POPULATION VIABILITY ANALYSIS FOR PLANTS: PRACTICAL RECOMMENDATIONS AND APPLICATIONS

by

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Stockholm 2006
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Abstract. Population viability analysis (PVA) is commonly used in conservation biology to predict population viability in terms of population growth rate and risk of extinction. However, large data requirements limit the use of PVA for many rare and threatened species. This thesis examines the possibility of conducting a matrix model-based PVA for plants with limited data and provides some practical recommendations for reducing the amount of work required. Moreover, the thesis applies different forms of matrix population models to species with different life histories. Matrix manipulations on 37 plant species revealed that the amount of demographic data required can often be reduced using a smaller matrix dimensionality. The population models of slow-growing woody species generally require less data than those of fast-growing herbaceous species to produce precise estimates of population growth rates. Despite the simple life cycle of annual species, the ability of single fitness components to predict changes in population dynamics varied among populations in the annual plant *Melampyrum pratense*. This indicates that specific fitness components alone are inadequate predictors of population viability and cannot be used to replace demographic data from all stages of the life cycle. Given that an individual’s fitness is affected by plant density or the frequency of different gender morphs, linear matrix models are unlikely to predict population dynamics correctly. Estimates of population size of the herb *Melampyrum sylvaticum* were sensitive to the strength of density dependence operating at different life stages, suggesting that in addition to identifying density-dependent life stages, it is important to estimate the strength of density dependence precisely. When a small number of matrices are available for stochastic matrix population models, the precision of population estimates may depend on the stochastic method used. To optimize the precision of population estimates and the amount of calculation effort in stochastic matrix models, selection of matrices and Tuljapurkar’s approximation are preferable methods to assess population viability. Overall, these results emphasize that in a matrix model-based PVA, the selection of a stage classification and a model is essential because both factors significantly affect the amount of data required as well as the precision of population estimates. By integrating population dynamics into different environmental and genetic factors, matrix population models may be used more effectively in conservation biology and ecology in the future.
This thesis is based on the following articles, which will be referred to in the text by their Roman numerals:


II **Ramula, S.** Among-population variation in the ability of fitness components to predict population viability in an annual herb. – Submitted manuscript.


IV **Ramula, S.** Sensitivity of population estimates to density dependence in an annual plant, *Melampyrum sylvaticum*. – Submitted manuscript.

V **Ramula, S., Toivonen, E. and Mutikainen, P.** Demographic consequences of pollen limitation and inbreeding depression in a gynodioecious herb. – Submitted manuscript.

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1. INTRODUCTION

To prevent species from becoming extinct, it is essential to develop methods of evaluating population viability. One popular and common method is population viability analysis, PVA (Groom and Pascual 1998, Menges 2000, Oostermeijer et al. 2003). Although PVA can take many forms, its aim is to assess population viability in terms of population growth rate and risk of extinction. Furthermore, it aims to identify the most critical life stages for population viability which can be used to guide management actions.

PVAs of plants are usually based on linear matrix population models that assume exponential population growth. Given that plant density or the frequency of different gender morphs in a population affects population dynamics, nonlinear matrix models are preferable to estimate population viability (Caswell 2001). Matrix population models consist of fecundity transitions and transition probabilities among different life, size, or age stages (Caswell 2001). To estimate these transitions, individuals from all stages of an organism’s life cycle are observed in permanent plots or transects for a certain period of time. Observations from consecutive time steps, usually from consecutive years, result in demographic data (i.e. data on birth, growth, and death) which are used to calculate population growth rate and other population parameters such as the sensitivity of growth rate to perturbations.

Estimates of population viability result from either deterministic matrix models that assume constant transition rates over time, or stochastic matrix models that include variability in the transition rates over time. Variation in the transition rates may be due to environmental stochasticity (e.g. weather, herbivory, pathogens), demographic stochasticity (e.g. uncertainty in life history traits due to a small population size), or sampling stochasticity (e.g. sampling a finite number of individuals) (Lande 1988, Alvarez-Buylla et al. 1996).

