

**ADAPTATION, POPULATION
VIABILITY AND COLONIZATION-
EXTINCTION DYNAMICS OF *SILENE
TATARICA* IN RIPARIAN HABITATS**

**ANNE
JÄKÄLÄNIEMI**

Faculty of Science,
Department of Biology,
Oulanka Research Station,
University of Oulu

OULU 2005



ANNE JÄKÄLÄNIEMI

**ADAPTATION, POPULATION
VIABILITY AND COLONIZATION-
EXTINCTION DYNAMICS OF *SILENE
TATARICA* IN RIPARIAN HABITATS**

Academic Dissertation to be presented with the assent of
the Faculty of Science, University of Oulu, for public
discussion in Kuusamonsali (Auditorium YB210),
Linnanmaa, on September 16th, 2005, at 12 noon

OULUN YLIOPISTO, OULU 2005

Copyright © 2005
University of Oulu, 2005

Supervised by
Professor Juha Tuomi
Docent Pirkko Siikamäki

Reviewed by
Associate Professor Johan Ehrlén
Docent Veikko Salonen

ISBN 951-42-7819-4 (nid.)
ISBN 951-42-7820-8 (PDF) <http://herkules.oulu.fi/isbn9514278208/>
ISSN 0355-3191 <http://herkules.oulu.fi/issn03553191/>

OULU UNIVERSITY PRESS
OULU 2005

Jäkäläniemi, Anne, Adaptation, population viability and colonization-extinction dynamics of *Silene tatarica* in riparian habitats

Faculty of Science, Department of Biology, University of Oulu, P.O.Box 3000, FIN-90014
University of Oulu, Finland; Oulanka Research Station, University of Oulu, Liikasenvaarantie 134,
93999 Kuusamo, Finland

2005

Oulu, Finland

Abstract

Plants in riparian environments have to tolerate disturbances like floods and erosion. In the absence of disturbances, habitats will gradually become unfavorable for early-successional species. This can have fundamental consequences not only for adaptation at the individual level, but also for the viability of local populations as well as for the persistence of the species on a regional scale.

Silene tatarica is a rare perennial plant exposed to annual floods of the Oulanka River. After sand burial most plants formed vertical rhizomes and new meristems by bud ramification. The special anatomical features of these fleshy underground structures seemed to allow the plants to be very resilient against fast-flowing water. Seed structure may enhance long-distance dispersal by water. Selection gradients for plant height were positive at the individual and group levels, but for the number of stems they were in opposition, as selection at the group level favored a smaller number of stems. This can be associated with pollination and herbivory, since taller and larger plants often attract more pollinators and mammalian herbivores.

At the local level, population growth was most sensitive to the survival and growth of juvenile individuals. The populations showed different fates, and according to stochastic simulations some of them will disappear in the near future. Their colonization and extinction rates varied between the years, but their balance over the study period was positive. Small patches had the highest risk of extinction and recolonization of extinct patches was very rare. Elasticity analysis indicated that the survival of patches made a much greater contribution to patch dynamics than did the production of new patches.

The short-term dynamics of *S. tatarica* depend primarily on local dynamics but, in the long run, the species will track the availability of habitat, and its persistence will depend on successful colonizations. The amount of suitable habitat depends on river disturbance. Conservation of this species requires the creation of new suitable open sites for colonization, a dispersal process leading to successful colonizations, and favorable habitats for survival. These conditions can be maintained either by natural processes of river disturbance or by active conservation management.

Keywords: conservation, demography, flood, habitat tracking, local population, metapopulation, regional population, stochasticity

Acknowledgements

I warmly thank my supervisor Juha Tuomi for his considerable support, scientific discussions and help during my work and Pirkko Siikamäki for her comments and support for my work. I would like to extend my thanks collaborators Anneli Kauppi, Antti Pramila and Kalle Vähätaini in plant morphology study and Jouni Aspi for collaborating in the selection study. The discussion with Henry Väre was of great assistance in the beginning of this research. Kari Lehtilä kindly gave me an opportunity to use his excel-program developed for the analyses of population matrixes. The official referees Johan Ehrlén (University of Stockholm) and Veikko Salonen (University of Jyväskylä) gave valuable comments on thesis. I also thank many people in the University of Oulu for their comments on manuscripts.

