

Regional distribution and local abundance in the grassland plant *Carlina vulgaris* in two landscapes in Sweden

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Despite a considerable research interest in relationships between abundance and distribution across species not so many studies have examined this relationship within species. We investigated the relationship between regional distribution and local abundance in the grassland plant *Carlina vulgaris* (Asteraceae) within and between two regions in southern Sweden. In contrast to what is usually hypothesised, no positive relationship was found between the distribution and abundance of *C. vulgaris* within the regions, and between regions there was a negative relationship between large-scale distribution and local abundance. A seed-sowing and transplantation experiment suggested that there is no difference in the amount of suitable but unoccupied habitats between the regions, and unoccupied sites were more favourable than occupied sites. The mechanism behind the observed abundance distribution pattern in *C. vulgaris* could be either a time-lag in population change response, or a negative correlation in resources between the regions.

Key words: habitat fragmentation, regional population dynamics, seed dispersal, seed limitation, semi-natural grasslands, unoccupied sites

Introduction

Patterns of species distribution and abundance have been an important issue in ecology for a long time (Willis 1922, Andrewartha & Birch 1954, Krebs 1972, Brown 1984, Gaston 1998, Guo *et al.* 2000). One general conclusion is that widespread species often are locally abundant, whereas species with restricted distributions often tend to be rare also at the sites at which they occur, i.e. that there is a positive relationship between distribu-

tion and abundance across species (Brown 1984, Gaston & Lawton 1990, Hanski *et al.* 1993, Gaston *et al.* 2000). This relationship has been suggested to occur also within species (Lawton 1993), although this is poorly explored for most groups of organisms. One exception is for fish, where the relationship between distribution and abundance is of interest for commercial harvesting (e.g. Winters & Wheeler 1985, Swain & Morin 1996). The studies of abundance–distribution relationships within bird species (Newton

1997, Blackburn *et al.* 1998, Fahrig & Jonsen 1998, Gaston & Curnutt 1998, Venier & Fahrig 1998, Tellería & Santos 1999), butterfly species (Pollard *et al.* 1995, van Swaay 1995) and plant species (Boeken & Shachak 1998) have found both positive and negative relationships, or no relationships.

No consensus has been reached concerning the mechanisms behind a positive relationship between abundance and distribution (Gaston 1994, Brown *et al.* 1995, Hanski 1999), although most studies have focused on two main groups of mechanisms. The relationships have been suggested to reflect the niche-requirements of species and the spatial distribution of resources where generalist species or species using abundant resources are expected to have both a high abundance and a wide distribution (Brown 1984, Brown *et al.* 1995). Alternatively, the positive relationship could result from metapopulation dynamics (Hanski 1982, 1999) where a dense distribution increases migration among populations and thereby increases local abundance, and a high local abundance is expected to decrease the extinction risks and therefore enhance distribution.

Knowledge about if, and why, positive abundance–distribution relationships occur within species is of importance because the ongoing destruction and fragmentation of many natural habitats causes reductions in the distribution and/or abundance of many species. If there is a positive relationship caused by metapopulation dynamics (Hanski 1999) the loss of populations could lead to a decrease in the population size of the remaining ones, and a decrease in local population size could lead to loss of populations. This would imply that the changes are more severe for the species than the first-hand picture would reveal (Lawton 1993, Gaston 1999).

Within a species, the relationship can be investigated by monitoring changes in distribution and abundance over time in the same area (Boeken & Shachak 1998, Conrad *et al.* 2001). An alternative approach is to measure regional distribution and local abundance in different areas or patch networks (Hanski *et al.* 1995). Whereas local abundance is a quite straightforward concept and mostly measured as the number (or density) of individuals in local popu-

lations, the term “distribution” has been used to denote size of geographic range (e.g. Gaston & Lawton 1990), absolute number of occupied areas (e.g. Newton 1997), and the fraction of occupied suitable sites (e.g. Venier & Fahrig 1998). The latter definition is used in theories that hypothesise that the positive relationship between local abundance and regional distribution results from metapopulation dynamics. By using a specialised butterfly as study species, empty but suitable locations could be found by mapping the two plant species that host the butterfly larvae (Hanski 1999). For plants it is much more difficult to define empty but suitable sites. The most common method has been to transplant seeds or juveniles to potentially suitable sites and then following the fate of these transplants (e.g. Ehrlén & Eriksson 2000, Franzén & Eriksson 2003).

