

Demographic variability and population viability of an endemic variety of the Siberian primrose

Taina Björnström¹, Marko Hyvärinen^{1,4,*}, Pirkko Siikamäki^{2,3},
Hanna Strengell¹, Henry Väre^{1,4} & Juha Tuomi¹

¹ Department of Biology, P.O. Box 3000, FI-90014 University of Oulu, Finland (*corresponding author's e-mail: marko.hyvarinen@helsinki.fi)

² Oulanka Research Station, Thule Institute, Liikasenvaarantie 134, FI-93999 Kuusamo, Finland

³ Present address: Metsähallitus, Natural Heritage Services, Torangintaival 2, FI-93600, Kuusamo, Finland

⁴ Present address: Botany Unit, Finnish Museum of Natural History, P.O. Box 7, FI-00014 University of Helsinki, Finland

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We used matrix population models to analyse spatial and temporal variation in the demography of the Siberian primrose (*Primula nutans* ssp. *finmarchica* var. *jokelae*), an early successional species of seashore meadows in the Gulf of Bothnia. We compared the dynamics of populations in habitats that were partially overgrown by woody shrubs with those in open ones. The major threat to the populations was the invasion of the habitat by woody plants, as population growth was very sensitive to a change in the transition from a sterile rosette to a flowering one and this transition occurred less frequently in overgrown meadows. This transition also had the greatest contribution to the differences in population growth rates between habitats. Although the invasion of shrubs negatively influenced population growth rate, most populations are still expected to persist and only two small populations out of eleven examined populations were expected to disappear within 50 years. However, with proper habitat management the problem of coarse-scale interactions, such as asymmetric competition for light with shrubs, can be substantially alleviated.

Introduction

Due to water level fluctuations seashores are challenging habitats for species to establish themselves (Dijkema 1990). This concerns also the Gulf of Bothnia (Baltic Sea) shores, characterized by flat topography and relatively rapid post-glacial isostatic land uplift (ca. 6.9 mm yr⁻¹, Johansson *et al.* 2004). The land uplift leads to

primary succession from open shores toward the meadow vegetation and, in the absence of grazing or mowing, eventually into woodlands or occasionally into peat-forming wetlands (Jutila 1997, Rautiainen *et al.* 2004). Hence, the uplift can be considered the main force shaping seashore vegetation in a long-term (at the scale of decades), whereas changes in management practices govern short-term changes (e.g. annual

variation). First, the density of taller herbaceous plants increases, and as stronger competitors they can suppress the abundance of smaller meadow species. The seashore meadows have experienced a long history of grazing and hay-making. The cessation of the traditional management procedures has reinforced reeds, tall grasses, and woodland species (e.g. Bakker 1985, Vestergaard 1985, Jutila 1997). The removal of the taller competitors should thus improve the success of smaller meadow species.

Second, more extensive vegetation changes are likely to occur when the woody plants invade the community previously consisted of herbaceous plants (Zobel *et al.* 1996, Wahlman & Milberg 2002). Zobel *et al.* (1996) made an important distinction between coarse-scale and fine-scale interactions between plants. If species are spatially separated (e.g. trees *vs.* herbaceous plants) one calls the interaction a coarse-scale one, whereas in the case of herbaceous plants of approximately similar height the interaction is regarded as a fine-scale one. According to Zobel *et al.* (1996), coarse-scale interactions determine the direction of rapid changes during the first stages of community succession as the invasion of woody plants changes light conditions in a way that favours shade-tolerant species. On the other hand, vegetation changes may take place very slowly if fine-scale interactions among herbaceous plants dominate in the meadow community (Hellström *et al.* 2006).

In the present study, we investigated the demography and population growth of an endemic variety of Siberian primrose (*Primula nutans* ssp. *finmarchica* var. *jokelae*) in the Gulf of Bothnia area. This is a rare endemic variety, which declined considerably in the Gulf of Bothnia region during the recent decades, as approximately one-fourth of the populations have gone extinct (Rautiainen 2006). We studied the demography in eight localities by annual censuses of individual plants in permanent study plots from 1999 to 2002 inclusive. Matrix population models were constructed in order to reveal those life-history stages and vital rates that are most valuable for population growth rate (Caswell 2001). Specifically, we focused on the significance of life-history transitions in explaining spatial and temporal variation in the growth rates

of the focal populations (e.g. Caswell 1996, Horvitz & Schemske 1995, Oostermeijer *et al.* 1996, Horvitz *et al.* 1997) because the variation in population growth between sites and years may reflect variation in different transitions (Jongejans & de Kroon 2005, Jäkäläniemi *et al.* 2006).

Although many primrose species may tolerate shading, the performance of individual plants as well as population growth of primroses are often enhanced in good light conditions (Whale 1984, Valverde & Silvertown 1997a, 1997b, 1998). Hence, we tested for the effects of shading (i.e. asymmetric light competition) by woody plants at three sites where we had a sufficiently large number of individuals both in open habitats and in ones partially overgrown by shrubs. Our main hypothesis was that the overgrowing of meadows by taller herbs and later on by shrubs and trees is the main threat for the population viability of the primrose. We predicted that population growth is reduced in overgrown habitats as compared with that in open meadows due to less successful flowering. We compare the present results with a parallel management study testing the effects of mowing and shrub removal on the performance of individual plants (Rautiainen *et al.* 2007). Together they provide strong evidence that the coarse-scale interactions with woody plants have important life-history consequences and influence the population viability of *P. nutans*.

