

Management actions are required to improve the viability of the rare grassland herb *Carlina biebersteinii*

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Small population size of many rare or endangered plant species makes a quantitative assessment of population status challenging because of the lack of detailed demographic data on different life-history stages. However, an urgent assessment is often required to start possible management actions. We performed a count-based population viability analysis (PVA) using discontinuous time series to quantitatively assess the viability of a rare, monocarpic, grassland herb *Carlina biebersteinii* Bernh. ex Hornem. (synonyms: *C. vulgaris* L. ssp. *longifolia*, *C. vulgaris* L. ssp. *stricta*) and examined demographic and environmental factors contributing to its viability. Based on 12 abundance counts of eight *C. biebersteinii* populations in Finland, we found that seven out of the eight population sizes declined during the observation period, and that annual population growth rates were slightly synchronised among the populations. Synchrony in annual population growth rates declined with increasing geographic distances among the populations, while fluctuations in the number of flowering plants were unrelated to geographic distances among the populations. According to stochastic simulations, the risk of losing all flowering individuals during the next 20 years will be high for unmanaged populations. To prevent the populations from gradually declining, our results suggest that summer grazing or removal of woody vegetation is required to increase habitat openness and consequently, to improve fecundity and seedling recruitment.

Habitat degradation is the main threat for plant species (Schemske et al. 1994) and it affects population viability via underlying demographic rates such as survival, growth and fecundity. Habitat degradation may lead to smaller and fragmented populations, which often have an elevated risk of extinction (Eisto et al. 2000, Lennartsson 2000, Matthies et al. 2004). This is because of the reproductive problems that small populations face (Leimu et al. 2006). The small population sizes of many rare or endangered plant species make it difficult to collect the accurate demographic data on different life-history stages required to assess population viability with traditional matrix population models. Matrix population models constructed from a few individuals per life-history stage are likely to contain a large amount of sampling error (Vandermeer 1978, Moloney 1986), making the estimates of population viability unreliable. For small populations, it is therefore tempting to replace a demographic analysis with indirect estimates of population viability, such as estimates of the amount of genetic variation in a population, seed production or growth of individual plants (reviewed by Oostermeijer et al. 2003). Nevertheless, single estimates of plant fitness may not be good surrogates for population status because they are not necessarily related to population viability (Ehrlén 2003,

Ramula 2008). A demographic analysis is thus needed to quantitatively assess population status.

Although detailed demographic data on different life-history stages may be lacking for small populations, there often exist count data on abundance (Schemske et al. 1994, Morris et al. 2002, Jacquemyn et al. 2007). For rare or endangered species, abundance counts conducted in some years during a longer period of time may be the only demographic data available (Morris et al. 2002). These count data may be inadequate for advanced time series analyses, such as autoregressive models (ARMA and ARIMA), but population viability may be assessed using a count-based population viability analysis (PVA). A count-based PVA is the simplest demographic analysis, relying on annual abundance estimates from at least ten years (Morris and Doak 2002). Because the collection of demographic data is time-consuming and may critically delay the start of management actions, population status and possible management actions are needed to be assessed urgently. Therefore, for small populations, the only possibility of assessing population status quantitatively is to use relatively short time series, even if they may produce quite rough estimates. Here, we perform a count-based PVA using discontinuous abundance counts to quantitatively determine the viability of a rare, monocarpic,

grassland herb *Carlina biebersteinii* Bernh. ex Hornem. (synonyms: *C. vulgaris* L. ssp. *longifolia*, *C. vulgaris* L. ssp. *stricta*). We also seek demographic and environmental factors that may contribute to population viability for *C. biebersteinii*.

Rare species often have specific habitat requirements and their populations may occur in quite a small geographic area. Adjacent populations facing similar environmental conditions may exhibit synchronised dynamics so that a good year results in high population growth rates for all populations in the same geographic area, and a poor year results in lowered population growth rates. Synchronised population dynamics have been found for common annual plant species occurring on coastal plant communities and in road verges (Coomes et al. 2002, Crawley and Brown 2004). If population dynamics for rare plant species are synchronised, estimates from one population might be used as surrogates for other populations of the same species, which would considerably reduce the amount of effort required for collecting demographic data.

