoeris* and *Plantago*. Such a pattern could be interpreted in different ways, either as an effect of seed dispersal (rescue effect) or pollen dispersal (pollen limitation), or it could depend on the habitat distribution within the area. Patch size

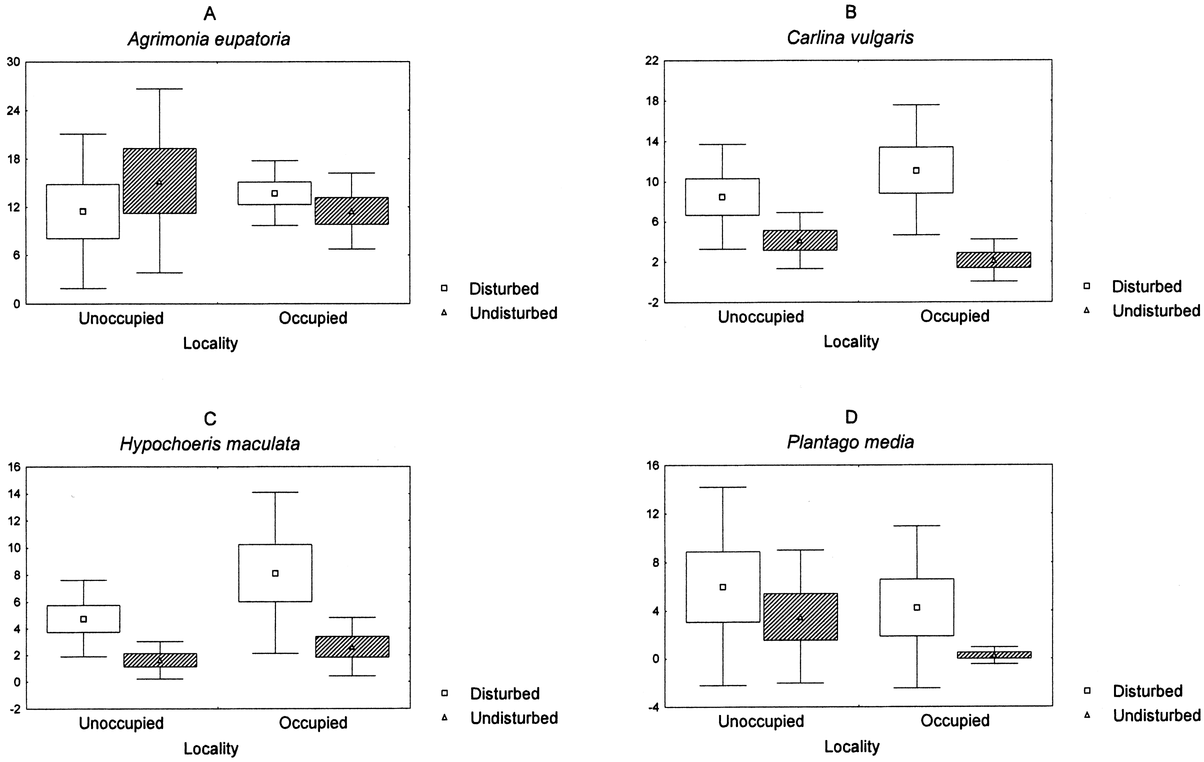

Figure 4. The recruitment success (fraction of successfully recruited seeds surviving two years after sowing) varied among the four examined species depending on locality and disturbance regime. Boxes denote standard error and whiskers denote the standard deviation.

could also be affected by edge effects, influencing the quality of habitats with different size and shape. In contrast to the other three species, the patch size of *Agrimonia eupatoria* was not negatively, but positively correlated to isolation (at least when α-values was set to 1). In general, it is difficult to distinguish between different isolation mechanisms (Ouborg 1993), and our study is no exception to that. According to Brown (1984), a patch size isolation relationship due to habitat or niche factors requires that environmental similarity is a decreasing function of distance between patches. This is violated whenever environmental variables are patchily distributed. We have not examined the distribution of different environmental factors in this study, although we have no a priori reason to reject a patchily distributions of environmental factors within the area. Instead we have tried to examine possible relationships between the distribution pattern of the species and the recruitment performance of the species within the study area.