Anna Kilpiä, Sirpa Marttila, Hannaleena Mäkipetäys, Niina Tuomas and Ulla Tiermas have done much work in the field. In addition, I thank many persons from Oulanka Research Station (e.g., Anne Ahola, Adam Denard, Sisko Hannula, Jouni Heikkilä, Erkki Jokelainen, Pekka Jokelainen, Anita Kellinsalmi, Erkki Kilpivaara, Aki Lämsä, Nicholas Money, Mauri Tiermas, Kimmo Tuuliainen, Liisa Viitala) as well as some volunteers (Virpi Karen, Aila Tarvainen) who have helped me in the field surveys. Special thanks also to Juho Palosaari and Markku Rontti for technical support during the field season. I also thank the staff of the Oulanka Research Station, specially Kalevi Kuusela and Anita Ala-Poikela, for arranging the practical things and laboratory work. Juhani Kinnunen is thanked for photographs. Keith Kosola revised the English of the summary.

I want to express my special thanks to my husband Pertti and our children Anna-Erika, Annukka, Greta and Meri-Maria for their patience and valuable support during my work. I also thank my parents to taking care of my children and making me possible to work long days in the field.

This thesis was financially supported by grants from the University of Oulu, Finnish Academy of Sciences (project #207621) and Nessling foundation. In addition, Metsähallitus gave travel support for the field work. I also extend my thanks to the publishers Blackwell Publishing (Journal of Ecology), NRC Research Press (Canadian Journal of Botany) and Allen Press (Evolution), which let me use the printed articles in my thesis.

In Jäkäläniemi, August 2005

Anne Jäkäläniemi

List of original papers

This thesis is based on the following papers, which are referred in the text by their Roman numerals:

- I Jäkäläniemi A, Kauppi A, Pramila A & Vähätaini K (2004) Survival strategies of *Silene tatarica* (Caryophyllaceae) in riparian and ruderal habitats. *Canadian Journal of Botany* 82: 491–502.
- II Aspi J, Jäkäläniemi A, Tuomi J & Siikamäki P (2003) Multilevel phenotypic selection on morphological characters in a metapopulation of *Silene tatarica*. *Evolution* 57: 509–517.
- III Jäkäläniemi A, Tuomi J & Siikamäki P (2005) Extinction probability of local populations and spatiotemporal variation in the demography of *Silene tatarica* (Caryophyllaceae) in riparian habitats. *Conservation Biology* in press.
- IV Jäkäläniemi A, Tuomi J, Siikamäki P & Kilpiä A (2005) Colonization-extinction and patch dynamics of the perennial riparian plant, *Silene tatarica*. *Journal of Ecology* 94:670–680.

These articles are reprinted with the kind permission of the publishers:

I NRC Research Press, II, Allen Press, IV Blackwell Publishing

Contents

Abstract	
Acknowledgements	
List of original papers	
1 Introduction	11
1.1 Dynamics and heterogeneity of riparian environments	12
1.2 Local dynamics and population structure	14
1.3 Metapopulation approach	15
1.4 Aims of the study	18
2 Materials and methods	20
2.1 Species	20
2.2 Study areas	20
2.3 Anatomical, morphological and physiological features	21
2.4 Field work	21
2.5 Selection analyses	23
2.6 Population and patch dynamics	24
2.7 Statistical methods	26
3 Results	27
3.1 Anatomical, morphological and physiological structures	27
3.2 Natural selection	28
3.3 Local population dynamics	30
3.4 Regional population dynamics	31
4 Discussion	32
4.1 Adaptations to river disturbance	32
4.2 Population and patch dynamics	34
4.3 Metapopulation concept and regional dynamics	36
4.4 Long-term persistence in transient environments	38
4.5 Conservation implications	40
5 Conclusions	43
References	