Because many herbaceous grassland plant species are weak competitors, they require an open habitat to be able to persist (Eisto et al. 2000, Lennartsson 2000, Löfgren et al. 2000). During past decades, a lowered grazing pressure has led to closing of open grassland habitats and consequently a decline of a number of grassland plant species in Europe. Our study species, *C. biebersteinii*, has also declined and has been classified as 'threatened' in Finland (Rassi et al. 2001). The occurrence of the species is restricted to open meadows and grasslands. Current populations are relatively small in size, usually containing less than 50 flowering individuals. We used eight *C. biebersteinii* populations to investigate the following questions: (i) what is viability of the short-lived, monocarpic herb *C. biebersteinii*? (ii) are population dynamics synchronised among closely situated populations? (iii) how are population size, lifetime seed production and vegetation cover related to population viability?

Material and methods

The species

In the first summer after germination, *C. biebersteinii* (Asteraceae) develops a rosette and in the third summer or later, a flowering stem about 30–60 cm high. Flowering is fatal and the plant dies after having flowered once. An individual plant usually has 1–7 capitula that are pollinated by bumble bees (*Bombus* spp.) but in favourable habitats plants can occasionally have up to 35 capitula (L. P. pers. obs.). *Carlina biebersteinii* reproduces by seed and there is no vegetative reproduction. The annual reproductive success of the species depends on the availability of pollinators as the germination of self-pollinated seeds is poor (Kemppainen et al. 1990). The seed bank of *C. biebersteinii* is probably absent. The studies show that at least closely-related *C. vulgaris* is not likely to have a persistent seed bank (Grubb 1986, Eriksson and Eriksson 1997). In Finland, *C. biebersteinii* is an archaeophyte that arrived with prehistoric immigrating people. The species occurs in open habitats such as meadows, abandoned fields and grassland strips by road verges (Kemppainen et al. 1990) but has declined during the past decades.

Populations and estimation of population sizes

We collected the annual counts of plant abundance from the Finnish Environmental Institute's database of threatened species, which contains data on threatened plant and animal species in Finland, their habitat sites, and observations or abundance counts of these species. The database is accessible to conservation authorities and land use planners, and others who need information on threatened species may order the data. The observations have been collected by conservation authorities at the regional environment centres, the regional units of Finnish Forest and Park Service, research scientists, volunteer specialists and amateur naturalists. For *C. biebersteinii*, abundance counts were based on the exact numbers of flowering plants. Non-flowering rosettes were only occasionally recorded and were not possible to use for population estimates because of the varying sampling procedure over time. As flowering plants were counted exactly for each population, they provided the most reliable estimate of annual population sizes. The number of flowering plants does not indicate the exact population size because populations always include non-flowering rosettes, usually 3–5 times more than flowering plants. The abundance of flowering plants, however, serves as an indicator of a population's viability for a short-lived species with no persistent seed bank.

We located eight out of 27 previously recorded flowering *C. biebersteinii* populations for which at least 12 annual abundance counts were available. These populations were situated within the area of 100 × 225 km in southeast Finland (61°40'N, 27°16'E), and occurred in abandoned fields and dry meadows (Table 1). We considered plants belonging to separate populations if the distance between them was ≥0.2 km, which was the distance between the nearest populations. The populations were mainly unmanaged, excluding population 3 in which woody vegetation was annually removed. The majority of the populations were small and usually contained less than 50 flowering individuals per year, while two of the populations were larger and contained more than 100 and 2000 flowering individuals, respectively (Table 1). We re-visited each of the eight populations during 2004–2005 and determined environmental conditions by estimating vegetation cover and the average lifetime seed production.

Vegetation analyses

To evaluate the influence of co-occurring vegetation on the performance of *C. biebersteinii*, we conducted vegetation analyses. For each population, we visually measured the moss cover and the field-layer cover (i.e. the vascular plant cover) from 5–10 1 × 1 m squares, depending on population size. We placed the first square in the middle of *C. biebersteinii* population and then placed the remaining squares systematically from the first square. To determine the total cover of field-layer vegetation, we summed up the cover of each vascular plant species in each square. Further, we visually measured canopy cover (i.e. the tree cover) from 1–4 randomly selected sites per population. We used the mean estimates of moss cover, field-layer cover and canopy cover for each population.