The recruitment experiments showed that all four species could recruit successfully at both occupied and unoccupied localities, which suggests that all four species are seed limited within the study area. However, the recruitment success and the effect of the factorial treatments, disturbance or locality, differed among the species. The recruitment of *Carlina*, *Hypochoeris* and *Plantago* was significantly higher in the disturbance treatment compared with the undisturbed. Thus, in this case successful recruitment is probably not only depending on availability of seeds and locality as such, but also on a "window of opportunity" because recruitment is facilitated by a disturbance event (Eriksson and Fröborg 1996; Jesson et al. 2000). Earlier recruitment studies in the same area confirm that *Carlina* (Löfgren et al. 2000), *Hypochoeris* (Eriksson 1997) and *Plantago* (Eriksson and Eriksson 2000) recruit better in disturbed areas where the sward is partly or totally removed. According to the recruitment experiment, *Plantago* and *Hypochoeris* also seem to have specific niche demands among certain localities. A combination of dispersal and "fluctuating site" limitation could possibly make these species extraordinary vulnerable to the effects of isolation. If the study area is surrounded by other types of habitats the probability for a seed to be dispersed to a site in the centre of the area is generally higher than the probability of a seed being dispersed to a site at the edge of the area (due to more "lost seeds" into unsuitable habitats at a peripheral site). After many generations time this may lead to more persistent and larger patches (fused patches) in the centre of the area. The results could be interpreted as congruent with the result of the isolation analyses, since the same three species that showed a negative relationship between isolation and patch size, *Carlina*, *Hypochoeris* and *Plantago*, were also affected by some of the factors in the recruitment experiment (which might strengthen the effect of isolation). In addition, the recruitment of *Agrimonia* did not differ between disturbance treatments or between localities, and there was not a negative relationship between patch size and isolation (even a positive correlation was found when the α-value was 1). *Agrimonia* is both a relatively good recruiter (germination and survival was not reduced by the grass sward and the average recruitment was high), and a good disperser. The ability to recruit successfully could to some degree be explained by the seed size of *Agrimonia*. Large-seeded species have generally recruited better than small-seeded species, for example found in studies in semi-natural grasslands (Jakobsson and Eriksson 2000) and in deciduous forests (Ehrlén and Eriksson 2000). *Agrimonia*-seeds are effectively dispersed by animals and the *Agrimonia* often grows along landscape elements like forest edges and road verges (Eriksson and Kiviniemi 1998). This may be one explanation to the distribution pattern of *Agrimonia*, since a large number of linear elements are abundant in peripheral parts of the area due to the border between cultivated area and forest.

Patch-specific changes between the surveys of 1996–97 and 2000 were negatively related to patch size for *Agrimonia* but not for the other species. The knowledge that *Agrimonia* often is found along road verges and fences could imply that *Agrimonia* might be favoured in an intermediate succession phase between intensely cultivated and overgrown areas. The relative high decrease in number of individuals in larger patches of *Agrimonia* could thus be an effect of succession, if these patches have reached and passed a succession optimum. There was also a trend of a decreasing *Agrimonia* population between the two surveys, which also could be explained by a succession process. *Hypochoeris* patch size had also a tendency to decrease between the first and the second survey and 5 patches went extinct. At least four of the five extinct patches were located in deciduous forest, indicating a succession effect in these patches that probably were established when the forest was grazed or mowed and less dense.

Demographic studies within the studied area suggest that all four focal species have a relatively high persistence (population may survive for decades even with a negative growth rate) (Kiviniemi 1999; Kiviniemi and Eriksson 1999; Eriksson and Eriksson 2000; Löfgren et al. 2000; Kiviniemi 2002 (in press)). However, the survival success of populations in a longer time perspective cannot only depend on local persistence, but also on the establishment of new patches. Hence, variation in recruitment ability (shown in this and in other studies) together with variation in dispersal ability may be key processes in explaining the difference in distribution patterns of species. A study of adhesive dispersal by domestic cattle showed that *Agrimonia* had a high ability to disperse (Kiviniemi and Eriksson 1999). *Plantago* (lacking seed dispersal characters) is often categorized as a poor disperser. *Hypochoeris* and *Carlina* have a similar ability to wind dispersal of seeds according to a seed drop experiment (A. Jakobsson, unpublished data), and might be classified as intermediate between the dispersal abilities of *Agrimonia* and *Plantago*. A good disperser and recruiter such as *Agrimonia* is probably favoured by the protection and management of suitable habitats and dispersal routes, keeping small-scale structures in the landscape, like fences and midlet islets, and mowing of all road verges. Our results suggests that *Agrimonia* is not as negatively affected by isolation as the other examined species are, but may be favoured in a landscape containing a number of different succession stages. If there is a relatively high turnover of *Agrimonia* patches (due to succession), the species is strongly dependent on the presence of dispersal vectors to establish new patches. *Plantago* is a poor disperser and recruiter and was probably more dependent on traditional management where mowing decreased light competition and the transport of hay between different meadows and hay barns helped the species to disperse. This implies that *Plantago* is especially sensitive to fragmentation, and active transport of seeds and sowing into different suitable patches may be necessary to keep a vigorous *Plantago* population. In agreement with our study, Ouborg (1993) also found *Plantago media* populations to be affected by isolation along the Dutch Rhine-system. *Carlina* and *Hypochoeris* need disturbed patches to recruit and persist in a long time perspective. Since they have intermediate dispersal abilities, seed sowing would have to be considered if the fragmentation of the landscape continues. For *Carlina* increasing the numbers of grazers in the grasslands would favour the species through increased disturbance by trampling and reduced competition by more intense grazing. *Hypochoeris* is also favoured by disturbance but *Hypochoeris* -flowers are often grazed, which suggests that mowing or late summer grazing could increase the population growth of *Hypochoeris*. Thus, in conclusion, all focal species are seed limited within the study area. *Hypocheris* and *Agrimonia* have decreasing populations. *Carlina, Hypocheris* and *Plantago* have specific demands for a successful regeneration and the distribution pattern of patches of these species suggest that isolation has a negative effect on patch size. To preserve the species in the long run we suggest a diversified and well-planned management within the area.