Material and methods

Study species

The distribution of the Siberian primrose (*Primula nutans*) is circumpolar. According to Mäkinen and Mäkinen (1964), the populations of *P. nutans* around the Gulf of Bothnia (Baltic Sea) and the White Sea belong to the variety *jokelae* of the subspecies *finmarchica*, and the populations in the Norwegian Finnmark at the coast of the Arctic Sea belong to the variety *finmarchica*. The species has probably spread to the Gulf of Bothnia after the Great Ice Age from the east. According to IUCN criteria, the species is classified as endangered (EN) in Finland (Rassi *et al.* 2000).

Primula nutans is a perennial rosette hemicryptophyte and usually produces one flower-

stem with 2–4 flowers in mid-June or early July. The flowers are insect-pollinated and the seeds dispersed by water currents (Ulvinen 1997). The species usually also spreads vegetatively by runners that originate from the axils of the lower leaves and form new rosettes or daughter-ramets (Mäkinen & Mäkinen 1964). Vegetative spread takes place in late August–early September and the runners connecting to the mother plant to its daughters wither and break up in winter (T. Björnström pers. obs.).

The species grows on low-growth seashore meadows on soil characterised by a mixture of sand and clay. Even though *P. nutans* seems to tolerate inundation for short periods due to flooding of rivers or wind-driven rise of the sea water level (Mäkinen & Mäkinen 1964), it is not able to invade the shore closest to the waterfront. The species prefers open habitats and starts its growth earlier in spring than its competitors. The distribution extends to the upper parts of seashore meadows where *Salix phylicifolia* and *Alnus incana* tend to overshadow lower vegetation (Rautiainen *et al.* 2007).

Field studies

Annual population surveys were carried out during 1999–2002 inclusive at eight study sites

(Table 1) on the Gulf of Bothnia shores in Finland. The *P. nutans* individuals growing at the same site were considered to comprise a population. The distance between the study sites ranged between 5 and 50 km. At the sites 1–3, plant demography was surveyed both in open meadow habitat and in more closed habitat that was partially overgrown by woody plants, mainly *S. phylicifolia*. In closed habitats, a minimum of 40% of the area was overshadowed by willows in the beginning of the study. However, the willow cover varied between years mainly due to wintry ice scouring that was especially extensive in the spring 2000 at site 1.

The individuals of *P. nutans* were tagged in five permanent quadrats per habitat and site. The places for the quadrats were chosen to represent a maximum density of 50 *P. nutans* individuals per 40 × 40 cm plot. The plant individuals were marked with metal tags with codes on them. For monitoring newly emerged seedlings, additional sketches were drawn from the plots in order to be able to localize the plants during subsequent years. At sites 4–8, only open habitats were available. On average (\pm SD), there were 116 ± 37 plants in the habitats studied (Table 1).

The marked individual plants were classified into three stages: seedlings, sterile rosettes, and flowering plants. At the time of the survey (mid-June–first week of July), sterile rosettes

Table 1. The study populations listed by site (1–8), location, habitat type (open = a meadow with no woody plants, closed = a meadow partially overgrown by woody plants) and spatial area of population (continuum from few m² = very small to about 0.5 ha = very large). Estimated population parameters: $(N_{t+1}/N_t)_{\text{gmean}}$ = geometric mean of observed annual finite growth rates in the study plots, λ_{gmean} = geometric mean of projected annual finite growth rates obtained from transition matrices, P_e = probability of extinction in 100 years for the subpopulations in the study plots, and E_{year} = expected time for extinction (≤ 100 yr). The average number of individuals in the study plots was taken as the initial population size (N_0) in the stochastic simulations.

Site	Location	Habitat	Size	$(N_{t+1}/N_t)_{\text{gmean}}$	λ_{gmean}	N_0	P_e	$E_{\text{year}} \pm \text{SD}$
1	Papinkari	Open	Large	1.09	1.10	183	0	39 ± 7
		Closed	Very small	0.91	0.91	108	1.00	
2	Riutta	Open	Large	1.15	1.01	89	0.03	
		Closed	Very small	1.10	1.02	158	0.42	
3	Villeniemi	Open	Large	1.09	0.99	86	0.01	
		Closed	Very small	1.11	1.07	111	0	
4	Harisoja	Open	Small	1.10	1.10	76	0.18	
5	Naistenletto	Open	Very small	1.20	1.17	143	0	
6	Praava	Open	Very small	0.86	0.90	76	1.00	29 ± 3
7	Uppi	Open	Very large	1.20	1.17	148	0	
8	Välitörmä	Open	Small	0.99	0.99	96	0	