1 Introduction

It has been estimated that 5.6% of all vascular plants in Finland are presently threatened (Rassi *et al.* 2001). Compared to the situation in 1991 (Rassi *et al.* 1992) an additional 30 species have now been estimated as threatened (Rassi *et al.* 2001). The classification of threatened species and the establishment of conservation areas have been the main conservation actions in Finland, while active monitoring and management to improve the population viability and persistence of endangered species is rather limited compared to many other countries (see Rassi *et al.* 2001, Bell *et al.* 2003). Conservation assessment of species consists of determining current and expected future population trends, identifying the demographic vital rates, which are currently depressed, determining the environmental and biological factors that cause the depressed rates, and then examining what could be done to correct these limiting factors (see Caughley 1994, Schemske *et al.* 1994). In practice, in order to estimate its probability of persistence, the viability of a species is often expressed as a risk of extinction within a given time interval (Akçakaya & Sjögren-Gulve 2000, Menges 2000, Reed *et al.* 2002). Population viability analyses (PVAs) are usually done for single local populations, but recently it has become increasingly popular to evaluate the viability of the species over larger spatial scales. For the analyses on regional scales, useful methods have been developed in order to estimate the capacity of fragmented landscapes to maintain viable metapopulations and to predict extinction thresholds in relation to the amount of available suitable habitat (Lande 1988a, 1993, Hanski 1997, Hanski & Ovaskainen 2002). However, these methods have not yet been widely applied in analyzing the viability of threatened plant species in Finland (Rautiainen *et al.* 2004) or the relative abundance of plant species in fragmented landscapes (Ouborg & Eriksson 2004).

Preserving a certain geographical location for a species may not always be sufficient to ensure its long-term persistence. This especially concerns plant species growing in transitional environments along succession gradients. The management of meadow plant communities, for instance, requires regular mowing or grazing, which keep the vegetation sufficiently low to ensure successful recruitment and survival of rare species, which are grazing tolerant but competitively inferior to taller plants (e.g., Huhta 2001, Hellström 2004). Accordingly, the survival of early successional species on riversides is critically dependent on natural disturbance processes (Menges 1990, Falk 1992), such as floods.

The survival of riparian species relies not only on their physiological tolerance of physical stress, but also on their ability to keep in track of habitat changes that occur as a consequence of succession and flood disturbances. Therefore, preservation of natural dynamics by itself or maintaining natural processes by management activities is the key element in the conservation of species growing in transient environments.

Silene tatarica (L.) Pers. (Caryophyllaceae) is a perennial herbaceous plant growing on riversides. In the present thesis I have investigated the viability and survival of this threatened species at the levels of individual plants, local and regional populations in relation to the structure and dynamics of riparian habitats.

1.1 Dynamics and heterogeneity of riparian environments

The causes of local extinction may be either stochastic or deterministic. Deterministic extinctions are typical to successional environments, where populations disappear as their habitat becomes unsuitable or too fragmented (Harrison 1991). The stochastic aspect can be classified as demographic, genetic and environmental stochasticity and catastrophes (Shaffer 1981). Demographic stochasticity concerns the changes in population size caused by randomness in birth and death rates, and it is independent among individuals. Genetic stochasticity refers to the loss of genetic diversity caused by drift or inbreeding. Environmental stochasticity causes random fluctuations in the population growth rate, driven by variation in external factors, such as fire, flood or weather. Fluctuations caused by demographic stochasticity are inversely proportional to population size, while fluctuations caused by environmental stochasticity can occur regardless of population size (Lande 2002). Demographic and genetic stochasticity concern small populations which are just established or are declining to extinction (for a discussion, see Harrison 1991). The most important cause of extinctions in regional populations is probably environmental stochasticity, including catastrophes (Harrison 1991, Caughley 1994). It has been shown to have an effect on population dynamics in many plant species by destroying old habitats and creating new open ones suitable for colonization (e.g., Menges 1990, Husband & Barret 1998, Watkinson *et al.* 2000).

S. tatarica grows on the shores of the Oulanka River, which is a meandering river with a natural disturbance regime. It grows in a succession area between the water-line and forest. On a worldwide scale the meanders of the Oulanka River can be included among those which cut into their banks most rapidly in Fennoscandia, and bank erosion along the river is regarded as highly exceptional (Koutaniemi 1984). The intensity of spring floods varies yearly and along different stretches of the river, forming erosion slopes and accumulation shores (Fig. 1, Koutaniemi 1984). Therefore, the location of the river channel change over the years. In addition to sand and gravel movement from upstream to downstream, ice jams and scours and bank slumping are typical during floods. Dead trees felled by riverbank erosion and carried by water can have a dramatic scouring effect on the shores. Consequently, the disturbance of the river exerts pressures on the survival of *S. tatarica* in the area.