In this study, we investigate the relationship between regional distribution and local abundance in the monocarpic plant *Carlina vulgaris* by comparing regional distribution and local abundance of populations within and between two regions in Sweden. We also examine whether the regions differ in the fraction of suitable sites inhabited by *C. vulgaris*, by a seed sowing and transplantation experiment.

Methods

The species

Carlina vulgaris (Asteraceae) is a monocarpic perennial thistle, which starts to flower after one to several years, depending on the size of the rosette (Watt 1981, Klinkhamer *et al.* 1991). The florets are yellow or violet, tubular, protandrous, insect-pollinated or self-pollinated if insect pollination fails (Grime *et al.* 1988). Each seed is attached to a pappus, so *C. vulgaris* is considered a wind-dispersed species. Flowering occurs in late July to August and seeds ripen in September. In Sweden, *C. vulgaris* has a south-easterly distribution. Its main habitat is dry semi-natural grasslands, it benefits from grazing (Rydberg & Wanntorp 2001), and disturbance has a positive influence on recruitment (Löfgren *et al.* 2000, Franzén & Eriksson 2003).

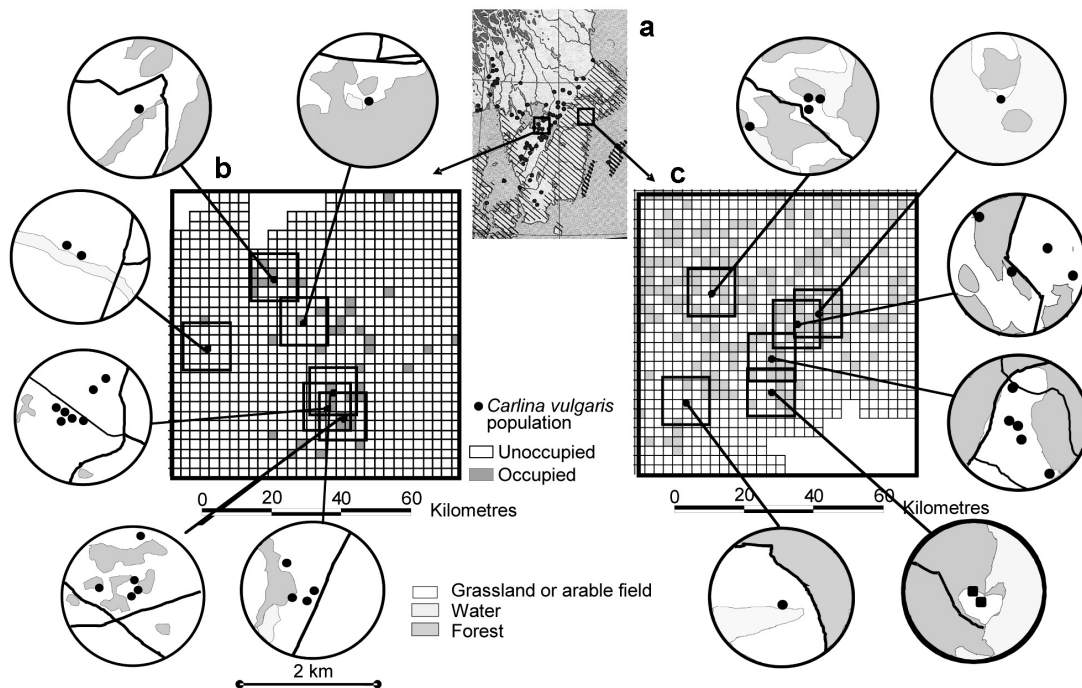


Fig. 1. Distribution patterns of *Carlina vulgaris* in Sweden, where *C. vulgaris* has a south-easterly distribution (a). In the county of Västergötland (b) and the county of Södermanland (c) presence/absence of the species was noted in 2.5×2.5 km squares. Regional distribution and local abundance was recorded in six areas in each region. Regional distribution was estimated at a large spatial scale as the number of occupied 2.5×2.5 km squares within quadrats with the side 12.5 km, and at a small spatial scale as the number of populations of *C. vulgaris* within circles with a diameter of 2 km.

Regional distribution and local abundance

The study areas were situated in two regions of Sweden (Fig. 1a), the county of Västergötland (Fig. 1b) and the county of Södermanland (Fig. 1c) which are separated by approximately 300 km. Estimates of regional distribution and local abundance of *C. vulgaris* were made in six areas in each region. The areas were centred on randomly selected *C. vulgaris* populations in each region. In summer and autumn 2001 the number of populations within a circle with a diameter of 2 km was counted. A population of *C. vulgaris* was defined as an aggregation of individuals separated from all other aggregations of individuals by at least 100 m. If the distance between two aggregations of *C. vulgaris* was between 100–200 m they were classified as separate populations if not connected with suitable habitat. This restriction was to ensure that the populations

were not connected with sparsely scattered individuals and therefore should be counted as one population. The number of flowering individuals was counted in each population.

