
Habitat Change and Demography of *Primula veris*: Identification of Management Targets

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Abstract: *Although the effects of deterministic factors on population viability often are more important than stochasticity, few researchers have dealt with the effect of deterministic habitat changes on plant population demography. We assessed population viability for the perennial herb Primula veris L. and identified targets for management based on demographic data from five different habitat types representing different degrees of canopy closure. We conducted replicate studies at the border of the distribution area and in more central parts. Demographic patterns were similar between the two regions. Most study populations had a positive population growth, and only populations in late phases of forest succession showed consistently negative trends. The populations of open habitats had high seedling recruitment, and the populations of early and middle forest succession had high seed production. The importance of survival for population growth rate increased with increasing habitat closure, whereas the importance of growth and reproduction decreased. Results of the elasticity analysis suggested that the best method to manage decreasing late-successional populations is to increase survival of the largest individuals. The life-table response experiment (LTRE) analysis, however, showed that survival of the largest individuals contributed little to differences in population growth rates of different habitats, whereas seed production and growth of small individuals were more important. Moreover, direct perturbation of the performance of the largest stages showed that late-successional populations would not attain positive population growth even if the largest stages had no mortality at all. We conclude that restoration of recruitment is the only possibility for positive population growth in late-successional populations of P. veris, although the elasticities of recruitment transitions are low. Our results also suggest that retrospective demographic methods such as LTRE constitute an important and necessary complement to prospective methods such as elasticities in identifying management targets.*

Keywords: elasticity, habitat closure, life table response experiment analysis, population growth rate, population viability, restoration

Cambio de Hábitat y Demografía de *Primula veris*: Identificación de Objetivos de Conservación

Resumen: *Aunque los efectos de factores determinísticos sobre la viabilidad poblacional a menudo son más importantes que la estocasticidad, pocos investigadores han abordado el efecto de los cambios determinísticos del hábitat sobre la demografía de poblaciones de plantas. Evaluamos la viabilidad poblacional de la hierba perenne Primula veris L. e identificamos objetivos para su gestión con base en datos demográficos obtenidos en cinco tipos de hábitat diferentes que representan diferentes grados de oclusión del dosel. Realizamos estudios replicados en el límite del área de distribución y en áreas más centrales. Los patrones demográficos eran similares en las dos regiones. La mayoría de las poblaciones estudiadas tenían un crecimiento poblacional positivo, y solo mostraron tendencias consistentemente negativas las poblaciones en fases avanzadas de*

sucesión del bosque. Las poblaciones en hábitats abiertos tenían alto reclutamiento de plántulas, y las poblaciones en bosques en sucesión temprana y media tenían alta producción de semillas. La importancia de la supervivencia para la tasa de crecimiento poblacional aumentó con el incremento de la oclusión del hábitat, mientras que disminuyó la importancia del crecimiento y la reproducción. Los resultados del análisis de elasticidad sugieren que el mejor método para manejar poblaciones decrecientes de etapas tardías de sucesión es el incremento de la supervivencia de los individuos más grandes. Sin embargo, el análisis de experimento de respuesta de tabla de vida (ERTV) mostró que la supervivencia de los individuos más grandes contribuyó poco a las diferencias en las tasas de crecimiento poblacional en hábitats diferentes, mientras que la producción de semillas y el crecimiento de individuos pequeños fueron más importantes. Más aun, la perturbación directa del funcionamiento de las etapas mayores mostró que las poblaciones de sucesión tardía no llegarían a tener crecimiento poblacional positivo aun si no hubiera mortalidad en las etapas mayores. Concluimos que la restauración del reclutamiento es la única posibilidad de crecimiento poblacional en poblaciones de P. veris de sucesión tardía, aunque las elasticidades de las transiciones de reclutamiento sean bajas. Nuestros resultados también sugieren que los métodos demográficos retrospectivos, como ERTV, constituyen un complemento necesario e importante de los métodos prospectivos, como las elasticidades, en la identificación de objetivos de conservación.

Palabras Clave: análisis de experimento de respuesta de tabla de vida, elasticidad, oclusión de hábitat, restauración, tasa de crecimiento poblacional, viabilidad poblacional

Introduction

Demographic analysis constitutes an important tool for population management (Caswell 2001; Beissinger & McCullough 2002; Morris & Doak 2002). Demography is affected by both stochastic and deterministic factors. In demographic studies of plant populations, stochastic variability among populations has received more attention than deterministic differences (Menges 2000; but see Silvertown et al. 1993; Oostermeijer et al. 1996). Yet, environmental trends such as successional dynamics are often decisive for extinction probabilities, and extinctions often follow on extended periods of population decline (Fieberg & Ellner 2000; Lande et al. 2003).

Population response to stochastic variability and deterministic changes may differ in different parts of the distribution area. Peripheral populations are assumed to be more affected by habitat deterioration and prone to extinction because individuals living in the margin of the distribution area of a species experience harsher environmental conditions than do individuals in central populations (Nantel & Gagnon 1999). Peripheral populations may also be more fragmented, if there are fewer suitable habitats because of more strict habitat demands (Lennon et al. 1997). On the other hand, if the distribution area of the species is not decreasing, then the state of populations should not differ between central and peripheral regions (Carter & Prince 1985; Prince et al. 1985).