Table 1. The habitat, approximated distance from the first population, survey period, number of abundance counts (n), latest population size as the number of flowering plants and population growth rate μ (variance of growth rate in parentheses) for eight *Carlina biebersteinii* populations in southeast Finland.

Population and habitat	Distance (km)	Survey period		Latest pop. size	Population growth rate
		Years	n		
1 Open mixed forest		1984–2006	14	138	−0.02 (0.74)
2 Open mixed forest	0.2	1985–2006	13	4	−0.15 (0.32)
3 Road verge	20	1982–2003	13	2055	0.14 (0.16)
4 Abandoned field	30	1986–2006	16	22	−0.11 (0.43)
5 Dry meadow	50	1984–2006	12	0	−0.05 (0.91)
6 Abandoned field	60	1988–2006	13	11	−0.08 (1.00)
7 Abandoned field	220	1987–2006	14	6	−0.06 (0.71)
8 Meadow and deciduous trees	225	1989–2006	12	30	−0.05 (0.45)

Calculation of lifetime seed production

To determine the average lifetime seed production for each population, we counted the number of capitula from every flowering plant for the small populations and from several haphazardly sampled flowering plants for the large populations. We then multiplied the mean number of capitula per flowering plant by mean seed number per capitulum. For the mean seed number per capitulum, we used estimates from the previous studies of *C. biebersteinii* conducted in the same populations (Kempainen et al. 1990, Puhakainen 2006). This enabled us to roughly estimate seed production per flowering plant.

Population viability estimates

In a count-based population viability analysis (PVA), abundance counts are ideally performed annually over many years. This results in a continuous series of estimates of population size which can be used to estimate the long-term population growth rate. Population growth rate can also be estimated from a discontinuous time series with different lengths of census intervals (Morris and Doak 2002). According to Morris and Doak (2002), ten years of annual counts is the minimum for conducting a count-based PVA. Still, longer time series than ten years are often required to produce accurate and unbiased population estimates (Thomas et al. 2002, Lotts et al. 2004).

We used discontinuous time series of eight *C. biebersteinii* populations to predict population viability into the future. To make time series consisting of different numbers of abundance counts (range: 12–16 counts, Table 1) comparable among the study populations, we used the 12 latest counts of each population and omitted the rest. Hence, the length of time series varied among the populations (range: 17–22 years) but always consisted of 12 abundance counts of population size. To estimate population growth rates, we used the maximum likelihood method according to Dennis et al. (1991) and calculated a change in logarithmic population size for each census interval as $\log(N_{t+1}/N_t)$, where N denotes the number of flowering plants in a population. Note that $n+1$ abundance counts are needed to produce n estimates of changes in population size. Abundance counts were not performed every year and therefore, we corrected the logarithmic changes in population sizes with the length of each census

interval as described in Morris and Doak (2002). We then used a linear regression of the yearly change in population size with zero intercept to estimate population growth rate (μ) and the variance of growth rate (σ^2) (Dennis et al. 1991).

For each population, we predicted population size for 40 years with a stochastic simulation. Stochasticity here refers to annual changes in population growth rates resulting from demographic variation and/or environmental variation. In the simulations, we randomly selected population growth rate for each year based on its mean value (μ) and variance (σ^2) using a normal distribution for μ (Foley 1994). We started the simulations from the first observed population size for each population and performed 10 000 trajectories per year. We predicted population size as $S_{t+1} = \mu_t + S_t$, where population growth rate (μ) and logarithmic population size (S) vary over time. We also examined the dependence of population dynamics on plant density separately for each population by correlating changes in logarithmic population size against the number of flowering plants. Although the data analyses showed a weak negative density dependence for populations 6, 7 and 8, we omitted density dependence from the final simulations because of a poorer fit of the density-dependent models than the density independent models. The poor fit may have resulted from small numbers of flowering plants and consequently unreliable estimates of density dependence, or arbitrarily set carrying capacities for the density-dependent models. There was no sign of a positive density dependence in any of the populations. Further, we did not include possible temporal autocorrelation in our simulations because only short continuous time series were available for each population. The longest continuous time series was seven years for population 3, and four or five years for the rest of the populations. Several studies have reported that such short time series are likely to produce unreliable estimates of autocorrelation (Foley 1994, Swanson 1998). We conducted all stochastic simulations in Matlab version 5.0.