Local abundance in an area was calculated as the mean number of flowering individuals in all the populations in the area in 2001. Regional distribution in an area was defined as the number of populations found in the area in 2001. To estimate distribution also at a larger spatial scale information from botanical surveys that were made during 1980 to 2001 in Södermanland (Rydberg & Wanntorp 2001) and during 1985 to 2002 in Västergötland (Bertilsson *et al.* 2002) was used. Quadrats with the side 12.5 km were centred on the circular areas and the number of occupied 2.5×2.5 km squares in the quadrats was compiled from the botanical surveys. Local abundance in the circular areas was considered to be representative also of the local abundance in the quadrats. The quadrats were partly over-

lapping so a separate test with six randomly selected non-overlapping quadrats in each region was performed. The large-scale distribution may overestimate the distribution since the botanical surveys had accumulated information during several years. However, we consider this unlikely since we used a coarse estimate (absence or presence of at least one population in a 2.5×2.5 km square), and populations of *C. vulgaris* in grasslands with constant management regimes have been observed to have rather stable population dynamics (Grubb 1986, van der Meijden *et al.* 1992, Löfgren *et al.* 2000). Information of the total distribution in each region, calculated as the percentage of occupied 2.5×2.5 km squares, was also obtained from the botanical surveys (Rydberg & Wanntorp 2001, Bertilsson *et al.* 2002).

Differences between the two regions in local abundance and distribution were investigated using one-way ANOVA. The relationships between local abundance and regional distribution within each region were investigated with correlation analyses. Regional distribution and local abundance was log-transformed to meet the assumptions of the models.

Estimation of empty but suitable sites

To investigate if our estimate of distribution was compatible with Hanski's definition of distribution, i.e. the fraction of suitable habitat that is occupied (Hanski 1999), we investigated whether the fraction of suitable sites occupied by the species differed between the two regions. A study area of $2 \text{ km} \times 1.5 \text{ km}$ was chosen in each region ($58^{\circ}17' \text{N}$, $013^{\circ}41' \text{E}$ for Västergötland and $50^{\circ}50' \text{N}$, $17^{\circ}24' \text{E}$ for Södermanland). In the study area in Västergötland an inventory was made during 2000 and in Södermanland data on location of populations of *C. vulgaris* was obtained from a previous study in the area (Franzén & Eriksson 2003). Twelve unoccupied but potentially suitable sites were identified in each area. An unoccupied suitable site was identified by the following criteria: (1) the presence of dry grassland, and (2) the suitability of the site with consideration to the aspect (south, south-west or south-east) and turf height (low to medium).