Despite the fact that PVA is commonly used in conservation biology, it has been criticized because of its uncertainty (Ludwig 1999, Coulson et al. 2001, Ellner et al. 2002). To produce precise estimates of population viability, PVA requires a lot of data and field work. Bierzychudek (1999) examined the reliability of the estimates of population viability in two populations of the perennial plant *Arisaema triphyllum*. She found that a matrix model based on three years of data failed to predict population viability over 15 years in one population but succeeded better in the other population. The failure was due to inadequate sample sizes, data based on too few years, or ignorance of density dependence (Bierzychudek 1999). The precision of a PVA is generally affected by the following three main factors. First, the precision is highly dependent on the number of individuals sampled per stage (Gross 2002, paper I). Although methods exist to sample and classify individuals for a transition matrix to achieve a precise estimate of population viability (Vandermeer 1978, Moloney 1986, Gross 2002), the lack of adequate demographic data is still a common problem in the PVAs of plants (Schemske et al. 1994, Menges 2000). This is mainly because of a small population size of threatened plant species (Ouborg 1993, Endels et al. 2002) and a shortage of time for conducting the PVA. Second, the precision of a PVA is affected by the number of years monitored (Lotts et al. 2004, Doak et al. 2005). On average, four years of demographic data are used in the PVAs of plants (Menges 2000). According to Fieberg and Ellner (2000), such a short observation period is
inadequate to predict the risk of extinction. Third, the outcome of a PVA may depend on the stochastic method (Kaye et al. 2001, Morris and Doak 2002, Kaye and Pyke 2003, paper III) or the programme package (Mills et al. 1996) used to estimate population viability.

This thesis examines the possibility of conducting PVA for plants with limited data, covering plant species with different life histories as well as different forms of matrix population models. Specifically, I will investigate under which conditions it is possible to reduce the amount of demographic data in the PVAs of herbaceous and woody species by using a smaller matrix dimensionality (paper I), and whether demographic data can be replaced by the measurements of specific fitness components alone for an annual plant with a persistent seed bank (paper II). Papers III and IV concentrate on stochastic matrix models and investigate the reliability of different stochastic methods in relation to a number of matrices (paper III), and the sensitivity of the estimate of population size to density dependence (paper IV). Finally, by integrating demographic data into data on pollen limitation and inbreeding depression, I will apply a two-sex stochastic matrix model to simulate the impacts of pollen limitation and inbreeding depression on population dynamics in a perennial plant that has two gender morphs (paper V). The aim of the thesis is to produce practical recommendations for the future PVAs of plants. Although the focus is on plants, the results can often be applied to the PVAs of other organisms as well.

2. MATRIX POPULATION MODELS

A large number of matrix models exist from simple deterministic matrix models to complex metapopulation models that may include population genetics, dispersal, and species interactions (Alvarez-Buylla et al. 1996, Beissinger and Westphal 1998, Caswell 2001). The simplest, linear deterministic matrix model can be expressed as \( \mathbf{n}(t + 1) = \mathbf{An}(t) \) or

\[
\begin{pmatrix}
  n_1 \\
  n_2 \\
  n_3
\end{pmatrix}
= 
\begin{pmatrix}
  a_{11} & a_{12} & a_{13} \\
  a_{21} & a_{22} & a_{23} \\
  a_{31} & a_{32} & a_{33}
\end{pmatrix}
\begin{pmatrix}
  n_1 \\
  n_2 \\
  n_3
\end{pmatrix}
\]

where \( \mathbf{A} \) refers to a population matrix and \( \mathbf{n}(t) \) refers to population size at time \( t \) (Caswell 2001). The population matrix consists of matrix elements \( a_{ij} \) each of which describes an average probability for an individual in stage \( j \) to transfer to stage \( i \). For fecundity elements, \( a_{ij} \) describes an average contribution of an individual in stage \( j \) to stage \( i \). The linear deterministic matrix model assumes population growth to be exponential and ignores variability in demographic transitions over time.