were one year old or older, and flowering plants were at least two years old. In a greenhouse, the germinating plants may form rosettes and flower in the same growing season, but according to our field observations the growing season is too short for this. Both sterile and flowering plants can clonally produce daughter-ramets. Because the inter-ramet connections had decayed during the winter, we could not follow the mother–daughter relationships in the field. By following the fate of the marked individuals we obtained data for the following life-history transition probabilities from year to year: SV = growth of a seedling to a 1-year old sterile rosette, VV = the survival of a sterile rosette as sterile and production of sterile daughter-ramets by sterile rosettes, VR = the change from a sterile to a flowering rosette and production of flowering daughter-ramets by sterile rosettes, RV = the change of a flowering plant to a sterile rosette and production of sterile daughter-ramets by flowering plants, and RR = the survival of a flowering rosette as a flowering plant and production of flowering daughter-ramets by flowering plants. An estimate of seedling production or fertility (RS) for a flowering plant in the year t in a given study population was obtained by dividing the total number of seedlings in the study plots in the year $t + 1$ by the number of flowering plants in the year t . Consequently, the estimate includes seedling production, germination success, and seedling survival to the time of the census. It ignores seed dispersal and recruitment from the seed bank. This simplification seem to be justified though, since out of 165 soil samples collected in 2002 from 8 sites (area of 177 cm² and 10 cm depth per sample, totalling ca. 3 m² area studied) during the third week of June before the seed-rain only 12 seedlings emerged after 2.5 months. Moreover, after samples were stored in +4 °C for four months (mimicking winter conditions) only one seedling emerged. Obviously the seed bank is transient.

Population structure and growth

From the study plots, we obtained the observed stage distributions and the total number of individuals (N_t) in the year t . These data were used to

calculate the observed finite rates of population growth as N_{t+1}/N_t , and to compare the observed stage distributions of open and closed habitats at sites 1–3. Population growth rates for open and closed habitats within populations were obtained for three intervals 1999–2000, 2000–2001, and 2001–2002. The geometric mean of the annual growth rates was used to estimate the observed annual growth rate for a given study population over the whole study period.

From the demographic surveys, we obtained separate annual transition matrices for each population. We used stage-structured matrix population models to analyse density independent population growth (Caswell 2001). The effect of intraspecific density-dependence was assumed to be negligible as there were large areas of similar habitat available for the populations to spread. The projected finite rate of increase (λ) corresponds to the population growth rate when the population has reached a stable stage distribution. Population increases exponentially for $\lambda > 1$, remains stationary for $\lambda = 1$, and declines for $\lambda < 1$. We quantified the magnitude of the temporal and spatial variability in λ by calculating the coefficient of variation (CV) separately by year and by site using arithmetic means. The overall population trend over the study years is indicated by the geometric mean of annual growth rates (λ_{gmean} , Table 1). Stochastic simulations were used to estimate the risk of extinction. The number of individuals in different stage classes in the study plots (average over the study years) defined the initial population structure. In simulations with 1000 replicated runs, the three annual transition matrices were assigned an equal probability of random sampling, and the population was considered extinct if its size dropped below one individual. For each population, we first calculated the probability of extinction in 100 years for the subpopulation in the study plots (P_e). If $P_e > 0$, we continued the simulations in order to estimate the expected time of extinction (E_{year}). We report only $E_{\text{year}} \leq 100$ years. The matrix calculations as well as the simulations concerning the extinction probability were done using the Microsoft Excel-based program KARISMA, a special application for matrix analysis made by Kari Lehtilä.

Sensitivity and LTRE analyses

The importance of stage classes was evaluated in terms of stable stage distributions and reproductive values. The standard sensitivity and elasticity analyses were used to evaluate the importance of the life-history transitions for population growth (de Kroon *et al.* 1986, Caswell 2001). Sensitivity yields an absolute effect of a change in a given life-history transition to the population growth rates, whereas elasticity gives a proportional effect to it. Therefore, the sum of elasticities in a matrix equals 1. Life table response experiment (LTRE) analyses were used to study how variation in life-history transitions contributes to the variation in λ (Caswell 1996, 2001, Horvitz *et al.* 1997, Jongejans & de Kroon 2005). LTRE decomposes treatment effects on a population growth rate into contributions from differences in the parameters that determine that variable (Caswell 2010). Hence, LTRE is very useful when comparing different population matrices.

To decompose the variation in λ , we applied fixed LTREs in order to compare the magnitude of effects associated with site, year, and habitat (for sites 1–3), and site and year (for sites 4–8). The decomposition to the main effects of the site, the year, and the habitat, and to the two-way interactions of site and year, site and habitat, and year and habitat, and to the three-way interaction by site, year, and habitat was done using the grand mean transition matrix as the reference matrix. Because the decomposed contributions can be positive as well as negative, the magnitudes of the effects were compared by calculating means and standard deviations for the absolute values of the given main and interaction effects (Jongejans & de Kroon 2005). Moreover, the contribution of life-history transitions to LTRE effects associated with the main effects was done by calculating the mean of absolute values of the magnitude of contributions for RS, SV, $V = VV + RV$, and $R = VR + RR$. Since we were comparing only two different habitats, it was possible to use the matrix for open habitats as the reference matrix and compare transitions in closed habitats against it.

Results

Population growth rates

According to both the observed and projected growth rate estimates, the majority of populations were more or less stationary or slowly increasing (Table 1). Two populations were clearly declining (the closed one at site 1 and the open one at site 6) and they were expected to go extinct within 30–40 years (Table 1). On average, populations of the sites 1–3 had a higher extinction risk (\pm SD) in the closed habitat (0.473 ± 0.502) than in the open habitat (0.013 ± 0.015) and at sites 4–8 (0.236 ± 0.434). The observed and projected growth rates correlated well although the projected λ tended to be slightly higher than the observed one for declining and lower for increasing populations (Table 1). Correlation between plant density, i.e. the average number of individuals per plot, and population growth was weakly positive (observed growth: $r = 0.434$, $df = 9$, $p = 0.181$; projected λ : $r = 0.631$, $df = 9$, $p = 0.037$).