Synchrony in population dynamics

To examine the possibility of using viability estimates from one *C. biebersteinii* population as a surrogate for other populations within the same geographic region, we visually examined the synchrony of annual population growth rates

among the eight study populations. Because the study populations were quite closely situated (Table 1), we included all the populations in the comparison. We were able to examine synchrony for five different years from which population growth rates were available for at least seven populations. For population 1, some management actions were performed in 2004–2005 and therefore, we only included the growth estimates before the management actions for that population. Hence, all the estimates of population growth rates included in the synchrony comparison mainly originated from unmanaged populations.

Statistical tests

To investigate the dependence of population growth rate (μ) on population size, lifetime seed production, moss cover, field-layer cover and canopy cover, we performed a multiple linear regression (PROC REG in SAS ver. 9.1.) across the study populations. The number of flowering plants from the latest abundance census was used as population size for each population, the variable was $\log(x+1)$ -transformed. Collinearity analysis revealed significant negative correlations between seed production and canopy cover, and between field-layer cover and canopy cover. Due to these correlations, we only included canopy cover in our final regression model and omitted seed production and field-layer cover. We used a stepwise linear regression to fit the best model. We also conducted forward and backward regressions but they produced the same final model as the stepwise regression. We only present results from the stepwise regression. The homogeneity of data was visually examined from the residuals.

To determine whether synchrony in population dynamics is related to geographic distances among the populations, we conducted a Mantel test which calculates a correlation between two distance matrices of the same size. To construct matrices, we first calculated spearman correlation coefficients between pairs of the populations for annual population growth rates and the number of flowering plants, resulting in two 7×7 correlation matrices. All data available from unmanaged populations were used for these correlation coefficient calculations ($n = 4$ – 11 common years for pairs of the populations). Further, we calculated a 7×7 matrix based on geographic distances between pairs of the populations (Table 1). We then ran a Mantel test with 1000 permutations to compare the matrices of the annual population growth rates and the geographic distances of the populations, and the matrices of the number of flowering plants and the geographic distances of the populations using R 2.4.1. Only the lower halves of the matrices were used for the tests. A negative correlation between the matrices indicates that populations geographically close to each other are more alike in their dynamics than populations that are geographically more apart.

Results

Viability and synchrony of populations

Population viability analyses (PVAs) based on discontinuous time series predicted seven out of eight *C. biebersteinii*

populations to be declining (annual decline 2–15%). The second largest population (population 1) showed the slowest annual decline, while only the largest and annually managed population (population 3) was increasing in size (Fig. 1, Table 1). According to the stochastic simulations, the risk of losing all flowering individuals during the next 20 years will be high for majority of the populations (Fig. 1). This suggests that without any management actions the populations are going to go extinct in the near future, except for the two largest populations. Since all simulations resulted in wide confidence intervals for population size (Fig. 1), the estimates of future population sizes are unsure but the simulations clearly show which of the populations are dramatically declining.

Population dynamics were somewhat synchronised for three out of five years (1988, 1989 and 2005), although the growth rates greatly varied among the populations particularly in 1988 (Fig. 2). For the other two years (1995 and 2004), the population growth rates varied from positive to negative among the populations within the same year, showing asynchrony (Fig. 2). Synchrony in annual population growth rates significantly declined with increasing geographic distances among the populations ($r = -0.40$, $p = 0.018$, Mantel test, Fig. 3a). There was no spatial autocorrelation among the populations for the number of flowering plants ($r = 0.04$, $p = 0.825$, Mantel test, Fig. 3b). For the number of flowering plants, correlation coefficients were often positive (Fig. 3b), suggesting that the number of flowering plants tended to fluctuate similarly among all the eight study populations regardless of the geographic distances among them.