Variability in the demographic transitions can be modelled using a linear stochastic matrix model \( \mathbf{n}(t + 1) = \mathbf{A}_t \mathbf{n}(t) \), where both the transition matrix (\( \mathbf{A} \)) and population size (\( \mathbf{n} \)) vary over time (\( t \)) (Caswell 2001). Stochastic population growth rate can be estimated either analytically using Tuljapurkar’s approximation or numerically using simulations. Tuljapurkar’s analytical approximation produces a rough estimate of stochastic population growth rate based on the observed matrices, and the variances and covariances of matrix elements (Caswell 2001, Fieberg and Ellner 2001). In simulation-based stochastic models, population dynamics are simulated into the future with a large number of projections. The estimate of stochastic population growth rate is then calculated as an average taken from all projections at \( t + 1 \). Three different simulation methods are currently used to estimate stochastic population growth rate. First, in the matrix selection method, an entire population matrix is randomly selected at each time step from a set of population matrices originated from different years. Second, in the matrix element selection method, one can produce
3. POPULATION PARAMETERS

Population growth rate describes the finite rate of a population to increase and to converge to its stable stage or age distribution (Caswell 2001). At the stable stage distribution, the proportion of each stage in the population remains constant although the population size may vary. The expression of population growth rates differs between deterministic and stochastic population models. In the deterministic models, the population with a growth rate ($\lambda < 1$) is declining and the population with a growth rate >1 is increasing. In the stochastic models, a logarithmic form ($\log \lambda_{st}$) is common. A negative growth rate ($\log \lambda_s$) indicates a declining population, whereas a positive growth rate indicates an increasing population.

Sensitivity measures the sensitivity of population growth rate to an absolute change in any matrix entry, and elasticity measures the sensitivity of population growth rate to a proportional change in any matrix entry (Caswell 2001). Elasticities sum to unity within matrices and are thus comparable among different matrices sharing the same dimensionality (Enright et al. 1995). Sensitivity can be calculated for each matrix transition, whereas elasticities can be calculated only for non-zero matrix transitions. Matrix transitions with the highest elasticity or sensitivity values are usually considered most critical to population viability (Benton and Grant 1999, Mills et al. 1999, Caswell 2000, de Kroon et al. 2000).

Risk of extinction is commonly expressed as the risk of quasi-extinction, i.e. the risk of population size declining to a threshold number of individuals (Caswell 2001).

Reproductive value, the left eigenvector ($\mathbf{v}$) of the transition matrix, predicts the relative contribution of each matrix stage to the future population growth rate (Caswell 2001). Reproductive values tend to be

\[ A \] matrices by selecting each matrix element from its distribution based on the mean and variance of the given matrix element. In contrast to the selection of entire matrices, this method does not automatically take correlations among matrix entries into account but it is possible to estimate and to include the correlations in the simulations. The inclusion of correlations is often important (Morris and Doak 2002, paper III) because survival, growth, and fecundity rates tend to covary in nature (Horvitz and Schemske 1995, van Tienderen 1995, Caswell 2001) resulting in covarying matrix entries. Moreover, the sign of correlations among matrix entries affects the estimates of population growth rate and the risk of extinction (Tuljapurkar 1982, Ferson and Burgman 1995, Fieberg and Ellner 2000, 2001). The third simulation-based method to estimate stochastic population growth rate is to produce \( A \) matrices by selecting vital rates. In this method all matrix elements are broken down into survival, growth, and fecundity components, so called vital rates. The vital rates are then randomly selected from their distributions based on the means and variances of the rates. Finally, the vital rates are converted back to matrix elements before calculating the stochastic population growth rate. Similar to the selection of matrix elements, the selection of vital rates ignores correlations among matrix entries unless they are estimated and added to a model.

Given that population dynamics is density-dependent or frequency-dependent, a nonlinear matrix model is appropriate to describe it as \( \mathbf{n}(t+1) = A \cdot \mathbf{n}(t) \), where the matrix elements of \( A \) change as a function of plant density or frequency in a population at time \( t \) (Caswell 2001). By varying matrix elements for projected years in a simulation, it is possible to include stochasticity in the nonlinear models.
lower for younger life stages than reproductive stages, indicating a lower probability for young individuals to survive to a reproductive stage and to contribute to population growth (Horvitz and Schemske 1995, Caswell 2001, Knight 2004, paper V). Reproductive values are also low for individuals that have already passed their reproductive age (Caswell 2001).