In most populations, the year 1999 was poor as $\lambda < 1$ in ten out of eleven cases (Fig. 1). In turn, the year 2000 was good with $\lambda > 1$ in ten cases. The year 2001 was rather variable between the sites as $\lambda < 1$ in four and $\lambda > 1$ in seven cases. The overall variability was greater among the years than among the sites. At sites 1–3 (Fig. 1a), the temporal variability was almost fourfold as compared with the spatial variability (between years: $CV = 15.74$; between sites: $CV = 4.02$). Sites 4–8 (Fig. 1b) were more heterogeneous as the spatial variability ($CV = 13.02$) was of the same magnitude as the temporal variability ($CV = 16.65$).

It should be noted that in spite of rather low growth rates the meadow population at site 8 did not go extinct in the stochastic simulations because of low variation in λ among years (Fig. 1b and Table 1). In contrast, the overgrown population at site 2 went extinct in 42% of simulation runs (Table 1), although it had positive population growth in two study intervals (Fig. 1a). The populations with the lowest geometric mean growth rates and the highest risk of extinction (Table 1) had λ values close to 0.8 in two study intervals (Fig. 1a: the overgrown population at site 1; Fig. 1b: the open meadow population at site 6).

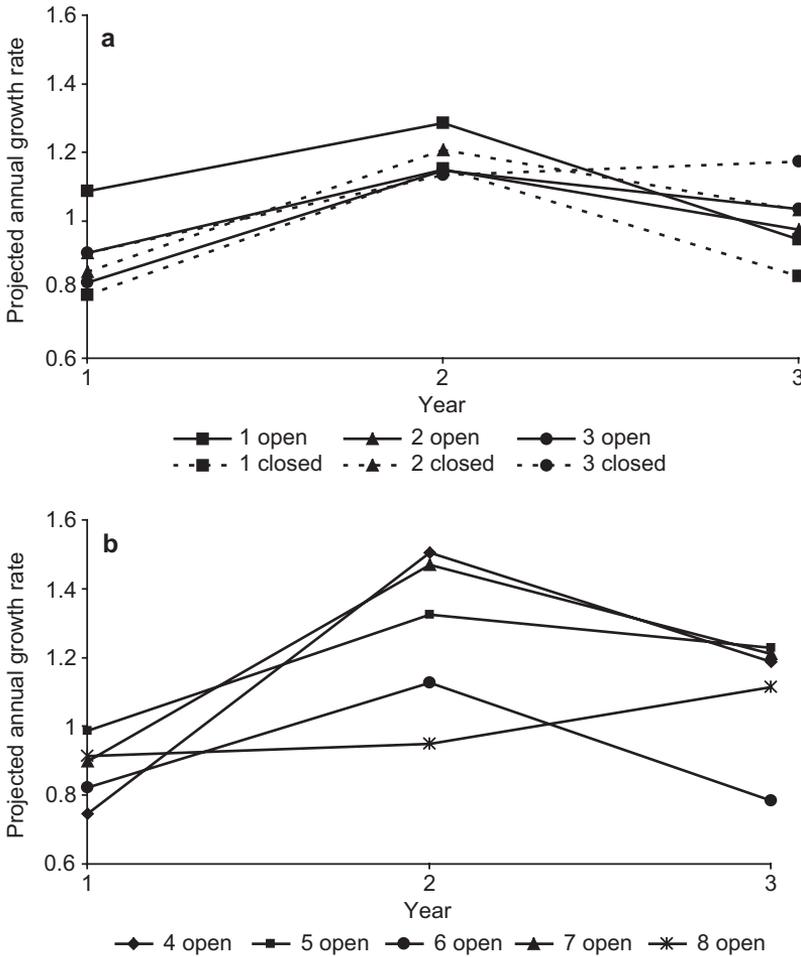


Fig 1. The projected annual rates of population growth (λ) in three-year intervals (1999–2000, 2000–2001, and 2001–2002). — **a:** Open and closed habitats at sites 1–3. — **b:** Open habitat at sites 4–8.

Importance of stage classes and transitions

Sterile rosettes dominated the observed stage distributions (Table 2). In closed habitats of sites 1–3, the sterile stage was even more pronounced than among open habitats (pooled $G = 13.9$, $df = 2$, $p < 0.001$). Also according to the stable stage distributions (Table 2), sterile rosettes were expected to be the most abundant among the stage classes. This was most pronounced in the closed habitat where, on average, sterile rosettes comprised 81% of the population, whereas the flowering plants were less abundant (6%) as compared with the open habitat (19%). The reproductive value of flowering plants was 3–5-fold and that of sterile rosettes 2.5-fold higher than that of seedlings (Table 2).

There were no large differences in the mean transition matrices of closed and open habitats (Table 3). The transitions from the sterile and flowering stages to the sterile stage (VV and RV) were slightly more prominent in the closed habitat. On the other hand, the transitions to the flowering stage (VR and RR) occurred less frequently and seedlings survived less well to the sterile stage (SV) in the closed habitat. Seedling production (RS), however, was higher in the closed habitat.