Stochastic and deterministic environmental factors determine population dynamics through vital rates such as reproduction, recruitment, growth, and survival. Silvertown et al. (1993, 1996) used the elasticity analysis of matrix population models to describe how demographic patterns change along the successional gradient and under different disturbance regimes. Silvertown et al. (1993)

categorize the transitions from smaller to larger stages as the growth component, the transitions dealing with seed, seedling, and clonal offspring production as the reproduction component, and the remaining transitions as the survival component. In an interspecific comparison, they showed that species of open and disturbed habitats often have high fecundity and growth elasticities, whereas species of closed, undisturbed habitats are characterized by high survival elasticities. Silvertown et al. (1996) suggest that the same pattern also works within species. Empirical studies usually support this hypothesis (e.g., Horvitz & Schemske 1986; Oostermeijer et al. 1996; Silvertown et al. 1996; Valverde & Silvertown 1998).

Elasticities can also be used to identify management targets in conservation biology (de Kroon et al. 1986; Caswell 2000, 2001). Because transition rates with high elasticities have a strong effect on population growth rate, λ , such transition rates are good candidates for management targets provided that there are management methods available to manipulate them. Decreasing populations in closed habitats often have high elasticities in the survival component and low elasticities in growth and especially in the reproduction component (Oostermeijer et al. 1996; Silvertown et al. 1996). Elasticity analysis thus suggests that managing populations of closed habitats should include enhancing the survival of established individuals. Oostermeijer et al. (1996) and Silvertown et al. (1996) recommend, however, to give priority to management for higher reproduction and growth because they suffer more from habitat closure than survival.

Sensitivities and elasticities are prospective methods that predict how population growth rate varies as a function of transition rates (Horvitz et al. 1997). Retrospective methods such as life-table response experiment (LTRE) methods, on the other hand, can be used to compare

demography of different populations. An LTRE shows how variation in transition rates contributes to variation in population growth rates (Horvitz et al. 1997; Caswell 2001). Because LTRE analysis is based on extant variation in realized data, some contend that LTRE methods cannot be used to identify potential management targets (Caswell 2000, 2001).

We used demographic analyses of *Primula veris* L., a perennial herb of grasslands and young forests, as a case study to develop methods to assess the most relevant management targets. We compared the population dynamics of *P. veris* among different habitats and between central and peripheral populations. We examined how population growth rate most effectively could be increased in different populations according to an elasticity analysis, and whether other demographic methods gave similar results.

Study Area and Methods

Study Areas and Species

Primula veris (Primulaceae) is a hemicryptophytic perennial herb. It forms a rosette, and vegetative reproduction is rare (Tamm 1972). Individual plants may live for several decades (Inghe & Tamm 1988). *P. veris* has one or a few inflorescences that emerge in spring. Each stalk usually has 5–10 flowers, which open synchronously in May. Flowering continues for 2–3 weeks, and the seeds ripen in late July and August. *P. veris* is an obligate outbreeder (Wedderburn & Richards 1990), and the flowers are distylic. Seed predation is common in some populations (Leimu et al. 2002). The main seed predators of *P. veris* are larvae of the plume moth (*Amblyptilia punctidactyla* [Pterophoridae]).

The main distribution area of *P. veris* is the temperate zone of central and eastern Europe (Hultén 1971; Hultén

& Fries 1986). *P. veris* is common in the central parts of its distribution area, but in some regions of Finland, outside our study area, and in some other peripheral regions it is considered endangered. The central populations we studied were located in the Tullgarn area in Sweden, about 60 km south of Stockholm. The peripheral populations were in southwestern Finland. The populations were located in habitats with varying management regimes and successional stages (Table 1). All populations consisted of at least several hundred individuals. The pasture populations had a long history of experiencing grazing throughout the summer. As a part of conservation management programs, the meadow populations were kept open with mowing in the middle of July (Swedish meadow) or with a combination of mid-July mowing and late-summer grazing (Finnish meadow). The early successional populations had no specific management of the field layer, but bush and tree canopy was sparse because of continuous thinning. The middle-successional populations were in open deciduous or mixed deciduous-coniferous forests with sparse field vegetation. In the late-successional populations the forest canopy was closed.

Field Studies and Demographic Analysis

From 6 to 20 permanent quadrats of 0.6 m², the number depending on the population density, were haphazardly placed in each population. We examined all *P. veris* individuals within quadrats. We used a frame to map the coordinates of individuals. Mapping was carried out twice a summer, in early June and in mid-July. The July census was decisive in classifying the state of the individuals. We used length of the leaf blade of the largest leaf as an index of plant size because it is closely correlated with the total leaf area (K.L. & K.S., unpublished data). The number of inflorescences and the number of intact, damaged, and aborted fruits were counted. We collected 10–30 infructescences outside the plots and estimated the

Table 1. Population growth rates (λ) of *Primula veris* in central populations (Sweden) and peripheral populations (Finland) representing different habitat types.*

Population	1995–1996	1996–1997	1997–1998	Mean matrix
Pasture, Sweden		0.932	1.277	1.097
Pasture, Finland		0.877	1.365	1.137
Meadow, Sweden	1.167	0.881	1.084	1.096
Meadow, Finland		1.060	0.889	0.982
Early succession, Sweden		0.989	1.035	1.010
Early succession, Finland 1		1.005	1.032	1.045
Early succession, Finland 2		1.127	1.088	1.119
Middle succession, Sweden		1.004	1.276	1.128
Middle succession, Finland 1		1.031	0.999	1.029
Middle succession, Finland 2		1.024	0.975	1.003
Late succession, Sweden	0.944			0.944
Late succession, Finland 1		0.708	0.855	0.781
Late succession, Finland 2		0.925	0.957	0.930

*An empty cell represents a year when no data were collected from the focal population.

number of seeds per fruit for each population and year to determine seed production. All populations except the Swedish late-successional population were surveyed in 1996, 1997, and 1998. The survey was started in the Swedish meadow and late-successional populations already in 1995, but the study had to be interrupted in the Swedish late-successional population after 1996 because the plots were destroyed by forest thinning in 1997.