4. METHODS

Transition matrices of smaller dimensionalities require less data than larger matrices. Smaller matrices might therefore be used to reduce the amount of work required, given that they predict population dynamics precisely. To examine under which circumstances matrix dimensionality can be reduced, I used demographic data on 37 plant species (18 herbaceous and 19 woody species) collected from literature and in the field (paper I). By reducing matrix dimensionality from one to three stages for each species, I examined changes in population growth rates, the variances of growth rates, and the elasticities of growth rates in relation to matrix dimensionality. I also compared the distance from the stable stage distribution and the time to converge to it between the herbaceous and woody species.

Since it is time-consuming to collect demographic data from all stages of an organism’s life cycle, I examined whether changes in single fitness components could be used as surrogates to predict changes in population viability for annual plants (paper II). I conducted biomass removal treatments in four populations of the annual herb *Melampyrum pratense* to induce changes in eight fitness components such as the probability of plants to remain vegetative, the probability of vegetative plants to flower, the survival of flowering plants, and seed production. I then examined how changes in single fitness components contributed to changes in population growth rates.

Estimates of stochastic population growth rate and the risk of extinction may vary depending on the stochastic method used. Further, the amount of calculation effort required to estimate a stochastic population growth rate varies to a large degree among different stochastic methods. Based on demographic data on the perennial herb *Primula veris*, I compared the stochastic population estimates produced by four different stochastic methods: selection of matrices, selection of matrix elements, selection of vital rates, and Tuljapurkar’s approximation (paper III). Specifically, I investigated the importance of the inclusion of correlations among matrix entries in the model in relation to a number of transition matrices. I also examined the possibility of replacing correlations among matrix entries from another data.

Although plant density often affects plant population dynamics, density dependence is rarely included in the PVAs of plants. To examine the role of density dependence in population dynamics of the annual herb *Melampyrum sylvaticum*, I conducted density manipulations during two consecutive years in the field (paper IV). I compared the estimate of population size produced by a linear stochastic model to that produced by a nonlinear stochastic model. Further, I studied the sensitivity of the estimate of population size to the strength of simulated density dependence occurring at different stages of the life cycle.

In the gynodioecious perennial plant *Geranium sylvaticum*, where the maintenance of female plants among hermaphroditic plants is problematic, I studied the effects of pollen limitation and inbreeding depression on population growth rate and sex ratio (paper V). I combined data on experimental hand pollinations with demographic data collected from three
populations and conducted stochastic simulations using a two-sex matrix population model.

5. RESULTS AND DISCUSSION

5.1. Matrix dimensionality and data requirements

In matrix population models each transition represents an average transition probability or an average contribution. Therefore, all individuals within a stage should ideally have homogeneous survival, growth, and fecundity rates to produce precise estimates of population viability (Vandermeer 1978, de Roos 1992, Caswell 1997). A high precision of transition rates and consequently population estimates is achieved by sampling a large number of individuals for each stage. However, due to small population sizes as well as time and monetary constraints, large sample sizes are sometimes impossible to achieve. In practice, sample sizes of some stages may be very low, even less than ten individuals (e.g. Piñero et al. 1984, Moloney 1988, Charron and Gagnon 1991). In such cases estimated demographic transitions are naturally imprecise and likely to produce biased estimates of population viability. Schemske et al. (1994) found that demographic data in the recovery plans of 98 plant species were insufficient in the majority of the plans, indicating that the lack of adequate data is indeed a common problem in population models.

A key factor that affects the number of individuals required to produce precise estimates of population viability is matrix dimensionality. Larger matrices consisting of several stages require considerably more data than smaller matrices consisting of only a few stages. Matrix dimensionality in demographic studies may vary from three stages (e.g. Fiedler 1987) up to 15 stages or even more (e.g. Nault and Gagnon 1993, Hoffmann 1999) being larger for woody than for herbaceous species (Silvertown et al. 1993, paper I).