Factors contributing to population viability

In the multiple regression model with population size, canopy cover and moss cover as explanatory variables, canopy cover was not statistically significantly related to population growth rate ($b \pm SE = -0.15 \pm 0.09$, $t = -1.61$, $p = 0.182$, Fig. 4a). After canopy cover was dropped from the model, population growth rate increased significantly with population size ($b = 0.03 \pm 0.01$, $t = 4.11$, $p = 0.009$) and decreased marginally significantly with moss cover ($b = -0.16 \pm 0.07$, $t = -2.46$, $p = 0.057$) (Fig. 4b, 4c). In this final model, population size and moss cover explained 76% of the variation in population growth rate ($F_{2,7} = 12.18$, $p = 0.012$).

Discussion

Based on discontinuous time series of abundance counts of eight *Carlina biebersteinii* populations, our results indicate that the studied populations are in a state of general decline, and that the risk of losing all flowering individuals during the next 20 years will be high. The exceptions are the two largest populations (populations 1 and 3), in which some management has been conducted. Although the populations were generally declining, their population dynamics were only slightly synchronised and population growth rates often varied from negative to positive among the populations within the same year. In general, geographically

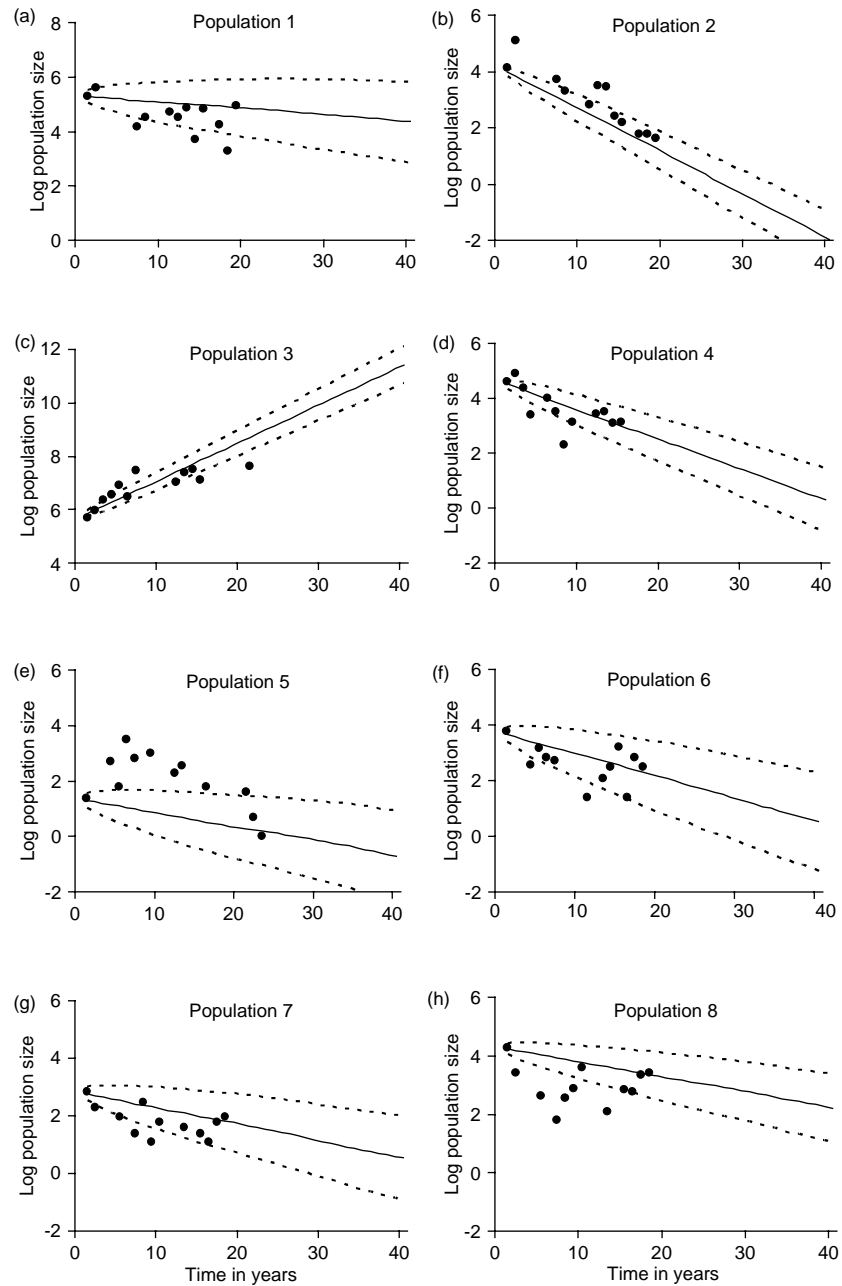


Figure 1. Predicted population sizes (mean \pm 95% confidence interval) in relation to observed population sizes for eight *Carlina biebersteinii* populations. Population size is log ($x + 1$)-transformed. Predictions are based on stochastic simulations for 40 years with 10 000 trajectories.

closely situated populations exhibited more synchronised annual population growth rates than populations that were geographically more apart. Our results indicate that viability estimates derived from one *C. biebersteinii* population might be used as rough surrogates for other closely situated populations of the same species when demographic data are lacking. However, these surrogates should only be considered as approximate because environmental conditions are likely to vary in a small spatial scale, causing fluctuations in local population dynamics.