The population growth rate is most sensitive to a change in the transitions from the most abundant stage class to the stage class of the highest reproductive value. In both open and closed habitats, VR had the highest sensitivity and VV had 50%–70% of the highest sensitivity. In turn, RS had the lowest sensitivity, roughly

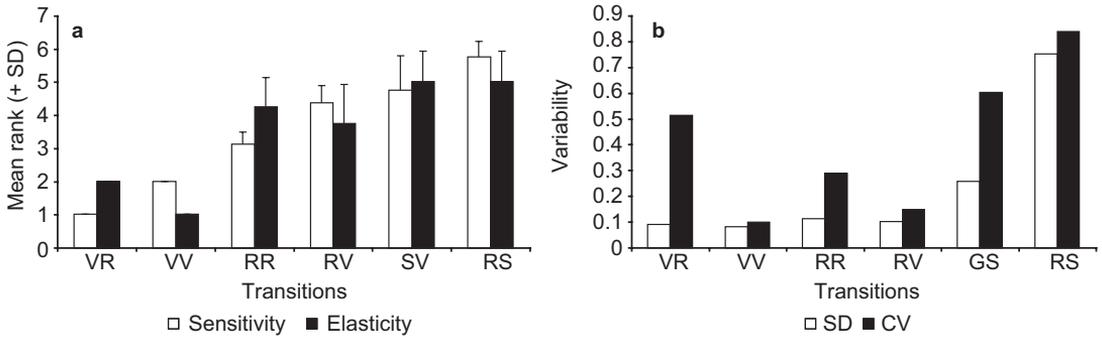


Fig. 2. (a) The mean rank (+ SD) of transitions in relation to sensitivity (empty bars) and elasticity (black bars), and (b) absolute (+ SD) and standardized variability (CV) of the transitions calculated over the eight meadow populations. Population-specific mean matrices over years were used. Transitions are denoted as in Table 3.

1%–3% of the highest value. Three most important transitions (VR, VV, and RR) were the same in all populations (Fig. 2a). In six out of eight cases, RV was the fourth most important (rank ranging from 4 to 5) and RS was the least influential transition (rank ranging from 5 to 6). The rank order of SV varied from 4 to 6.

Elasticity was highest for VV (open habitat: 0.50; closed habitat: 0.72). VR had the next highest values (open: 0.17; closed: 0.10), and the other transitions had lower elasticity (open:

0.05–0.11; closed: 0.04–0.05). Two most important transitions (VV and VR) were the same in all cases. In 6 of 8 cases, RR and RV were third–fourth important, whereas SV and RS were the two least influential transitions (Fig. 2a).

LTRE effects of site and year

Sites 1–3 were rather homogeneous since the decomposition of the variation in λ revealed that

Table 2. Stable stage distributions and reproductive values of the three stage classes (seedlings, vegetative and reproductive [flowering] rosettes) corresponding the mean matrices of the given sites and habitat types. Observed stage distributions were calculated by taking the mean distributions over years for each population and then pooling the data over sites.

	Sites	Habitat	Seedlings	Vegetative	Reproductive
Observed distribution	1–8	Open	8.25	73.58	18.17
	1–3	Closed	8.49	86.21	5.31
Stable distribution	1–8	Open	13.39	67.28	19.33
	1–3	Closed	12.32	81.10	6.58
Reproductive value	1–8	Open	1.00	2.47	3.58
	1–3	Closed	1.00	2.52	5.13

Table 3. Stage classes (seedlings, vegetative and reproductive rosettes) and transitions from the year t to the next ($t + 1$) in the grand mean matrices of the open habitat (sites 1–8) and the closed habitat (sites 1–3) in 1999–2002.

Stage in year $t + 1$	Stage in year t			Open habitat			Closed habitat		
	Seedling	Vegetat.	Reprod.	Seedling	Vegetat.	Reprod.	Seedling	Vegetat.	Reprod.
Seedling	–	–	RS	–	–	0.752	–	–	1.940
Vegetative	SV	VV	RV	0.440	0.806	0.671	0.411	0.913	0.731
Reproductive	–	VR	RR	–	0.193	0.413	–	0.060	0.299