Seeds were collected in the autumn of 1999 and juveniles were raised in a common garden in the summer of 2000. Seeds and eight-week-old juveniles were planted in twelve unoccupied and ten occupied sites in each study area. At each site a slight disturbance was made in five 1 dm^2 plots, and twenty seeds were sown in each of four plots. One plot was kept empty to control for natural seed rain. Furthermore, at each site five juveniles were planted and watered immediately after planting to enhance rooting. Germination, survival, rosette size and flowering were recorded in spring and autumn in 2001 and 2002. Rosette size was estimated by counting the number of leaves, and measuring the longest leaf in each rosette. An index of rosette size was calculated as log length of the longest leaf \times number of leaves. In the analyses only rosette size measured in autumn 2002 was used. For germination the sum of all germinated seeds during the period was used. The criterion for a site to be denoted as suitable for *C. vulgaris* was that at least one juvenile originating from the transplanted seeds (hereafter called seedlings) had survived and at least one juvenile originating from the transplanted juveniles (hereafter called juveniles) had survived or flowered until autumn 2002. One occupied site in Västergötland was lost due to missing markers. The difference in suitability between occupied and unoccupied sites was analysed using a χ^2 test. Differences in seedling and juvenile rosette size between occupied and unoccupied sites in autumn 2002 were analysed as site means in one-way ANOVA. Differences in proportion of germinated seeds and survived seedlings were analysed with site as a block factor in a logistic model in SAS genmod module. Differences in proportion of survived juveniles and flowering individuals between occupied and unoccupied sites were analysed with site as a block factor in a generalised linear model.

Statistical analyses

The statistical analyses were performed in the SAS system 8 for windows (SAS Institute Inc, Cary, USA) and in Statistica 6.0 (StatSoft Inc, Tulsa, USA).

Results

Distribution and abundance

The two regions, Västergötland and Södermanland, did not differ in regional distribution of *C. vulgaris* at the smaller spatial scale (Table 1). The average number of populations within circular areas with a 2 km diameter was 3.2 (S.E. = 0.95, $n = 6$) in Västergötland and 3.0 (S.E. = 0.82, $n = 6$) in Södermanland. At the larger spatial scale, there was a significant difference in regional distribution where the average number of occupied 2.5×2.5 km squares within areas with 12.5 km sides was 5.5 (S.E. = 1.48, $n = 6$) in Västergötland and 13.5 (S.E. = 2.0, $n = 6$) in Södermanland (Table 1). The difference between the regions in large-scale distribution was even more pronounced when tested for the non-overlapping areas (Table 1). In total *C. vulgaris* occurred in 4.5% of all 2.5 km squares in Västergötland, and in 24% of the squares in Södermanland (Fig. 1a and b). Further, *C. vulgaris* had a significantly higher local abundance in Västergötland, where the mean number of flowering individuals in populations within circular areas was 570 ($n = 6$, S.E. = 289) as compared with that in Södermanland, where it was 73.3 ($n = 6$, S.E. = 34.3) (Table 1). Thus, at the larger spatial scale we found a negative relationship between abundance and distribution.

No relationship was observed between local abundance and regional distribution at the smaller spatial scale within the regions ($p = 0.07$, $n = 6$ for Västergötland and $p = 0.18$, $n = 6$

for Södermanland), or between local abundance and regional distribution at the larger spatial scale ($p = 0.13$, $n = 6$ for Västergötland and $p = 0.92$, $n = 6$ for Södermanland).