We constructed stage-structured population matrices from information gathered from permanent plots. Matrices consisted of six categories: seed bank, seedlings, small plants, middle-sized plants, large plants, and reproductive plants. Obviously, only the plants of the last category flowered and fruited. By definition, newly germinated seedlings moved to small plants the next year. The upper class limit separating small plants from middle-sized plants was defined as the largest leaf size attained by first-year seedlings (leaf length of 17 mm). The lower class limit for large plants was defined as the threshold plant size (leaf length) for reproduction. The threshold was kept the same for different years in the same population but was different for different populations because plants of closed habitats had large shade leaves and plants of open habitats had small, thick sun leaves. We calculated transition probabilities for stage i as the number of plants going from stage i to stage j the next year, divided by the number of plants in the stage i in the current year ($i, j = 2 \dots 6$). Rare events of fission (vegetative reproduction) were handled by enabling two simultaneous transitions from stage i to stage j by the same plant.

In the late-successional populations the number of small- and middle-sized plants was low (≤ 5). Confidence intervals of the transition rates were thus large and the resulting population dynamics was problematic to analyze, especially if the life cycle was broken because all individuals of the same stage died or if all individuals remained in the same stage. We therefore used the beta-binomial model to calculate empirical Bayes estimates of transition rates (Link & Hahn 1996). In empirical Bayes methods, the original estimates are adjusted toward an overall mean by a factor based on the precision of the estimates. We calculated overall mean from all available data from the three late-successional populations involved. All analyses were carried out with both original and Bayes-adjusted transition rates. The results were similar with original and Bayes-adjusted transition rates, except in two cases, where all small individuals survived and stayed in the same stage (Swedish late-successional population, 1995–1996, five small individuals; Finnish late-successional population 2, 1997–1998, one small individual). Dynamics without Bayes adjustment was then totally dominated by stasis of small individuals (elasticity of stasis of small individuals = 1, population growth rate = 1). Bayes estimates were used for the analyses presented in results.

We examined the fate of seeds by randomly sowing 50 seeds to four 1-dm² quadrats each year in every popula-

tion and recording seedling germination and survival in the following years. We estimated from individual seed production and the dispersal pattern of seeds that the seed density in sown plots was similar to the density of seeds after natural dispersal. Judging from seed-sowing experiments with variable seed densities (Ehrlén et al. 2005), however, our results are also robust if actual seed densities were slightly higher in some places. We also carried out seedling counts in the same number of control plots to measure background germination. These counts were subtracted from the values recorded from the experimental quadrats.

We calculated survival in the soil seed bank by carrying out identical sowing experiments at the same site in consecutive years and recording germination in each sowing plot over several years. Because of limited availability of data, we calculated only one estimate of survival of seeds in the soil seed bank (s). The probability of a seed released from a fruit to survive and germinate t years after sowing, G_t , is equal to the probability of surviving in the seed bank and not germinating each year up to year $t - 1$ times the probability of germinating in year t and can be written as $(s - g_1) \times (s - g_2) \dots \times (s - g_{t-1}) \times s \times g_t$, where g_t is the probability that a seed that has survived in the seed bank will germinate at time t . We estimated the proportion of seeds that survived and germinated from a given cohort each year (G_1, G_2, G_3 , etc.) directly by monitoring sowing plots.

Assuming germination probabilities were similar for different seed-sowing cohorts, we were able to estimate the size of the seed bank in older plots from germination rate in newer plots at the same site sown in the previous year. For example, if plots sown with 50 seeds in year $t - 1$ had 10 seedlings in year t , the probability of surviving and germinating was $s \times g_t = 20\%$ in that year. If old plots sown with 50 seeds in year $t - 2$ had 5 new seedlings in year $t - 1$ and 4 new seedlings in year t , we estimated that their seed bank size in year $t - 1$ was 20 seeds (20 seeds \times 20% = 4 seedlings). There were thus 25 survivors in year $t - 1$ (20 seeds and five seedlings) from 50 seeds sown in year $t - 2$, which gives an estimate of 25/50 = 50% as the survival probability s . We used this value to estimate that the proportion of seeds that survived the next year, s , was on average 57.1%. Using a constant value of s underestimates the effect of variability of seed bank survival on population dynamics, but the elasticity of the seed bank was always low, even when seed-bank transitions were artificially varied from low to high values.

The seedling production of an average flowering individual was calculated as $s \times g \times f$ and the yearly input to seed bank as $s \times (1 - g) \times f$, where f is the number of seeds produced per individual. The transition from seed bank to seed bank was calculated as $s \times (1 - g)$, and from seed bank to seedlings as $s \times g$. In three populations (Finnish pasture, meadow, and late-successional population 2) we were unable to establish sowing plots, and the seedling

recruitment was estimated from total number of seeds produced in the current year and the number of seedlings in the permanent quadrats the next year. To take into account the number of seedlings germinated from the seed bank in estimating seedling recruitment, we used average values of vital rates of seed bank from other similar habitats. Data from the 10 populations where both estimates from permanent plots and sowing plots were available suggested that they yield similar values of germination.