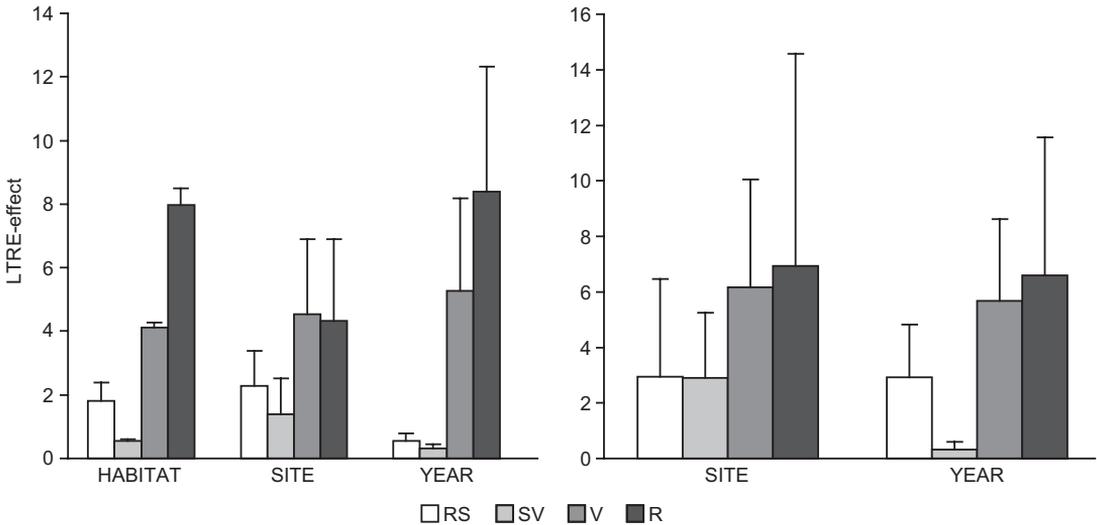


Fig. 3. Contribution of life-history transitions to LTRE effects associated with (a) the main effects of site, year and habitat at sites 1–3, and (b) the main effects of site and year at sites 4–8. The mean of absolute values of the magnitude of contributions ($\times 100$) are shown for RS = fecundity, SV = growth of seedlings to sterile rosettes, V = survival as a sterile rosette, production of sterile ramets, and retrogression of a flowering plant to the sterile stage, and R = transition of a sterile rosette to the flowering plant, production of flowering ramets, and survival as a flowering plant.

the year effect was about four times stronger than the site effect (Table 4). There was, however, some heterogeneity among the sites since the site and year interaction was large in relation to the main effect of the site. Sites 4–8 showed a greater site effect, while the year effect was of about the same magnitude as at sites 1–3. The site \times year interaction effect was only slightly smaller than the main effects, indicating heterogeneity among the populations at sites 4–8 (Table 4).

Table 4. Decomposition of LTRE effects on transition matrices of the sites 1–3 (by site, year and habitat) and the sites 4–8 (by site and year). The mean (\pm SD) of the absolute values of the decomposed effects ($\times 100$) are shown.

LTRE-effect	Sites 1–3	Sites 4–8
Site	3.03 \pm 2.39	12.34 \pm 3.77
Year	12.26 \pm 7.47	12.94 \pm 8.57
Habitat	2.60 \pm 0.88	
Site \times Year	6.32 \pm 3.45	9.82 \pm 7.02
Site \times Habitat	5.04 \pm 2.34	
Year \times Habitat	3.08 \pm 1.01	
Site \times Year \times Habitat	2.97 \pm 2.00	

The site-effect contributions of transitions concerning the mature stages (V and R) were greater than those of seedling production and establishment (RS and SV). The later transitions had a greater importance in between-site than in between-year variation in λ (Fig. 3). At sites 1–3, the between-year variation in population growth rate was almost completely associated with V and R (Fig. 3a). At sites 4–8, the year effect of RS was larger (Fig. 3b). It is notable that SV contributed very little to the variation of λ between years (Fig. 3).

When the study years were compared (data not shown), the year 1999 was below and 2000 above the average with respect to all transitions. The year 2001 was close to the average, except that at some sites seedling production was weak. V and R had opposite site effects at sites 2–3, but not at site 1 (Fig. 4a). Among the open meadow populations 4–8, the largest and most viable population (site 7) had R much above, whereas the very small and least viable population (site 6) had R much below the average (Fig. 4b). At site 6, VR and RR were low in 1999 (0.06 and 0.18, respectively), better in 2000 (0.16 and 0.53), and there was no flowering in 2001 (VR = RR = 0). The

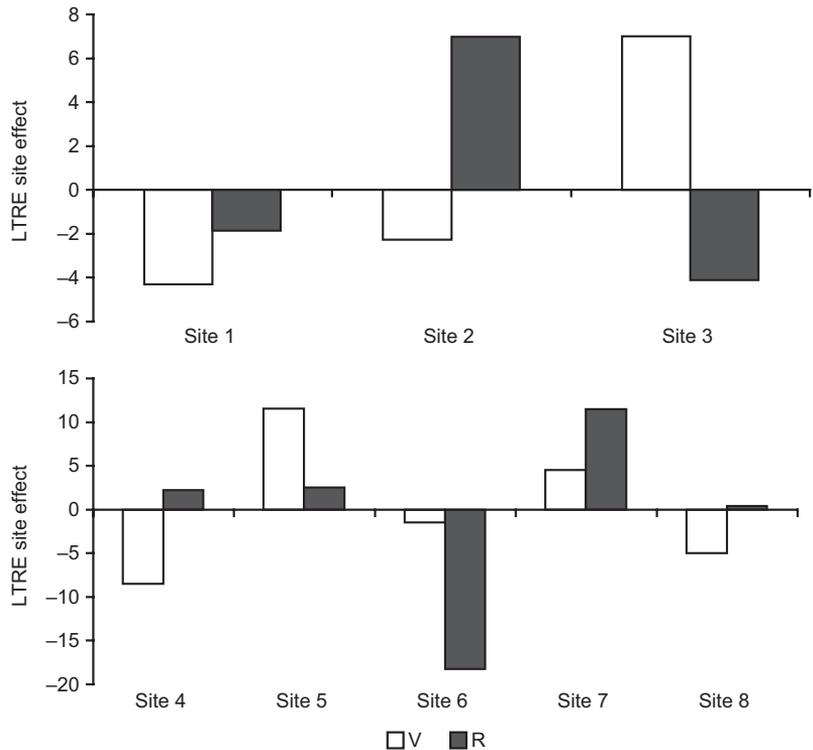


Fig. 4. The site LTRE effects of the combined transitions V and R (a) at sites 1–3 and (b) at sites 4–8. For explanation, see the legend of Fig. 2.

trend was similar but less extreme in the poorly viable population in the closed habitat of the site 1 (VR in 1999–2001: 0.02, 0.18, and 0.13; RR in 1999–2001: 0, 0.55, and 0.01).