I examined the effect of matrix dimensionality on population growth rates ($\lambda$), the variance of growth rates, and the elasticity of growth rates using data from 37 plant species. I found that combining adjacent stages in a matrix sometimes decreased the variance of $\lambda$ and thus, improved the precision of $\lambda$ as a result of an increased sample size per stage (paper I). In other cases, combining stages reduced the precision of $\lambda$ because of an increased heterogeneity in the combined stage (paper I). Whether it is possible to use a smaller matrix without reducing the precision of an estimated population growth rate depends on the distance of the population structure from its stable stage distribution and the difference in the combined transition probabilities weighted by their reproductive values (paper I). In general, when a population is near or at its stable stage distribution, stages in a matrix can be combined without substantial changes in population growth rates (paper I). Furthermore, the adjacent stages that have approximately similar transition rates, and low reproductive values and sensitivities can be combined without decreasing the precision of the population growth rate (paper I). This result clearly shows that in many cases it is unnecessary to construct large matrices to be able to estimate population growth rate precisely. By using a small matrix dimensionality, population growth rate can be assessed quite well also when data is sparse. Nevertheless, it is important to note that even though population growth rate may remain virtually constant despite the number of stages in a matrix, the elasticities of population growth rates are still affected by matrix dimensionality (Enright et al. 1995, paper I). The elasticity of population growth rates to survival and fecundity transitions tends to increase with decreasing matrix dimensionality (Enright et al. 1995, paper I), whereas the elasticity of
population growth rates to growth transitions tends to decrease (Yearsley and Fletcher 2002, paper I). The dependence of elasticity values on matrix dimensionality matters when the importance of different life stage transitions is needed to compare among different species, or among different habitats within the same species.

The number of individuals required per stage in a matrix varies among species with different life histories. Matrix manipulations of 37 different plant species revealed that the population models of herbaceous species often require more data than those of woody species to achieve a high precision (paper I). Despite the fact that matrix dimensionality can often be reduced for perennial plants, demographic data collected from all life stages cannot be replaced by the measurements of single fitness components, such as adult survival, growth, and/or fecundity (Ehrlén and Eriksson 1995, Louda and Potvin 1995, García and Ehrlén 2002, Ehrlén 2003). Even in the annual herb *Melampyrum pratense*, which has a persistent seed bank but a simpler life cycle compared with that of perennials, the ability of single fitness components to predict population viability varied among populations (paper II). Changes in fitness components contributed directly to changes in population growth rates in some populations but not in others (paper II). The varying ability of fitness components to predict population viability mainly resulted from the different sensitivity of growth rates to fitness components (paper II). Hence, without constructing a transition matrix, it is difficult to assess whether a change in a single fitness component (or some components) is large enough to cause a change in population viability of annual plants with a seed bank. For annuals without a persistent seed bank, changes in fitness components might be better predictors of population viability. Given that the recruitment of annuals without a seen bank is not limited by the availability of suitable habitats, the average lifetime offspring production of an individual plant should generally equal population viability (e.g. Silvertown and Charlesworth 2001).

5.2. Reliability of stochastic matrix models

Demographic data from several years are often required to capture variability in demographic transitions. Stochastic simulations based on only a few years of data tend to underestimate or overestimate stochasticity leading to erroneous estimates of population viability (Bierzychudek 1999, Ludwig 1999, Fieberg and Ellner 2000, Lotts et al. 2004, Doak et al. 2005). There has been a lot of debate on the length of demographic data (i.e. the number of years) in relation to the precision of population estimates. According to McCarthy et al. (2003), ten years of data is enough to approximately predict the relative risk of extinction for the following 100 years. The results of Fieberg and Ellner (2000) are much more pessimistic suggesting that ten years of data would allow predictions only for the following one or two years.