Many grassland species require an open habitat to be able to persist (Eisto et al. 2000, Lennartsson 2000, Löfgren et al. 2000). The present study suggests that habitat

openness is essential also for *C. biebersteinii* to ensure seedling recruitment. In shady populations, suitable microhabitats are probably scarce because of moss cover and the accumulation of litter. Based on seed sowing experiments, Kemppainen et al. (1990) observed quite low germination rates in unmanaged *C. biebersteinii* populations (range 0–16%), whereas removal of surrounding vegetation increased germination up to 26%. Keizer et al. (1985) also observed that moss cover impeded seed germination of *C. vulgaris*. Our finding that population viability declines with moss cover should be, however, interpreted cautiously. Many *C. biebersteinii* populations had a high moss cover and the negative relationship between population growth

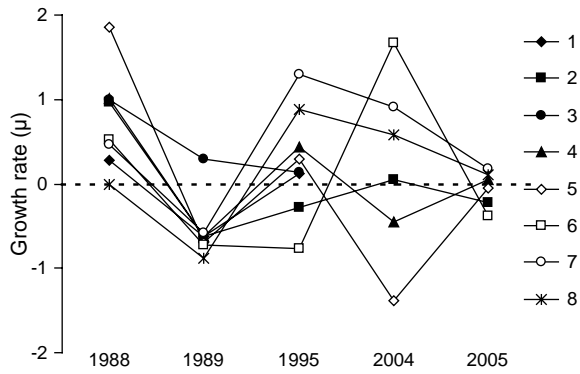


Figure 2. Synchrony of population growth rates (μ) among eight *Carlina biebersteinii* populations for five years. Zero population growth is indicated with a dashed line.

rate and moss cover was mainly due to one population with a high population growth rate and a low moss cover. In addition to the amount of moss cover, a significant negative relationship between lifetime seed production and canopy cover indicates that seed production is lower in shady populations than in open populations. Because *C. biebersteinii* is unlikely to have a permanent seed bank, the recruitment of the species highly depends on its annual seed production. A failure in seed production in one summer will result in few seedlings in the next year and finally a small cohort of flowering plants.