We used standard methods of population matrix modeling (Caswell 2001) to calculate basic population parameters and to conduct an elasticity analysis and an LTRE. We used two-way factorial design for LTRE, with successional stage and country as factors. Interaction effects are part of the model, but for brevity they are not presented in the results section. We calculated the mean matrix over yearly transitions for each population. In Finland we had two early, middle-, and late-successional populations, so we calculated a mean of these populations for the LTRE.

Silvertown et al. (1993) proposed that transition rates can be grouped into three different life-history components for an elasticity analysis. The growth component contains all transitions that represent movement of a plant to larger stages. The survival component contains transitions in which individuals stay in the same stage (stasis) or regress to earlier stages (retrogression). The reproduction component has transitions that deal with seed production. We used this scheme to present the results, but we divided the growth component into two parts: (1) growth of adult individuals (middle-sized, large, and reproductive plants) and (2) establishment of new individuals, including seed bank germination, seedling survival (transition from seedlings to small plants), and growth of small individuals. The elasticities of transitions from reproductive individuals to seed bank and from seed bank to seedlings were equal. Similarly, the transitions from reproductive individuals to seedlings, from seedlings to small individuals, and from small to middle-sized individuals had very similar elasticities. The reproduction component and the growth component of early life-history stages are thus closely related. We merged these groups in some of our elasticity analyses and called them the recruitment component.

Conditional life spans were calculated using the equation given in Cochran and Ellner (1992). One year was subtracted from the result because the original equation gave estimates of life span that were too high (Ehrlén & Lehtilä 2002). We used the average total life span of individuals that had germinated the year after seed dispersal, without entering the seed bank, on the condition that they reached the large or reproductive stage (depending on which of the estimates was highest) as our measure of conditional life span. Harmonic mean was used to take an average of life span estimates of different years of the same population (Ehrlén & Lehtilä 2002).

Results

Population Growth Rates and Transition Rates

The population growth rates of mean matrices were > 1 in all populations except in the late-successional populations and in the Finnish meadow population (Table 1). In most of the populations, however, at least one of the yearly transitions yielded a growth rate < 1 .

Management regime and successional stage had a strong effect on plant fate. For instance, growth of the middle-sized and large individuals and seed production were highest in early and middle succession (Figs. 1f, 1g). Seedlings and small individuals were especially responsive to habitat type. In pasture and meadow, seedlings had high survival (Fig. 1b, transition 2–3) and small plants had high growth probability (Fig. 1d). In the early and middle-successional populations, seedling survival was also high (Fig. 1b, transition 2–3), but small plants had low probability to grow to larger stages (Fig. 1d). Seed production and seedling recruitment were low in late-successional populations (Figs. 1a, 1b).

Population growth rates did not differ between central populations (Sweden) and peripheral populations (Finland) (paired t test of $\log_e \lambda$, $t = 1.074$, $p = 0.343$, $df = 4$, populations paired according to the successional stage; Table 1). The central and peripheral populations differed by 4.0%. According to the power analysis, the design would have detected 16% difference in population growth rates with 80% statistical power. On average, Finnish populations had lower survival (average survival of all stages except seed bank, Sweden 0.80, Finland 0.70). On the other hand, growth probabilities of middle-sized and large individuals were higher in Finland (results not shown). These differences may have affected life span of the individuals because Swedish populations had a longer life span in all successional stages except middle succession, but the difference between countries was not statistically significant (paired t test after \log_e transformation, $t = 0.404$, $p = 0.707$, $df = 4$). In other than middle-successional populations, life span of *P. veris* ranged from 12 to 88 years and was from 8 to 30 years higher in Sweden than in Finland when values of the same habitat type were compared. In the middle-successional habitat, life span was 37 years in Sweden and on average 155 years in Finland because one of the Finnish middle-successional populations had very low mortality.

Elasticities and LTRE

Elasticities of survival, growth, and reproduction components showed clear trends along the successional gradient (Fig. 2). The elasticities of the transitions involving the seed production, recruitment, and growth of the small individuals decreased through succession and approached 0 in the late-successional populations (Figs. 2a, 2b, 2c).