In addition to demographic data input to a population model, the stochastic method used in the simulation may affect the outcome of the model (Kaye et al. 2001, Morris and Doak 2002, Kaye and Pyke 2003, paper III). The selection of entire matrices is still the most common method in stochastic simulations (reviewed in Fieberg and Ellner 2001) but an increasing number of studies have used the selection of matrix elements or the selection of vital rates (Doak et al. 1994, Maschinski et al. 1997, Gross et al. 1998, Pfab and Witkowski 2000, Kaye et al. 2001, Doak et al. 2005). The selection of matrix elements and the selection of vital rates are considered more flexible methods compared with the selection of matrices and Tuljapurkar’s analytical approximation (Fieberg and Ellner 2001, Morris and Doak 2002).
2002), which may explain their increasing popularity in PVAs. Moreover, the use of the selection of vital rates makes it possible to reduce the observation error, i.e. the error that is caused by sampling a finite number of individuals per stage (Morris and Doak 2002). Despite the flexibility of the selection of matrix elements and the selection of vital rates, they require most calculation and one challenge in the simulations based on these methods is the estimation and inclusion of correlations among matrix entries. Correlations are often ignored in stochastic matrix simulations (Maschinski et al. 1997, Kaye et al. 2001, Kaye and Pyke 2003) although their inclusion significantly affects the estimates of population viability (Doak et al. 1994, Ferson and Burgman 1995, Cisneros-Mata et al. 1997, Morris and Doak 2002). The importance of the inclusion of correlations was confirmed by the simulations based on varying numbers of matrices of the perennial herb, *Primula veris* (paper III). Furthermore, the simulations demonstrated that the magnitude of correlations increased with decreasing number of matrices, indicating that the inclusion of correlations is important particularly when simulations are based on only a few years of data and thus a small number of matrices (paper III). On the other hand, correlations estimated from a small number of matrices are sometimes erroneous (Morris and Doak 2002), and may produce population estimates that significantly differ from those produced by the selection of matrices and Tuljapurkar’s approximation (paper III). This result suggests that to increase the reliability of stochastic population estimates based on a small number of matrices, it is most safe to use the selection of matrices or Tuljapurkar’s approximation. Given that matrices from several years of the same population are available, the selection of vital rates may be preferred because it allows for a reduction in observation error (Morris and Doak 2002) that always exists unless the sample includes every individual in a population. The magnitude of observation error significantly affects the precision and bias of population estimates (Ludwig 1999).

Previous studies have reported that the choice of a stochastic method affects the estimates of population viability (Kaye et al. 2001, Morris and Doak 2002, Kaye and Pyke 2003). In contrast, Fieberg and Ellner (2001) observed that all three stochastic methods investigated produced similar estimates of stochastic population growth rates. I found that the selection of matrices and the selection of matrix elements often produced quite similar estimates of stochastic population growth rate (log $\lambda_s$) in *P. veris* (paper III). Further, the selection of vital rates generally produced the lowest and Tuljapurkar’s approximation the highest estimates of log $\lambda_s$ (paper III). Low log $\lambda_s$ values tend to indicate a higher risk of extinction and more pessimistic estimates of population viability (Caswell 2001). Nevertheless, this is not always the case because the risk of extinction also depends on the variance of log $\lambda_s$. In *P. veris*, the selection of matrices produced the highest variance of log $\lambda_s$ and therefore the highest risk of extinction although it did not produce the lowest log $\lambda_s$ (paper III). Thus, the selection of matrices produced the most pessimistic estimates of the risk of extinction, which again according to the precautionary principle, made it a preferable method to assess population viability (paper III).

### 5.3. Model selection

In PVA, a researcher must often try to optimize the precision of population estimates based on the data at hand. One may have to choose whether to use simple deterministic models that may be less realistic because of the lack of variation in demographic transitions (Doak et al. 1994, 2005, Alvarez-Buylla et al. 1996, Nations and Boyce 1997), or whether to use more complex stochastic models that may fail.
because of inadequate data (Ludwig 1999, Doak et al. 2005). There is no alternative to deterministic models if only one transition matrix can be constructed, whereas it is possible to use stochastic models when more than one matrix is available. Doak et al. (2005) compared population estimates produced by deterministic and stochastic models. They observed that with less than five years of data, population estimates produced by deterministic models were generally less erroneous than those produced by stochastic models, whereas the reverse was true for longer data sets.