Estimation of empty but suitable sites

There was successful recruitment in terms of germination and survival of at least one seedling and survival or flowering of at least one juvenile at almost all sites, both in Södermanland (11 of 12 unoccupied and 8 of 10 occupied, $\chi^2 = 0.63$, $p > 0.05$) and in Västergötland (12 of 12 unoccupied and 8 of 9 occupied, $\chi^2 = 1.40$, $p > 0.05$). Germination was higher at unoccupied sites in both regions (10.5% vs. 8.6% in Södermanland, and 14% vs. 8% in Västergötland), and in Västergötland survival of seedlings was higher at unoccupied sites (74% vs. 62%, Table 2). There was no difference in seedling size between the unoccupied and the occupied sites in any of the regions, but in Västergötland juveniles were larger at unoccupied sites (Table 3). Survival of juveniles did not differ among the sites in any of the two regions, but in Västergötland, flowering occurred more often at unoccupied sites (Table 4). In Södermanland, only one juvenile flowered, and this was at an unoccupied site. In summary these results show that *C. vulgaris* is limited by dispersal in both study areas, and that there are no indications of difference in the fraction of suitable but unoccupied site between the regions. Furthermore, there are indications of unoccupied sites being more suitable than occupied sites.

Table 1. The differences in regional distribution measured at two spatial scales and local abundance of *Carlina vulgaris* between two regions in Sweden. The measure of distribution at the larger spatial scale was centred on the measure of distribution in a small spatial scale, and was partly overlapping. Therefore an additional test with randomly chosen non-overlapping areas was performed. V = the county of Västergötland, S = the county of Södermanland. + = higher distribution/abundance, - = lower distribution/abundance. Analyses were made with one-way ANOVA. n.s. = non significant, * = $p < 0.05$, ** = $p < 0.01$.

Response variable	d.f. effect, error	MS	F	Direction	
				V	S
Regional distribution, small-scale	1,10	0.002	0.003	n.s.	
Regional distribution, large-scale	1,10	3.62	6.79	*	- +
Regional distribution, large-scale, non-overlapping	1,10	4.07	9.71	**	- +
Local abundance	1,10	13.87	12.59	**	+ -

Discussion

In contrast to the in general expected positive relationship between abundance and distribution (Gaston & Lawton 1990), we found no relationship between regional distribution and

local abundance in *C. vulgaris* within regions and a negative relationship between large-scale distribution and local abundance between regions. Thus it might appear that our results for *C. vulgaris* do not support the existence of positive feedback where local abundance and

Table 2. Germination and survival of *Carlina vulgaris* seedlings in occupied and unoccupied sites in two regions, the county of Södermanland and the county of Västergötland, Sweden. Differences were analysed in a logistic model with type 3 LR statistics. Status = occupied/unoccupied. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.0001$, n.s. = non significant.

Region	Response variable	Source of variation	d.f.	χ^2	Direction	
					Occup.	Unoccup.
Södermanland	Germination	Status	1	9.95 **	–	+
		Site (status)	20	86.61 ***		
	Survival of seedlings	Status	1	0 n.s.		
		Site (status)	20	251 ***		
Västergötland	Germination	Status	1	4.76 *	–	+
		Site (status)	19	82.05 ***		
	Survival of seedlings	Status	1	4.48 *	–	+
		Site (status)	17	53.31 ***		

Table 3. Juvenile and seedling size of *Carlina vulgaris* in occupied and unoccupied sites in two regions, the county of Södermanland and the county of Västergötland, Sweden. Differences between occupied and unoccupied sites were analysed on site means with one-way ANOVA. * = $p < 0.05$, n.s. = non significant.

Region	Response variable	d.f. effect, error	MS	F	Direction	
					Occup.	Unoccup.
Södermanland	Seedling size	1,18	0.52	3.66 n.s.		
	Juvenile size	1,18	0.001	0.004 n.s.		
Västergötland	Seedling size	1,18	211.2	1.81 n.s.		
	Juvenile size	1,19	3.27	5.5 *	–	+

Table 4. Survival of juveniles and flowering for *Carlina vulgaris* in occupied and unoccupied sites in two regions, the county of Södermanland and the county of Västergötland, Sweden. Differences were analysed in a generalised linear model with type 1 LR statistics. Status = occupied/unoccupied. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.0001$, n.s. = non significant.