LTRE effects of habitat

In the three way LTRE analysis (site, year, and habitat), the habitat effect was slightly lower than the site effect (Table 4: sites 1–3). The interaction terms including habitat were roughly of the same magnitude and larger than the habitat effect. The habitat-effect contributions of the transitions in Fig. 3a are similar to the site effects, except that R is more important than V, and SV is less important in the habitat effects. The LTRE analysis comparing the mean matrices of the two habitat types reveals that the most important habitat effect concerns VR:

	Seedlings	Vegetative	Reproductive
Seedlings	0	0	0.036 (RS)
Vegetative	-0.011 (SV)	0.072 (VV)	0.009 (RV)
Reproductive	0	-0.131 (VR)	-0.028 (RR)

This effect (-0.131) together with lower SV and RR reduces the growth rate of the populations in the overgrown in relation to the open meadows. Higher VV and RS in the overgrown meadows affect in the opposite direction. The overall effect is -0.05218 which corresponds well to the difference in projected growth rates $\Delta\lambda = -0.05198$ in favour of open meadow habitats.

Discussion

Temporal and spatial heterogeneity

The emphasis in the viability analyses of plant populations was on the demography and fate of single local populations. Recently, greater attention has been paid to temporal and spatial variation in the vital rates. This is, on one hand, due to the improved methods for the analysis of variation in demographic parameters (Caswell 1996, 2001, Horvitz *et al.* 1997, Jongejans & de Kroon 2005) and, on the other hand, greater focus on spatial dynamics of fragmented populations, especially on metapopulation dynamics (Eriks-

son 1996, Husband & Barrett 1996, Tilman & Kareiva 1997, Valverde & Silvertown 1997a, 1997b, Hanski 1999, Freckleton & Watkinson 2002, Ehrlén & Eriksson 2003, Jäkäläniemi *et al.* 2005, Rautiainen *et al.* 2007a). Jongejans and de Kroon (2005) found in a study of three perennial plant species that the magnitude of spatial and temporal components of heterogeneity can greatly vary among the species: some species show high spatial variation, others high temporal variation, or low spatial and temporal variation. In our case, the populations at sites 1–3 were temporally relatively synchronous. These populations were rather large, and the study plots in the closed habitat were not completely isolated from those in the open habitat closer to the sea. There was greater heterogeneity in vital rates, especially in those connected to the performance of reproductive individuals, among sites 4–8, probably because of the variation in the habitat characteristics (e.g. connection with the sea) and population structures.

It is notable that according to genetic analyses, the populations in the Gulf of Bothnia area have a low level of genetic differentiation, which suggests frequent gene flow between the populations (Kreivi 2009). This is most probably due to frequent seed dispersal among the populations, most likely via the sea water. This can be important for the maintenance of local populations as well as for the colonization of new sites. According to Larson and Barret (1998), periodic dispersal of floating seeds may constrain evolutionary divergence among island and mainland populations of *P. mistassinica* on Lake Huron shorelines.

In *P. nutans*, isolated and small populations at unfavourable sites are doomed to go extinct. As such, the present method for population dynamic analysis is not applicable to the smallest populations with only few individuals because the reliable data for transition matrices requires sufficiently large sample sizes for all the stage classes.

Population growth rates tended to correlate positively with plant density. Positive correlation between fruit production and population size has been reported in *P. elatior* (Jacquemyn *et al.* 2002) as well as *P. vulgaris* (Brys *et al.* 2004b) and other insect-pollinated species (e.g. Fischer & Matthies 1998). This may reflect the simple

fact that in a favourable environment a population ends up with a higher density and also the population growth rates below the carrying capacity may be higher.

Important life-history transitions vary temporally and spatially. For instance, Jongejans and de Kroon (2005) found in *Succisa pratensis* that fecundity was in a greater extent responsible for site effects and growth for year effects. Although fecundity and seedling survival were highly variable in *P. nutans*, they contributed very little to the spatial and temporal variation in population growth rate. In turn, the transitions involving sterile and flowering rosettes were more important. This concerned sensitivity, elasticity, as well as the LTRE analyses. The importance of the transitions to the flowering stage is highlighted by stochastic simulations where the risk of extinction in small populations was associated with a frequent failure in the start of flowering.