Due to the fact that population dynamics of plants are often affected by plant density and thus intraspecific or/and interspecific competition (e.g. Smith 1983, Watkinson et al. 1989, Watkinson 1990, Alvarez-Buylla 1994, Silva Matos et al. 1999, Blundell and Peart 2004, paper IV), linear matrix models are likely to produce erroneous estimates of population dynamics (Silva Matos et al. 1999, Tanner 2000, Henle et al. 2004, paper IV). So far, density dependence is taken into account in relatively few PVAs of plants (reviewed in Groom and Pascual 1998, Menges 2000). The sensitivity of population growth rate to changes in matrix transitions depends on the magnitude of growth rate and the life history of a species (Oostermeijer et al. 1986, Silvertown et al. 1993, 1996, de Kroon et al. 2000, Franco and Silvertown 2004). Therefore, species often vary in their response to density dependence operating in different matrix transitions. In the annual weed, *Tripleurospermum perforatum*, Buckley et al. (2001) observed that density-dependent mortality and flowering probability had a minor effect on population dynamics that was mainly regulated by density-dependent fecundity. In the annual herb, *Melampyrum sylvaticum*, an estimate of population size was sensitive to simulated density dependence in nearly all matrix transitions (paper IV). Moreover, the strength of density dependence often affected the estimate of population size significantly (paper IV). The different sensitivities of population dynamics to density dependence in these two annual species emphasize the variation among species even with similar life histories. Since it may be impossible to generalize the effects of density on population dynamics, the sensitivity of population estimates to density dependence should be studied for each study species in question. Given that population dynamics is highly sensitive to the strength of density dependence, the effect of density on different life stages needs to be carefully assessed before conducting a PVA (paper IV).

A number of studies have recommended comparing different population models in order to view possible scenarios before assessing population viability (Mills et al. 1996, Sæther et al. 1998, Doak et al. 2005, paper IV). Further, one should preferably compare the relative rather than absolute outcomes of different models (Beissinger and Westphal 1998, Lotts et al. 2004). Overall, this suggests that it is ultimately a researcher’s task to evaluate the most likely scenarios based on the knowledge of the study system.

### 5.4. Applications of matrix population models

Ecological factors, such as herbivores, pollinators, and neighbour plants play an important role in plant population dynamics (e.g. Horvitz and Schemske 2002, Lennartsson 2002, Ehrlén 2003, Blundell and Peart 2004). Further, threatened and small plant populations often suffer from inbreeding depression (Ellstrand and Elam 1993, Hendrix and Kyhl 2000, Severns 2003) that may lead to the loss of genetic diversity. Although the amount of genetic diversity has been estimated for a large number of rare and threatened plant species, this knowledge is rarely included in the PVAs of plants (Oostermeijer et al. 2003). Several studies have integrated pollen
limitation and/or herbivory into population dynamics (e.g. Calvo and Horvitz 1990, Ehrlén and Eriksson 1995, Parker 1997, Garcia and Ehrlén 2002, Ehrlén 2003, Knight 2004), whereas a few studies have integrated genetic problems into demographic studies in plants (Oostermeijer et al. 2003, paper V). In the gynodioecious perennial plant *Geranium sylvaticum*, where female and hermaphroditic plants co-occur in the same population, pollen limitation of both gender morphs as well as inbreeding depression of hermaphrodites reduce the fitness of individual plants (Asikainen 2004, Asikainen and Mutikainen 2005) and may thus affect the frequency of the gender morphs. However, a matrix model approach revealed that due to the different sensitivity of population growth rate to changes in demographic transitions, severe pollen limitation of either females or hermaphrodites had a smaller effect on population dynamics than inbreeding depression of hermaphrodites (paper V). This demonstrates that without a demographic approach, it is often difficult to quantify the total effects of different ecological and genetic factors on population dynamics. Matrix population models provide a tool to integrate population dynamics of different species making it possible to model population dynamics under species interactions (Thomson 2005). In addition to estimates of population viability, matrix models can be used, for instance, to assess control strategies against invasive species (Shea and Kelly 1998) and to determine a sustainable harvest level (Bernal 1998, Freckleton et al. 2003).

5.5. Viability of PVA

Due to uncertainty related to the estimates of population viability, it has been suggested that PVAs should not be conducted if demographic data are poor (e.g. Beissinger and Westphal 1998, Coulson et al. 2001). Although it is wise to be critical of the outcomes of PVAs, there are still several methods that have been developed to improve the precision of PVA. Some of the methods have focused on data collection to effectively sample individuals in a population to produce a precise estimate of population viability (Vandermeer 1978, Moloney 1986, Gross 2002, Münzbergová and Ehrlén 2005), and others have presented techniques to reduce observation error (discussed in Morris and Doak 2002). Moreover, this thesis has made several practical suggestions on how to construct transition matrices and to perform stochastic simulations in order to increase the reliability of matrix-based population models (paper I, III and IV).