The viability of *C. biebersteinii* populations was positively related to their size. There are at least three possible explanations for this positive relationship. First, small populations tend to attract less pollinators than large populations (Mustajärvi et al. 2001), and the lack of pollinators may have led to a reduced seed production

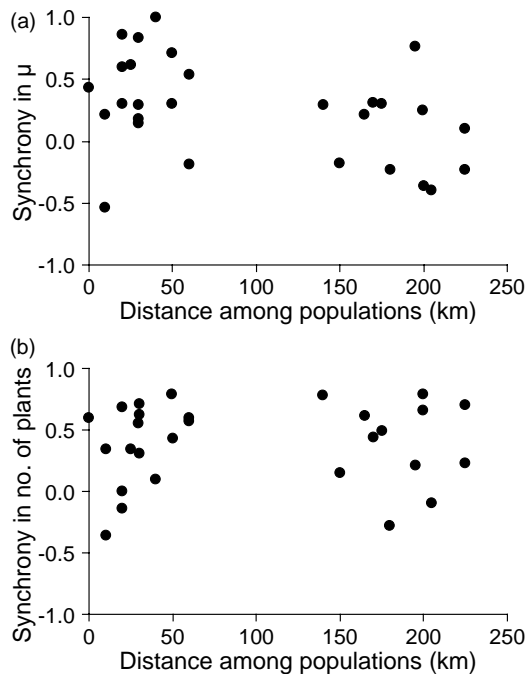


Figure 3. Synchrony in (a) annual population growth rates (μ) and (b) the number of flowering plants in relation to geographic distances among eight *Carlina biebersteinii* populations.

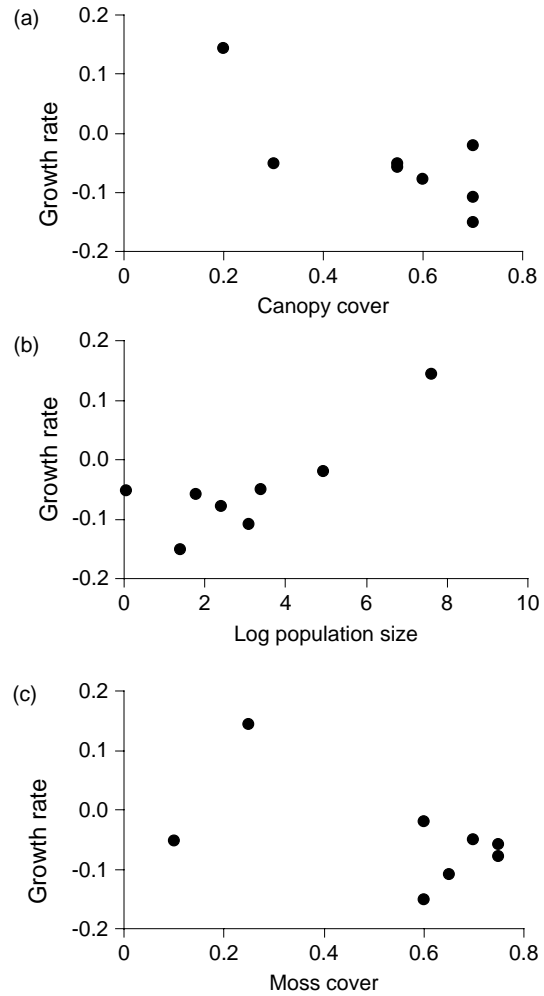


Figure 4. Population growth rate (μ) in relation to (a) canopy cover, (b) $\log(x+1)$ -transformed population size and (c) moss cover estimated from eight *Carlina biebersteinii* populations.

and consequently a reduced population growth rate for small populations. For *C. biebersteinii*, however, seed production was unrelated to population size, suggesting that seed production in small populations was not limited by pollen. Secondly, the lowered viability of small populations might have resulted from breeding with close relatives. Small *C. biebersteinii* populations often contain less than 50 flowering individuals and due to the lack of the persistent soil seed bank, quite a high proportion of flowering individuals within the populations is likely to be siblings. Breeding with relatives leads to a lowered offspring performance because of the loss of genetic variation (Young et al. 1996). Small and fragmented populations are also more prone to lose genetic variation due to genetic drift (Young et al. 1996), which may partly explain their lowered viability. On the other hand, many *C. biebersteinii* populations have been small in size for years (Fig. 1) and therefore, continuous inbreeding should have purged deleterious recessive alleles (Young et al. 1996). The third explanation for the positive relationship between population viability and population size is management actions conducted in the two largest populations during the data collection period. It is likely that removal of woody vegetation in

the two largest populations increased habitat openness, resulting in increased population performance. Moreover, land use intensity has declined over time as many populations currently inhabit abandoned fields (Table 1). Lack of regular disturbance, such as summer grazing, may have changed edaphic factors and nutrient balance in the unmanaged populations (Shariff et al. 1994), making growing conditions less favourable for *C. biebersteinii* over time.