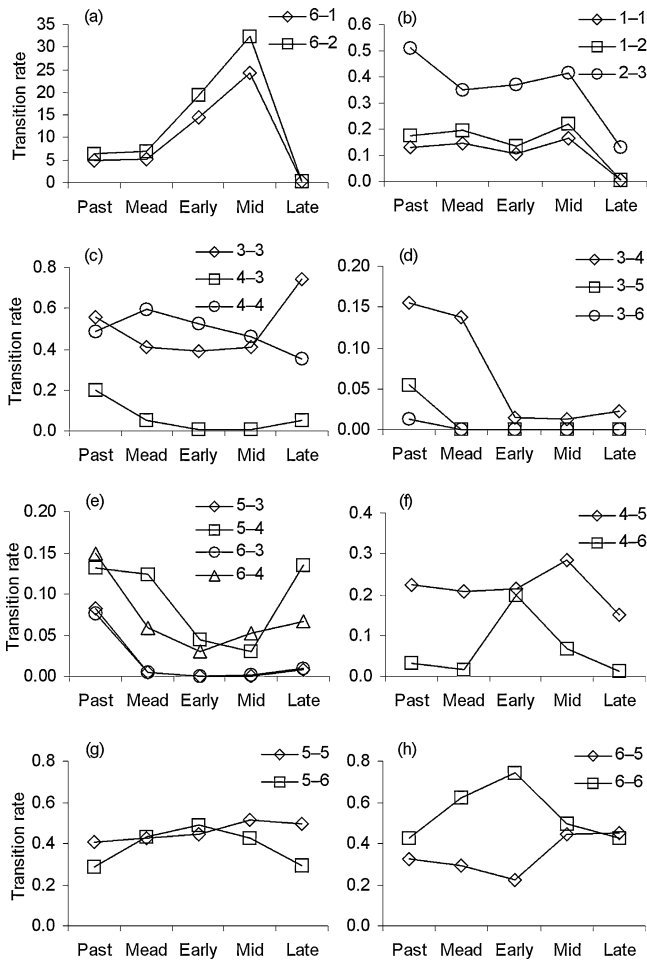


Figure 1. Transition rates between different life-history stages of *Primula veris* in different habitat types (life-history stage: 1, seed bank; 2, seedlings; 3, small plants; 4, middle-sized plants; 5, large plants; 6, reproductive plants; habitat type: past, pasture; mead, meadow; early, early succession; mid, middle succession; late, late succession). The transitions are grouped as follows: (a) seed production, (b) seed bank and seedlings, (c) stasis and retrogression of small and middle-sized plants, (d) growth of small plants, (e) retrogression of large plants and two retrogression transitions of reproductive plants, (f) growth of middle-sized plants, (g) stasis and growth of large plants, (h) retrogression from reproductive to large plants and stasis of reproductive plants.

Growth elasticities of the middle-sized and large individuals remained fairly constant throughout the succession (Fig. 2d). The combined elasticity of stasis and retrogression transitions was high and increased with succession (Fig. 2e).

Transitions that made large contributions to population growth rate, in terms of their elasticities in the average matrix of all habitats, varied less among habitat types than

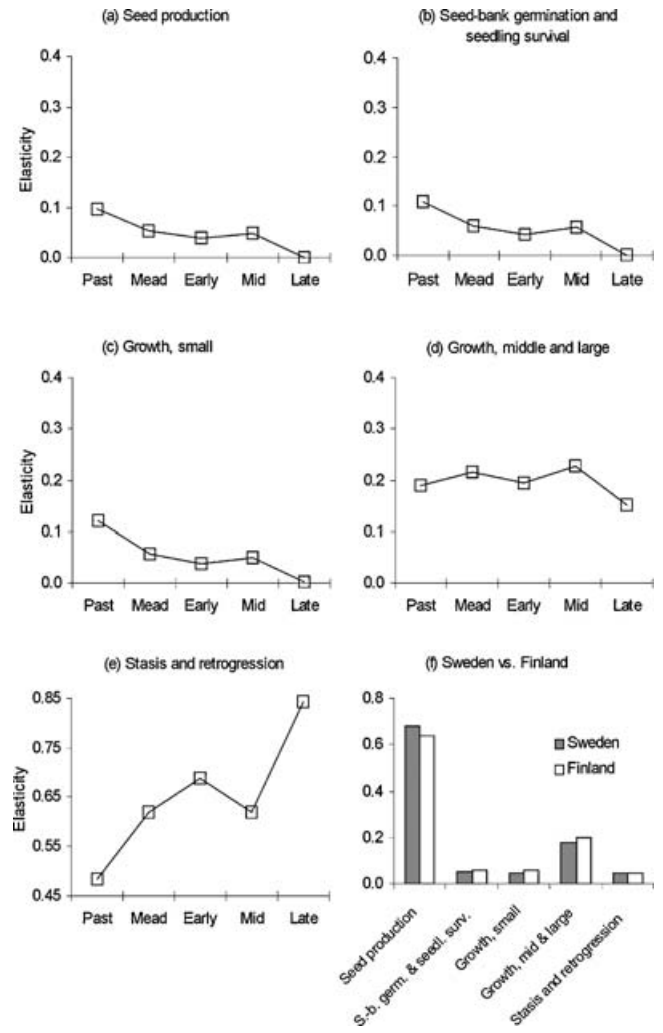


Figure 2. Combined elasticities (summed values) of *Primula veris* in (a–e) different habitat types and (f) in Sweden and Finland (combinations: (a) seed production, elasticities from reproductive plants to seed bank and from reproductive plants to seedlings; (b) seed-bank germination and seedling survival, elasticities from seed bank to seedlings and from seedlings to small plants; (c) growth small plants, sum of elasticities from small plants to larger stages; (d) growth middle-sized and large plants, elasticities from middle-sized to large plants, from middle-sized to reproductive plants, and from large to reproductive plants; and (e) stasis and retrogression, sum of elasticities of other elements; habitat types: past, pasture; mead, meadow; early, early succession; mid, middle succession; late, late succession).

transitions with smaller contributions (Pearson correlation between elasticity value and the coefficient of variation of each transition rate, $r = -0.6049$, $p = 0.004$, $n = 21$).