There is a current trend in the PVAs of plants towards more realistic models, which often means more complex models that include spatial dynamics. Some studies have used individual-based models in stochastic simulations for plants (e.g. Schwartz et al. 2000, Buckley et al. 2003). In such models demographic transitions are calculated separately for each individual keeping track of all individuals in the data set. Intuitively, this seems as a more realistic way to project population viability because all individuals within the same stage are not assumed to have identical transition rates. However, it is good to keep in mind that in addition to large data requirements, complex models require quite advanced programming skills. Furthermore, there is no guarantee that complex models are always worth constructing if the identical results can be achieved using simpler models.

Bayesian statistics is a technique that can greatly clarify and improve the interpretation of PVAs in the future (Ludwig 1996, Wade 2000, Marin et al. 2003, Dixon et al. 2005). Demographic data on rare and threatened species is often scattered and PVAs of such species, in particular, may benefit from Bayesian statistics. Based on the collected data and the existing knowledge of a study system, it
is possible to estimate a probability for any event, such as the risk of extinction, using Bayesian statistics. Despite this attractive approach, in which existing data can be included in the estimates of population viability, few studies have applied Bayesian statistics to demographic models. So far, the lack of easy programme packages may also limit the wider use of Bayesian statistic in conservation biology.

6. CONCLUSIONS

Sparse data lead to imprecise estimates of population viability and may limit the use of a PVA for threatened and rare species. Since the outcome of a model is often sensitive to the input parameters, it is essential to pay attention to the selection of a population model. This thesis provides some practical recommendations for the PVAs of plants, which increase the reliability of the PVAs and reduce the amount of work required. Although data requirements for PVA depend on the life history of a species, it is still possible in many cases to reduce the amount of demographic data by using a smaller matrix dimensionality. Smaller matrices can especially be used for woody species without decreasing the precision of the estimate of population growth rate. In stochastic simulations, one can considerably reduce the amount of calculation required by using a selection of entire matrices or Tuljapurkar’s approximation instead of a selection of matrix elements or a selection of vital rates. The selection of matrices and Tuljapurkar’s approximation are also preferable when only a small number of matrices are available for simulations. Despite the time-consuming field work required to collect demographic data, the construction of matrices is still often the only way to assess the role of different ecological and environmental factors in population dynamics. Due to the varying sensitivity of population growth rates to different demographic transitions, changes in specific single fitness components can rarely be used to predict changes in population viability. Overall, a matrix model approach provides a great opportunity to model population dynamics under different scenarios. Due to the many forms and applications of a PVA, it is currently and will in the future be an important tool in species conservation.

ACKNOWLEDGEMENTS

First of all, I would like to thank my supervisors Kari Lehtilä and Patrik Dinnétz for having provided me with this wonderful opportunity. Whenever I have needed it, Kari and Patrik have had time to listen to my problems, and their help in practical things especially during my first year in Sweden has been invaluable. I am pleased that Kari introduced me to programming and was open to my ideas. Patrik gave useful advice for field work and took care of many practical arrangements. Both Kari and Patrik were encouraging supervisors and shared their knowledge in our “literature club”.

I would like to thank all the co-authors with whom it has been a pleasure working. I am grateful to Professor Ove Eriksson from the Department of Botany at Stockholm University for helping with all kinds of formalities, and Södertörn University College for providing good working facilities.

Living in a country that is not your “home” is not always easy, and several surprising (amusing and less amusing) things tend to happen. I would like to thank my roommates for their good company and patience. Special thanks to Elin Boalt and Maria Thorsson who shared everyday problems and delight with me and made life much more enjoyable. I also owe thanks to my dear friends and relatives in Finland and Denmark whose visits, phone calls, and
e-mails have cheered me up and kept me updated. ☺ In particular, I would like to thank Heli Nykänen for the long discussions that took place at different cafés in Turku and which covered the whole spectrum of life. Roosa Leimu was a cheerful companion at different meetings and conferences. Maarit Kivimäki struggled with me during the first year at Södertörn and Paula Jokela always had time for nice chats. Ebba’s Dance Club in Stockholm kept me going by making me laugh and forget everything else except for the music. My deepest thanks go to Antti Kause for standing by me during all these years that I have spent in Sweden; you have been invaluable.

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