The two most important transitions were consistent among all studied *P. nutans* populations indicating that they could have been generalized from a study of a single population. Yet, the rank order of sensitivity and elasticity differed. Our results were thus more consistent across populations than those in the study of *Silene acaulis* by Morris and Doak (2005), who concluded that no single vital rate had the greatest influence on the stochastic growth rate in all study populations. A reason could be that they used a large number of stage classes (12) and hence the importance rank of a single vital rate may not be as robust as in our case with only three stage classes. Ramula and Lehtilä (2005) noted that the matrix dimensionality (i.e. the number of age or stage classes) can influence population growth and elasticity analyses. Therefore, they recommended the use of few stage classes especially when data are limited, and for relatively slow-growing species, such as *P. nutans*, with a simple matrix structure that mainly consists of stasis and growth to the next stage.

Life-history consequences of coarse-scale species interactions

We expected that the major threat for *P. nutans* is the increasing competition with the taller

herbaceous species (fine-scale interactions) and especially the invasion of shrubs and woody plants, which alters the vertical structure of the plant community (i.e. intensifying coarse-scale interactions among species, *sensu* Zobel *et al.* 1996). An increased density of herbaceous plants often influences adversely the establishment of seedlings, while the shading of woody plants may especially suppress flowering of shade-intolerant or gap-demanding species. Although the differences in population growth rates were rather small between open and closed habitats, the habitat shift had important life-history consequences on *P. nutans*.

First, flowering individuals had the highest reproductive value for population growth and their abundance was reduced in closed habitats. Second, population growth was most sensitive to a change in the transition from the sterile to flowering stage and this transition occurred less frequently in closed habitats. This transition also had the greatest LTRE contribution to the habitat-differences in population growth rates. Third, although seedlings were expected to be equally abundant in open and closed habitats when the population reaches a stable stage distribution, the weaker seedling survival and growth to a sterile rosette influenced negatively the population growth in the closed habitat as compared with that in the open habitat. Larger fecundity (seedling production) in closed habitat influenced in the opposite direction. Moist microclimate under the shrubs is probably favorable both for germination and seedling establishment.

According to Ehrlén *et al.* (2005) manipulations of fine-scale interactions of a closely related species, *P. veris*, either had no effect whatsoever on the growth rate or substantially improved it, depending on the nature of management. Cutting surrounding vegetation turned out to be ineffective unless it was combined with litter removal. The improvement mainly was due to better seedling establishment whereas the treatments did not affect the probability of flowering. In *P. farinosa*, all populations with continuously high grazing pressure survived whereas 60% of populations without grazing went extinct during a 70 year period in Sweden (Lindborg & Ehrlén 2002). Fertilization was even more detrimental (100% of populations went extinct) because of

increased vegetation height and stronger competition for light. Clipping experiments revealed that the treatment effects on population growth rate were in a large part due to flowering plants and especially seedling production (Lindborg & Ehrlén 2002). Accordingly, a comparison of demographic characteristics between different management regimes revealed that recruitment and plant density of *P. vulgaris* were highest in study plots subject to mowing and clearing of ditch banks whereas densities were lower along forest edges (Endels *et al.* 2004). In ditch banks, the major threat is competitive exclusion by much taller herbaceous species such as *Phragmites australis* or *Urtica dioica* (Endels *et al.* 2004). *Primula vulgaris* in woodland habitats is often associated with canopy gaps (Valverde & Silvertown 1995), and a simulation study of gap dynamics suggests that overall population growth rate of this species is enhanced by high gap opening rates (Valverde & Silvertown 1997b). These latter studies are highly consistent with the present study suggesting that changes in the vertical structure of plant communities have important life-history consequences for *Primula* species (Brys *et al.* 2004a).

Population viability and management

When overgrowing by reeds and shrubs proceeds, this influences negatively population growth rate of *P. nutans* by reducing flowering frequency and survival and growth of seedlings. On the other hand, as far as shading and competition are not too strong, the population can persist due to survival of sterile rosettes and clonal production of sterile ramets. Vegetative spread may also be important in open habitats especially when sexual reproduction fails more or less completely, e.g. due to flooding during the flowering period. Because the species reproduces both sexually and asexually, the populations are likely well buffered against moderate natural variation in vital rates.

In our parallel management experiments (Rautiainen *et al.* 2007b), mowing increased markedly the number of *P. nutans* individuals in all demographic stages studied (seedlings, sterile rosettes, and flowering individuals). The treat-

ment effects were seen from the second year onwards after the start of the mowing treatment. Mowing decreased both the cover of sedges and the amount of litter, thus influencing fine-scale interactions in the favour of *P. nutans*. In the shrub removal experiment, the total number of *P. nutans* individuals was higher in treatment quadrats compared to the control ones already in the following year after the start of the management. This was mostly due to the increased number of sterile rosettes and seedlings in the treated quadrats. Removal of shrubs also increased flowering of *P. nutans* in treated as compared to control quadrats where flowering plants were rare. This result further supported our working hypothesis that the coarse-scale interactions with the woody plants are detrimental for the success of *P. nutans*.

Although our demographic estimates may be biased because of a very limited number of annual matrices, the present estimates indicate that most study populations are viable and they are expected to persist provided that the environment does not change significantly. This especially concerns large populations in open habitats close to the sea. Smaller populations have a greater risk of extinction, and in our simulations two populations (out of 11) were expected to disappear within 50 years. Although demographic stochasticity may influence the smallest populations, it is most likely that environmental stochasticity (disturbances and annual fluctuations in the environment) or directional changes in the habitat (e.g. gradual invasion of woody plants) are the major threats for small populations.

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