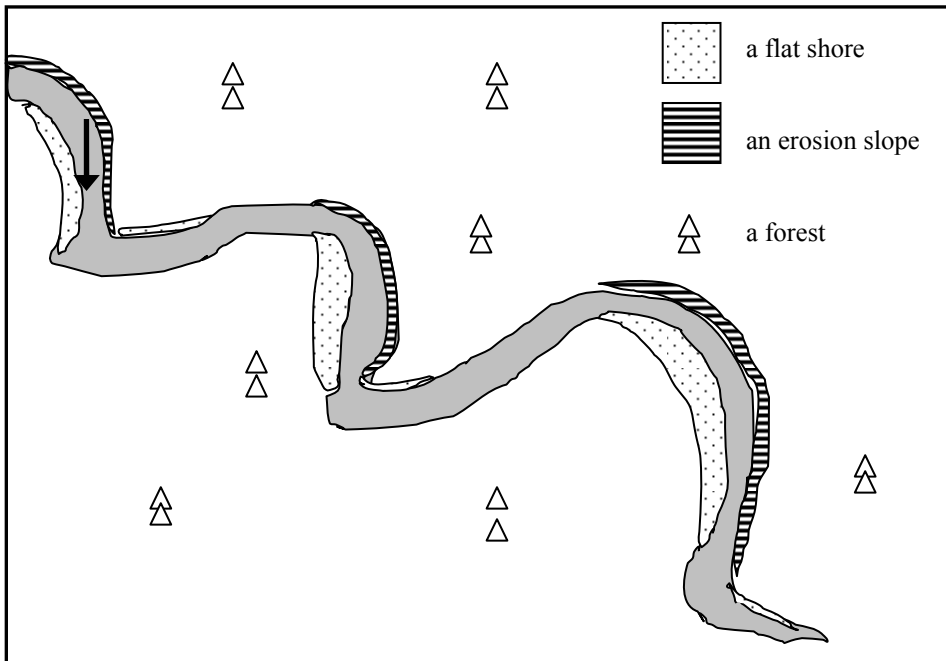


Fig. 1. Schematic diagram of a meandering river surrounded by forest habitats. Erosion slopes are located at the outer bends of the river and accumulation shores at the inner bends of the river. The arrow represents the direction of water flow.

Over evolutionary time, organisms evolve traits that enable them to survive, recover, exploit and even depend on disturbance, and such adaptations can carry both costs and benefits (Lytle & Poff 2004). An example of a cost can be a competitive disadvantage in the absence of floods and a benefit that the life-history strategy is synchronized in relation to the occurrence of flow regime events (Blom & Voeselek 1996, Lytle & Poff 2004). Because humans have altered the flow regimes of most rivers and streams, understanding the behaviour of species in natural riparian systems is crucial for the management and restoration of running water ecosystems. However, only little attention has been paid to how organisms have evolved in response to floods. Some plant species can survive due to their ability to tolerate physical stress like sand burial, submerging and mechanical damages. This can be due to the special morphological adaptations and resilience of structures (Lytle & Poff 2004). Disturbance is both a major source of temporal and spatial heterogeneity and an agent of natural selection in the evolution of life histories (Sousa 1984, Menges & Quintana-Ascencio 2003). Drought can also sometimes represent an important source of mortality, especially among seedlings and juvenile plants.

Plants can adapt to heterogeneous environments either genetically to local conditions which are rather predictable in time, or by means of phenotypic plasticity, i.e., the ability to alter allocation patterns, morphology, or physiology in response to environmental variation. These adaptations whether genetic or purely phenotypic, will influence the demographic vital rates of young and mature plants as well as the patterns of how these

vital rates will vary in time within a given local population and in space among populations occupying different habitats in relation to succession gradients and disturbance regimes.

1.2 Local dynamics and population structure

In riparian environments, the intensity of flooding varies between the years. The openness of the habitat is indicative of repeated, current and/or past disturbances, because in the absence of disturbance, succession will gradually lead to closed meadow and finally forest vegetation. Accordingly, *S. tatarica* grows in habitats ranging pure sand and gravel to almost closed vegetation and this spatial and also temporal heterogeneity in growing conditions should affect the dynamics of populations. In open habitats, intensive and frequent disturbances may reduce survival especially among juvenile individuals. If disturbances occur regularly each year, these populations will eventually become extinct. Successful establishment of new populations requires either that new colonizations occur in relatively open sites with low disturbance intensity and frequency or that the colonized site becomes more favorable to survival due to habitat changes associated with succession. When the succession proceeds, the vegetation becomes more closed. With increasing competition, the establishment of seedlings becomes increasingly difficult and juvenile survival declines. However, adult survival may be less affected. Eventually, the surrounding vegetation becomes so dense that seedling establishment becomes a rare event and even adult survival declines. As a consequence, the population as a whole begins to decline and dies out sooner or later.