According to LTRE, early life-history stages contributed positively to the population growth rate in open habitats,

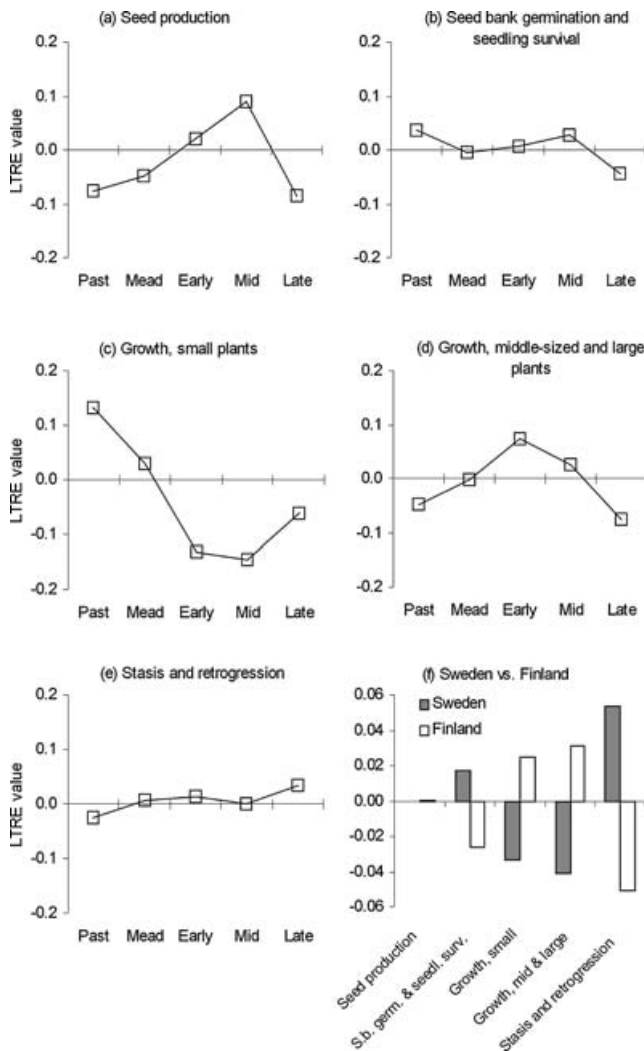


Figure 3. Life-table response experiment (LTRE) results of *Primula veris* in (a–e) different habitat types and (f) in Sweden and Finland (combinations: (a) seed production, LTRE values from reproductive plants to seed bank and from reproductive plants to seedlings; (b) seed bank germination and seedling survival, LTRE values from seed bank to seedlings and seedlings to small plants; (c) growth small plants, sum of LTRE values from small plants to larger stages; (d) growth middle-sized and large plants, LTRE values from middle-sized to large plants, middle-sized to reproductive plants, and large to reproductive plants; (e) stasis and retrogression, sum of LTRE values of the other elements; habitat types: past, pasture; mead, meadow; early, early succession; mid, middle succession; late, late succession). Summed LTRE analysis values are in y-axis.

whereas high growth and seed production of adult individuals increased the population growth rate in early and middle-successional populations (Fig. 3). Low seed production in pasture resulted in a negative contribution

to the population growth rate compared with the mean matrix, whereas the high growth transitions of the small individuals gave positive contributions to the growth rate (Figs. 3a, 3c). The LTRE contributions of the meadow populations were near 0 (i.e., transitions were near the mean matrix) (Fig. 3). In early and middle succession, growth transitions of the small stage were low, and the LTRE contributions were negative (Fig. 3c). Early successional populations had the most growth in middle-sized and large individuals, and middle-successional populations had the highest seed production (Figs. 3a, 3d). Contributions of late-successional populations were negative for all life-history components except stasis and retrogression (Fig. 3). The contributions of variation in stasis and retrogression were small in all successional stages (Fig. 3e).

Elasticities did not show any systematic differences between Sweden and Finland (Fig. 2f). According to LTRE, growth to larger stages increased the population growth rate in Finland, whereas seedling recruitment and stasis were important in Sweden (Fig. 3f).

Discussion

Demographic information is essential to the assessment of the factors underlying population decline and to the identification of targets for population and habitat management (Caswell 2001; Morris & Doak 2002). Ideally, assessment of population viability should be carried out in multiple populations of a species and over several years (Menges 2000). Sampling of several populations is especially important for species that have a wide habitat range, such as *P. veris*. This species grows in open habitats such as pastures and short- and tall-grass meadows, but also in various stages of forest succession, from quite open woodlands of early succession to late stages with a closed canopy. For efficient conservation management of species that have a wide habitat range, it is important to know which habitat types can maintain populations that are persistent in the long run, how transition rates vary in association with habitat, how this variation affects population dynamics, and how we can affect transition rates through management. We will discuss these factors with the demographic analysis of *P. veris* as an example.

Demographic Patterns

The demography and growth rate of *P. veris* in Sweden and Finland were similar. There was no difference in its population growth rates (λ) between the countries, and elasticities were similar in corresponding habitats. Survival was somewhat lower and growth probabilities often higher in Finnish populations. As a result the projected life span was shorter in Finland in all successional stages, except in middle succession. If Finnish plants are more short-lived than Swedish plants, population persistence in a deteriorating environment may be lower in Finland,

whereas Swedish populations may be able to maintain themselves until environmental conditions improve (e.g., forest thinning, or occasional good years for recruitment) (Higgins et al. 2000). On the whole, however, the similarity of demographic patterns in the two regions suggests that results can be generalized over a large part of the distribution area of *P. veris*.

Among-habitat demographic variation was substantial. The average population matrices had a positive growth rate in all habitat types except in late-successional populations and in Finnish meadow habitats. The late-successional populations are remnants from earlier successional stages. Even the late-successional populations seem to persist for a long time because *P. veris* is a long-lived species. The projected life spans of adult individuals of two of the late-successional populations were 27 and 37 years, so if some recruitment is possible and if the environment does not deteriorate further, extinction will take a long time (see also Eriksson 1996; Higgins et al. 2000). In the third late-successional population, the environmental conditions were so harsh that survival of established plants was poor and the projected life span of adult individuals was only 12 years.