Our count-based PVAs predicted most of the *C. biebersteinii* populations to be quite dramatically declining. The models may, however, have overestimated the rates of decline because we only counted the number of flowering plants in the populations and omitted non-flowering rosettes from the models. Given that the number of non-flowering rosettes remains quite stable from year to year or increases in number, the populations may be more viable than predicted by the current models. Monocarpic plants often delay their reproduction under unfavourable conditions (Klinkhamer et al. 1996, Falińska 1997). Such a delay in reproduction might even have increased the number of non-flowering rosettes in the shaded study populations. However, due to the fact that the number of flowering plants declines in many populations (Fig. 1), the number of non-flowering rosettes is also likely to be declining in this short-lived species. This suggests that *C. biebersteinii* indeed has recruitment problems in shady habitats.

The only increasing population (population 3) occurred in road verge where woody vegetation was annually removed, while the declining populations inhabited abandoned fields and mixed forests. Continuous disturbance, such as moderate summer grazing, is probably required to increase the viability of *C. biebersteinii* populations. Furthermore, mechanical removal of shrubs and trees in the shady populations would increase habitat openness and consequently seed production and the recruitment of seedlings. Due to the lack of persistent seed bank, populations are likely to rapidly respond to management actions. For instance, the removal and thinning of shrubs at the end of the observation period in population 1 might have resulted in a rapid increase in population size for that population in the last year.

According to Lotts et al. (2004), ten years of count data are suitable to assess only the relative risk of extinction among populations. We agree generally with this statement because short time series produce wide confidence intervals for estimates of population size and population growth rate. Moreover, short time series make it difficult to estimate and to include temporal autocorrelation (Foley 1994, Swanson 1998) as well as density dependence in the models. Both temporal autocorrelation and density dependence, when they occur, usually need to be included in the model to achieve higher accuracy of PVA (Morris and Doak 2002). The number of flowering plants fluctuated in many *C. biebersteinii* populations over time (e.g. populations 1, 6 and 7), indicating a negative temporal autocorrelation, while for some populations the number of flowering plants tended to gradually decline (e.g. populations 2 and 4), indicating a positive temporal autocorrelation. Given that population dynamics are density-independent, the inclusion of a negative temporal autocorrelation in stochastic simulations retards the decline of populations as a bad year is

followed by a good year. In contrast, the inclusion of a positive temporal autocorrelation in simulations speeds up the decline of populations as a bad year is followed by another bad year. Therefore, our estimates of population viability may be too pessimistic for populations with highly fluctuating annual population growth rates, while they may be too optimistic for populations showing a gradual decline. Unfortunately, the lack of long continuous time series made it difficult to estimate possible temporal autocorrelation in our case. Despite uncertainty related to discontinuous time series, they may be utilised for small populations of short-lived plants with no persistent seed bank to roughly assess population viability. As pointed out by Schemske et al. (1994), a count-based PVA may be unsuitable for long-lived perennials with a persistent seed bank. A long lifespan and high survival of flowering plants in long-lived perennials probably leads to overoptimistic estimates of population viability (Schemske et al. 1994).

Overall, our study illustrates that the populations of *C. biebersteinii* in Finland are declining and without management actions will go extinct in a few decades. The decline of the populations is probably because of diminished land use intensity followed by increased vegetation cover. Therefore, summer grazing or removal of shrubs and trees is required to keep habitats open and to improve fecundity and seedling recruitment.

Acknowledgements – We thank Heidi Kaipainen and Eija Kempainen from the Finnish Environment Institute for providing access to the monitoring data, and Peter Baxter for checking the language. Funding was provided by the Finnish Cultural Foundation and the Swedish Research Council Formas to SR, Societas pro Fauna et Flora Fennica, Kuopio Naturalists' Society and Finnish Biological Society Vanamo to LP, and the Academy of Finland to JS.

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