A short-term objective of PVA is to estimate the extinction risk and the expected time to extinction of populations and to find suitable management options (e.g., Ackakaya & Sjögren-Gulve 2000, Menges 2000, Reed *et al.* 2002). One method of this kind of analysis is stochastic simulation (Shaffer 1981, Caswell 1989, 2001, Tuljapurkar 1989, 1990, Menges 1992, Menges & Quintana-Ascencio 2003), which can be based on population growth trajectories formed by matrix projection models (Caswell 2001). The matrix population model shows the rate and direction of population growth. To acquire enough demographical data for matrix analysis it is necessary to follow marked individuals in different life stages and their reproductive output for several years and in many populations to get a more reliable estimate of spatial and temporal variation in population trends (Menges & Quintana-Ascencio 2003). On the basis of field data it is possible to estimate vital rates, i.e., the rates of transition from one stage to another. Consequently, matrix mathematics allows the calculation of the projected growth rate for populations in different years and, by sampling randomly annual matrices, the stochastic growth rate can be estimated.

Using more sophisticated analyses, it is possible to recognize the stages in the life cycle that contribute most to population dynamics, which can help in ranking management strategies for the species. Examples of these are prospective analyses, such as sensitivity and elasticity analyses (Goodman 1971, de Kroon *et al.* 1986, Caswell 2001), and retrospective analyses, such as life table response analysis (LTRE, Caswell 1989, 2001, Horvitz *et al.* 1996). Sensitivity analysis measures the absolute and elasticity

analysis the proportional contribution to the finite growth rate of a population given that there occurs an infinitesimal absolute or proportional change in the vital rate. This change can be due to intrinsic (genetic or physiological) or extrinsic (environmental) reasons. LTRE analysis is an extension of sensitivity analysis on the sense that it explains the observed variation in population growth rates in terms of variation in vital rates weighted by their sensitivity values.

The dynamics of local populations can have a significant effect on the dynamics and evolution of species in a regional level (see reviews in Ackakaya & Sjögren-Gulve 2000). In addition, regional processes can provide new insights into the dynamics of species, since the patterns of their abundance and distribution may not be predictable on the basis of local population dynamics alone.

1.3 Metapopulation approach

A long-term objective of spatial PVA is to indicate suitable conditions, in which species retain their potential for evolutionary change without intensive management, or to provide recommendations for management (e.g., Ackakaya & Sjögren-Gulve 2000). A spatial extension of the PVA analysis is the occupancy models of metapopulations (e.g., Hanski 1999, Ackakaya & Sjögren-Gulve 2000, Menges & Quintana-Ascencio 2003). Because it sheds light on patterns of distribution and population turnover rates on a regional scales, the metapopulation approach is especially useful in fragmented landscapes (Hanski & Simberloff 1997). The metapopulation framework also encourages to face issues such as long-distance dispersal, environmental heterogeneity over space and time, and the interplay between gene flow and local selection.

The classical metapopulation is subdivided into many local populations in discrete patches, and it has a limited dispersal, asynchrony in the dynamics of local populations and frequent local extinctions and recolonizations (Levins 1969, Harrison 1991, Gilpin & Hanski 1991, Hanski 1999). It has been suggested that few species actually exist in a balance between extinction and colonization, as assumed by the classical metapopulation model (Harrison 1991, Harrison & Taylor 1997, Baguette 2004, but see Hanski 2004) and even the same species can have many types of regional dynamics (Eriksson 1996). In the recent decade, the metapopulation view has broadened and several other types of metapopulations have been distinguished (Harrison 1991, Harrison & Taylor 1997, Hanski 1999). In mainland-island (Boorman & Levitt 1973) and source-sink metapopulations (Pulliam 1988) local extinctions occur only in the smallest populations, which can have a minimal effect on the regional persistence of the metapopulation (Harrison 1991, Harrison & Taylor 1997). In source-sink metapopulations the source areas export propagules to sink populations, while in mainland-island populations the source areas are very large with a minimal risk of extinction. Remnant populations or non-equilibrium populations are defined as systems of almost isolated local populations, in which some are maintained a long time in spite of low or negative population growth (Harrison 1991, Eriksson 1996). In such populations, extinction may take a long time because of the buffering effect of the long life span and relatively stable environment of the species (Harrison 1991, Eriksson 1996, Ouborg & Eriksson 2004). This time delay

can further lead to an extinction debt (sensu Tilman *et al.* 1994, see also Hanski & Ovaskainen 2002).