Among- and within-species comparisons indicate that plants of open habitats tend to have high fecundity and growth elasticities, whereas plants of closed habitats often have high survival (stasis and retrogression) elasticities (Silvertown et al. 1993, 1996; Oostermeijer et al. 1996). The elasticity analysis of our *P. veris* populations supports this hypothesis. Plants in open habitats (pasture and meadow) had lower survival elasticities than plants in habitats in later successional stages. Fecundity elasticities showed the reverse trend. The elasticities of the growth component of early life-history stages (germination from seed bank, seedling survival, and growth from small to middle-sized plants) also decreased with increasing successional development, but growth elasticities of large stages were similar in all types of habitats.

Elasticities as Conservation Tools

Even a small increase in transition rates with a high elasticity results in a large increase in the population growth rate, λ (de Kroon et al. 1986); therefore, such transition rates may be good candidates as management targets (Caswell 2000, 2001). Current data can be used to evaluate this prediction. In *P. veris*, the late-successional populations are in most immediate need of management. The search for effective management methods for late-successional populations may provide information for conservation of other species with a similar ecology because forestation and habitat closure is a threat for many endangered species in Sweden and elsewhere (Gärdenfors 2000).

In late-successional habitats the highest elasticities were in the latest life-history stages (large and reproduc-

tive individuals) and especially in stasis and retrogression transitions. The elasticity analysis thus suggests that the quickest way to increase λ in late-successional populations is to enhance the survival of individuals in the largest stages. This appears paradoxical because recruitment suffers most from canopy closure. One may therefore ask, Are there other types of demographic information that would indicate that managing recruitment would be effective? One possibility is that other parameters related to elasticity, such as sensitivities or loop elasticities, are more appropriate in this case. Sensitivity analysis of late-successional populations yielded results similar to results of the elasticity analysis: sensitivities of stasis and retrogression were 10–500 times higher than sensitivities of recruitment (results not shown). Van Groenendael et al. (1994) suggested that loop elasticities could be used to combine elasticities of several transition rates into an integrated measure of elasticity for a given life-cycle path. For the current data, loop elasticities showed the same patterns as the ordinary elasticity analysis: they suggested that management investments should be directed toward the well-being of adult plants rather than to enhance recruitment (results not shown).

Elasticities change when matrix elements change (Horvitz & Schemske 1995). Could management of recruitment substantially increase recruitment elasticities? We selected one of the late-successional populations, the Finnish late-successional population 2, to analyze how elasticity structure changes when the transition elements of recruitment are increased. Changes in the elasticity structure as a response to perturbation of transition rates can be studied with second derivatives of elasticities (Caswell 1996). According to the second derivatives, an increase in the transition rates of recruitment indeed decreased the stasis, growth, and retrogression elasticities of the largest stages (results not shown). We tested this result by increasing some recruitment elements of the Finnish late-successional population 2 (Table 2) to maximal values observed in other populations (Table 3). Several recruitment elements had to be changed simultaneously before the elasticity structures of the Finnish late-successional population 2 and the other populations became similar (Table 3; the largest recruitment elasticity and the elasticity of stasis of large plants used as the indicators of elasticities of recruitment and stasis, respectively).

Our elasticity and sensitivity analyses suggest that to manage decreasing populations of *P. veris*, one should invest in adult survival. Substantial enhancements in several steps of recruitment are needed before their elasticities increase to the level observed in growing populations.

Population Growth Rate after Direct Perturbation of Adult Survival

Would high adult survival be the best management target for late-successional populations, as the elasticity analysis

Table 2. Average population matrix and elasticities of *Primula veris* in Finnish late-successional population 2.

Population matrix	Seed bank	Seedlings	Small plants	Middle-sized plants	Large plants	Reproductive plants
Seed bank	0.005	0	0	0	0	0.362
Seedlings	0.006	0	0	0	0	0.482
Small plants	0	0.1	0.755	0.024	0	0.011
Middle-sized plants	0	0	0.023	0.289	0.030	0.043
Large plants	0	0	0	0.278	0.599	0.383
Reproductive plants	0	0	0	0.011	0.313	0.530
Elasticities						
seed bank	<0.001	0	0	0	0	<0.001
seedlings	<0.001	0	0	0	0	0.001
small plants	0	0.001	0.008	<0.001	0	<0.001
middle-sized plants	0	0	0.002	0.008	0.008	0.009
large plants	0	0	0	0.018	0.345	0.173
reproductive plants	0	0	0	<0.001	0.183	0.243

suggests? Adult survival cannot be increased without limits. Let us assume there is a management method to totally remove the mortality of the largest stages. In the Finnish late-successional population 2, survival rate of large and reproductive plants was 0.942 and 0.967, respectively. After removing mortality of large and reproductive plants, λ increases from 0.930 to 0.976. Also taking away mortality from middle-sized plants increased λ further to 0.997. The Finnish late-successional population 2 would thus decrease even if middle-sized, large, and reproductive plants did not have any mortality. In the unrealistic extreme case, where all middle-sized, large, and reproductive plants would survive and become reproductive the next year, λ is 1.005 (i.e., population would have virtually no growth). Increasing growth and stasis transitions to maximal values, as elasticities and sensitivities suggest, does not result in positive population growth of a late-successional population. That management for better survival has its limits—survival cannot exceed unity—may sound trivial, but it is easily forgotten when interpreting elasticities (e.g., Caswell 2000).