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References

Bastin L. and Thomas C.D. 1999. The distribution of plant species in urban vegetation fragments. Landscape Ecology 14: 493–507.

Brown J.H. 1984. On the relationship between abundance and distribution of species. American Naturalist 124: 255–279.

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

Cousins S.A.O. 2001b. Plant species diversity patterns in a Swedish rural landscape: Effects of the past and consequences for the future. Department of Physical Geography and Quaternary Geology, Stockholm University, Stockholm.

Ehrlén J. and Eriksson O. 2000. Dispersal limitation and patch occupancy in forest herbs. Ecology 81: 1667–1674.

Eriksson Å. and Eriksson O. 2000. Population dynamics of the perennial *Plantago media* in semi-natural grasslands. Journal of Vegetation Science 11: 245–252.

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

Eriksson O. 1997. Colonization dynamics and relative abundance of three plant species (*Antennaria dioca*, *Hieracium pilosella* and *Hypochoeris maculata*) in dry semi-natural grasslands. Ecography 20: 559–568.

Eriksson O. and Ehrlén J. 1992. Seed and microsite limitation of recruitment in plant populations. Oecologia 91: 360–364.

Eriksson O. and Ehrlén J. 2001. Landscape fragmentation and the viability of plant populations. In: Silvertown J. and Antonovics J. (eds), Integrating Ecology and Evolution in a Spatial Context. Blackwell Science, Oxford, pp. 157–175.

Eriksson O. and Fröborg H. 1996. "Windows of opportunity" for recruitment in long-lived clonal plants: experimental studies of seedling establishment in *Vaccinium* shrubs. Can. J. Bot. 74: 1369–1374.

Eriksson O. and Kiviniemi K. 1998. Site occupancy, recruitment and extinction thresholds in grassland plants: an experimental study. Biological Conservation 87: 319–325.

Franzén D. and Eriksson O. 2001. Small-scale patterns of species richness in Swedish semi-natural grasslands: the effects of local species pools. Ecography 24: 505–510.

Grubb P. 1986. Problems posed by sparse and patchily distributed species in species rich plant communities. In: Diamond J. and Case T. (eds), Community Ecology. Harper & Row Publishers, New York, pp. 207–226.

Hanski I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63: 151–162.

Hanski I. 2000. Metapopulation Biology. Oxford University Press, Oxford.

Jakobsson A. and Eriksson O. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. Oikos 88: 494–502.

Jennersten O. 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae): Effects of habitat fragmentation on visitation and seed set. Conservation Biology 2: 494–502.

Jesson L., Kelly D. and Ashley S. 2000. The importance of dispersal, disturbance, and competition for exotic plant invasions in Arthur's National Park, New Zealand. New Zealand Journal of Botany 38: 451–468.

Kiviniemi K. 1999. Evolution of seed attributes, dispersal and population dynamics of plants, with special emphasis on fragmented habitats. Dep. of Botany, Stockholm University, Stockholm.

Kiviniemi K. 2002. Population dynamics of *Agrimonia eupatoria* and *Geum rivale*, two grassland species in a fragmented grassland. Plant Ecology (in press).

Kiviniemi K. and Eriksson O. 1999. Dispersal, recruitment and site occupancy of grassland plants in fragmented habitats. Oikos 86: 241–253.

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

Ouborg N.J. 1993. Isolation, population size and extinction: the classical and metapopulation approaches applied to vascular plants along the Dutch Rhine-system. Oikos 66: 298–308.

Poschlod P. and Bonn S. 1998. Changing dispersal processes in the central European landscape since the last Ice age: an explanation for the actual decrease of plant species richness in different habitats? Acta Botanica Neerlandica 47: 27–44.

Primack R.B. and Miao S.L. 1992. Dispersal can limit local plant distribution. Conservation Biology 6: 513–519.

Pulliam H.R. 2000. On the relationship between niche and distribution. Ecology Letters 3: 349–361.

Watt A.S. 1947. Pattern and process in the plant community. Journal of Ecology 35: 1–22.

Whittaker R.H. and Levin S.A. 1977. The role of mosaic phenomena in natural communities. Theoretical Population Biology 12: 117–139.

Wolf A.T. and Harrison S.P. 2001. Effects of habitat size and patch isolation on reproductive success of the serpentine morning glory. Conservation Biology 15: 111–121.