Freckleton & Watkinson (2002, 2003) suggested a classification of regional and local populations of plants (Table 1). They considered that the regional availability of a suitable habitat is the key factor in a plant population structure. From regional populations they first isolated metapopulations, in which they include classical, mainland-island and source-sink populations. Typical for metapopulations is that regional processes dominate, patches are discrete, and extinctions, colonizations and recolonizations are common. Second, they isolated “regional ensembles”, where both regional and local processes are important and extinctions, colonizations and recolonizations are rare. The remnant metapopulations are included in this category. For the last category they suggested spatially extended populations, in which local processes dominate, and extinctions, colonizations and recolonizations are very rare or nil. According to Freckleton and Watkinson (2002), the only convincing case of plant metapopulations is *Eichhornia paniculata* (Husband & Barrett 1998). They included most of the *Silene* species in the regional ensembles (Table 1). However, their classification and especially their definition of ‘region’ has been criticized by Ehrlén and Eriksson (2003), who suggested that ‘metapopulation dynamics are largely a matter of spatial and temporal scales’. Furthermore, we actually know very little about the regional dynamics of plants. This can be due to the fact that there is a lack of appropriate field studies on a large enough spatial scale for a long enough time (Eriksson 1996, Harrison & Taylor 1997, Hanski 1997, Husband & Barrett 1996, Freckleton & Watkinson 2002, Bullock *et al.* 2002, Menges & Quintana-Ascencio 2003). The turnover rate of populations is faster in stochastic environments and some promising studies have been made of the regional dynamics of plants in seasonal pools (Husband & Barrett 1998) and in riparian environments (Menges 1990, DeWoody *et al.* 2004).

Table 1. Classification of plant regional dynamics used in the present thesis. For more comprehensive treatments and discussion, see the original references and Eriksson (1996), Husband and Barrett (1996), Hanski (1999), Ehrlén and Eriksson (2003), and Snäll and colleagues (2003). Regional dynamics of *Silene* is classified according to the Freckleton and Watkinson (2002).

Regional dynamics	Habitat	Extinction-colonization dynamics	Regional Dynamics in <i>Silene</i> ⁵
Equilibrium metapopulations ^{1,2}	Suitable habitat in discrete patches; static habitat structure	Extinctions and colonizations common and in balance; recolonizations common; asynchronous dynamics of local populations, regional dynamics dominate	
Remnant, non-equilibrium metapopulations ¹	Suitable habitat in discrete patches; static habitat structure	Extinctions > colonizations; low rate of recolonization; transient dynamics leading to extinction	
Habitat tracking, non-equilibrium metapopulations ^{1,3}	Suitable habitat in discrete patches; dynamic landscape	Extinctions and colonizations common; recolonizations rare; asynchronous dynamics of local populations related to habitat changes	
Regional ensembles ²	Patches of suitable habitat surrounded by large areas of unsuitable habitat	Extinctions, colonizations and recolonizations are rare; local and regional dynamics both important	<i>S. vulgaris</i> , <i>S. dioica</i> , <i>S. alba</i> ⁴
Spatially extended populations ²	Suitable habitat rather continuously distributed in space	High rate of dispersal within a large spatially structured or unstructured population; local dynamics dominate	<i>S. latifolia</i> ⁴

¹ sensu Harrison and Taylor 1997. ² sensu Freckleton and Watkinson 2002, Table 1. ³ sensu Thomas 1994. ⁴ *Silene latifolia* = *S. alba*, ⁵ Original papers: *S. vulgaris* (Taylor *et al.* 1999), *S. dioica* (Giles & Goudet 1997, Ingvarsson & Giles 1999), *S. alba* (McCauley *et al.* 1995, Antonovics *et al.* 1994), *S. latifolia* (Delmotte *et al.* 1999).