Enhancement of reproduction and recruitment is the only way to achieve healthy population growth in this case. Substantial increases, however, are needed in recruitment transitions of the Finnish late-successional population 2 (Table 3). Only when seedling production is increased simultaneously with one or both of the other two recruitment transitions does population growth rate become positive (Table 3). Management, to be effective, must simultaneously enhance several transition rates of recruitment. Management methods that produce habitat gaps, such as grazing or mowing, would give seedlings and small plants a competitive release. The transition rate increases must be substantial, but it is sufficient that they are within the range observed in other populations of *P. veris*.

Prospective and Retrospective Analyses

The use of prospective and retrospective methods in conservation has raised much discussion recently (e.g., Horvitz et al. 1997; Ehrlén & van Groenendael 1998; Caswell

Table 3. Largest elasticity of recruitment, elasticity of stasis of large plants, and population growth rate (λ) of Finnish late-successional population 2 of *Primula veris* after change of some life-history transition rates to maximal values observed in other populations.

Change of transition rate	Largest elasticity of recruitment*	Elasticity of stasis of large plants	λ
No change, mean value in the other habitat types	0.056	0.128	1.065
No change, Finnish late-successional population 2	0.002	0.345	0.930
From reproductive plants to seedlings, change from 0.482 to 35	0.041	0.236	0.988
Seedling survival, change from 0.1 to 0.6	0.008	0.326	0.937
From small to middle-sized plants, change from 0.023 to 0.18	0.012	0.314	0.941
Seedling survival, from 0.1 to 0.6; change from small to middle-sized plants, change from 0.023 to 0.18	0.035	0.252	0.974
From reproductive plants to seedlings, change from 0.482 to 35; from small to middle-sized plants, change from 0.023 to 0.18	0.082	0.156	1.119
From reproductive plants to seedlings, change from 0.482 to 35; seedling survival, from 0.1 to 0.6	0.076	0.165	1.097
From reproductive plants to seedlings, change from 0.482 to 35; seedling survival, change from 0.1 to 0.6; from small to middle-sized plants, change from 0.023 to 0.18	0.113	0.110	1.330

*Recruitment includes transitions from reproductive plants to seed bank and seedlings, seed-bank transitions, seedling survival, and transition from small- to middle-sized plants.

2000). Sensitivity and elasticity are prospective methods that analyze the dependence of λ on the transition rates. In prospective methods it is possible to analyze effects of all different types of changes in transition rates on population growth rate, irrespective of whether transition rate changes are easy to put into practice or totally unrealistic. Retrospective analyses such as LTRE methods express observed variation in λ as a function of observed variation in the transition rates. Essentially, LTRE values are among-population differences of transition rates weighed with sensitivity (i.e., the capacity of variation in transition rates to affect population growth rate according to the current data).

It has been claimed that LTRE results cannot be used to select optimal management targets (Horvitz et al. 1997; Caswell 2000, 2001). An LTRE considers only realized variation among the study populations. There may be management options available other than those we considered. The difference, however, between the random-model LTRE, where study populations are chosen randomly, and the fixed-model LTRE, where populations are chosen according to prior structure (Horvitz et al. 1997), is important. In the random-model LTRE, the fact that a large part of variation in λ is explained by one of the transition rates does not necessarily imply that this transition rate is the best management target. This is because variation in a transition rate might be due to factors that are not possible to modify by management (Caswell 2001). A transition rate may also be easy to manipulate and have a high sensitivity and elasticity, but it may have a low LTRE contribution because it is constant across the populations that were included to the study. In our study, transition rates that had the lowest elasticities varied most among habitat types. It has been suggested that this pattern is caused by stabilizing selection on those transition rates that have strongest fitness effects (Pfister 1998). The pattern may mean that it is easier to manipulate transition rates with low elasticities, such as reproduction in the case of *P. veris*.

It is easier to consider the implications of LTRE for management when the study populations represent the main potential management strategies and the analysis method is the fixed-model LTRE. The results then show how the management strategies included in the study affect transition rates and how this affects λ . A field experiment analyzed with a fixed-model LTRE can show why the best population is best and what is wrong with populations with a low growth rate (i.e., what the key elements are of a life cycle that suffers from bad conditions). In a prospective analysis the transition rates are varied in a computer; in a fixed LTRE different management methods affect transition rates in the field. An empirical study is not as clean as a computer simulation because several transition rates are affected simultaneously, with different strengths and sometimes in an unpredictable way, but the results are in a realistic context. In principle, a prospective analysis simi-

lar to LTRE can be based on predictions of the response of life-history stages to management if data on sensitivities are available. Such initial estimates of LTRE values can help in the evaluation of management strategies for experimental design or as an alternative to a full-scale field experiment.

We used LTRE with two factors, eccentricity of distribution area, which cannot be manipulated, and habitat, which can be controlled by habitat management. Management strategies other than those we included are possible. If, however, one wants to increase the growth rate of *P. veris* populations as a part of general habitat and landscape management without a custom-made management plan for a single species, LTRE results are highly relevant. Such management may help other species with ecologies similar to that of *P. veris*.

In our study the main difference between the LTRE results and the elasticity results was that the survival component (stasis and retrogression) had high elasticities but low LTRE contributions. Managing for high survival would thus not be a good strategy—at least with management methods of the study populations—because they do not generate enough variation in transition rates of the survival component. Moreover, increasing survival to unity in established plants would still yield negative population growth in late-successional populations as long as the other parts of the life cycle are unchanged.

Prospective methods help determine good candidate traits for management targets. If time and resources allow, the real value of potential management targets should be tested empirically. An LTRE helps in the analysis of the empirical tests. Prospective and retrospective methods can in this way be used together to find the optimal management strategy.

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