Region	Response variable	Source of variation	d.f.	χ^2	Direction	
					Occup.	Unoccup.
Södermanland	Juvenile survival	Status	1	0.85 n.s.		
		Site (status)	20	58.06 ***		
	Flowering	Status	1	1.11 n.s.		
		Site (status)	18	6.42 ***		
Västergötland	Juvenile survival	Status	1	0.30 n.s.		
		Site (status)	19	48.40 ***		
	Flowering	Status	1	9.89 **	–	+
		Site (status)	18	37.46 **		

regional distribution enhance each other through the mechanism of dispersal between populations (e.g. Hanski *et al.* 1993, Hanski 1999). However, a negative abundance–distribution relationship or an absence of such a relationship may be observed if there is a time-lag in the response of local population size to changed distribution, or vice versa (Gaston & Curnutt 1998). In Sweden, it is not unlikely that such a time-lag occurs for *C. vulgaris*. Semi-natural grasslands have declined drastically in Sweden during the last century (Eriksson *et al.* 2002) and so has probably also the distribution of *C. vulgaris*. On the other hand, populations of *C. vulgaris* in grasslands with constant management regimes have rather stable population dynamics (Grubb 1986, van der Meijden *et al.* 1992, Löfgren *et al.* 2000), which may delay the response of local abundance to a reduced distribution.

Hanski (1999) defined distribution as the fraction of suitable habitat that is occupied and this deviates from the way we estimated distribution. As in most other empirical studies we estimated distribution as the number of populations within an area, not as the fraction of suitable habitats occupied. This means that the abundance–distribution relationship in *C. vulgaris* may in fact be positive, if the number of suitable habitats is lower but more often occupied in the areas with a high local abundance. However, the sowing and transplantation experiment did not show any difference in fraction of unoccupied suitable sites between the regions. The experiment also showed that the distribution of *C. vulgaris* is limited by dispersal, similar to what has been found for many other grassland species (Primack & Miao 1992, Kiviniemi & Eriksson 1999, Turnbull *et al.* 1999, Franzén & Eriksson 2003). An unexpected result was that *C. vulgaris* performed better at unoccupied than at occupied sites. This could either be due to some kind of degradation of the habitat after colonisation affecting already occupied sites, for example by accumulation of pathogens, or simply due to the fact that plants are passively dispersed. Passive dispersal implies that *C. vulgaris* cannot direct its seeds towards the most suitable sites, so therefore it grows at places that are “good enough” but does not, at all times, occupy the most suitable sites in a landscape.

The negative relationship between abundance and distribution found between the regions could also result from the spatial distribution of resources suggested by Brown (1984), with the difference that in this case there is a negative correlation of resources instead of a positive. For *C. vulgaris* this is not unlikely, since the region with few but large populations is more heavily exploited by large-scale farming compared to the other region, and more resources may be available for *C. vulgaris* in that region due to the fact that it is more productive.

Gaston (1999) suggested that a positive abundance–distribution relationship implies a “double jeopardy” for declining species. As a corollary, a lack of such a positive relationship would provide a more optimistic picture. However, this conclusion is only valid if the pattern is not generated by a response time-lag, or if the time-lag is large enough to be considered as permanent in management perspectives. Also a positive relationship that is caused by correlation of resources would be more beneficial from a conservation point of view. Since plants often have properties that promote the development of remnant populations such as clonal propagation and seed banks (Eriksson 1996), time-lag effects can be expected to be very common in plants. To our knowledge only one previous study has investigated within-species relationships between distribution and abundance in plants (Boeken & Shachak 1998) and this study found both positive and negative abundance–distribution relationships within the examined species. Thus, a first step to understand the mechanisms behind abundance–distribution patterns within plant species is to continue to document these patterns.

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