The patch dynamics theory (e.g., Pickett & White 1985, Amarasekare & Possingham 2001), which has formed the basis of landscape ecology, focuses on changes in the state of patches themselves. According to Wiens (1997), metapopulation models have concentrated purely on the dynamics of species and have largely ignored landscape elements, which can have a great effect on the dynamics of species. Recently the metapopulation theories have approached landscape ecology, since more spatial elements and habitat properties have been added to the models (Hanski 1991, Fahrig 1992, Hess 1996, Thomas 1994, Keymer *et al.* 2000, Hastings 2003) and many empirical studies have shown that e.g., the spatial configuration, habitat properties and duration, life history of species and isolation affect the dynamics of many species (Hanski 1994, Overton 1994, Quintana-Ascencio & Menges 1996, Fleishman *et al.* 2001, Snäll *et al.* 2003). Despite the progress in theoretical and empirical research, most metapopulation models assume static landscapes, where physical patches are neither created nor

destroyed (see Keymer *et al.* 2000, Baguette 2004, Verheyen *et al.* 2004). Especially in transient environments, the interaction between the rate of change of landscape and the spatial or temporal arrangement of patches, determines the probability of a species' regional survival (see Pease *et al.* 1989, Fahrig & Merriam 1994, Stelter *et al.* 1997, Whittaker 1998, Travis & Dytham 1999, Johnst *et al.* 2002). For example, successional processes create a dynamic landscape, where the patch state is dependent on the time elapsed since the last disturbance (Stelter *et al.* 1997, Amarasekare & Possingham 2001) and individual patches are likely to disappear through habitat succession (Harrison 1994, Thomas 1994). According to the model of Pease *and colleagues* (1989), a species adapted to moving habitats must either track its habitat spatially, or adapt genetically to the new environmental conditions.

Most treatments of plant metapopulations are based on classical metapopulation models, which assume a static landscape and fast local dynamics of the species (e.g., Levins 1969). The dynamics of the system are usually described in terms of the equilibrium value (P^*) of the occupancy (P) of suitable habitat patches, which is determined by the colonization rate (c) of unoccupied suitable patches and the extinction rate (e) of occupied patches ($P^* = 1 - e/c$). Below I call this "equilibrium dynamics", which is characterized by a balance between colonization events, $cP(1 - P)$, and extinction events, eP , in the classical model, i.e., $cP^*(1 - P^*) - eP^* = 0$ (Levins 1969, Hanski 1997, equilibrium metapopulations in Table 1). By "non-equilibrium dynamics" I refer to transient regional dynamics in static or dynamic landscapes. In static landscapes, transient dynamics may refer to viable metapopulations ($e < c$), which are invading new areas but have not yet reached equilibrium ($0 < P^* = 1 - e/c$), or remnant populations which are slowly driven towards extinction ($c \leq e$). In dynamic landscapes, regional populations may more or less permanently remain at the transient phase if habitat dynamics are fast enough relative to the dynamics of the species so that the species, while tracking habitat changes, remain behind landscape changes (Fahrig & Merriam 1994, Harrison & Taylor 1997, habitat tracking, non-equilibrium metapopulations in Table 1). As far as succession and disturbance processes are driving habitat changes in riparian environments, the latter kind of regional dynamics can be common in riparian plants.

1.4 Aims of the study

S. tatarica needs special strategies to survive in riparian environments. First, individual plants have to tolerate stochastic disturbances that occur as a consequence of river movements, floods and erosion. Second, drought and sometimes herbivory can influence the survival as well as reproduction of individual plants. Third, in the absence of disturbances, vegetation density and composition will gradually change, and due to the increasing intensity of competition, will become unfavorable for the early-successional species. In this thesis, I intend to explore and outline how the variability and heterogeneity of riparian environments may influence the adaptation, population viability and local and regional dynamics of *S. tatarica*.

S. tatarica grows almost alone on disturbance-prone sand and gravel beaches and slopes. While I had no *a priori* predictions of how the species could possibly survive both

the physical stress of the floods and sand burial, it is almost inevitable that the species must have some morphological and physiological adaptations for tolerating physical stress as well as disturbance. In the first paper (I), I therefore explored the anatomical, morphological and physiological structures, which could enhance the survival of *S. tatarica* in disturbance-prone riparian habitats. I further compared whether there may be some differences in these characteristics between plants growing on riversides and in less disturbed roadside habitats.

Fruit and seed production of herbaceous plants often correlate positively with the size of an individual plant (e.g., Geber 1990). However, selection of plant height and, on the other hand, the number of stems can vary considerably, depending on the species and their preferred habitats (e.g., Aarssen and Irwin 1991, Aarssen 1995). In the second paper (II), I estimated the intensity of directional selection on plant height and the number of stems. It has recently been suggested that such estimates can vary greatly, depending on sample size (Kingsolver *et al.* 2001). The large data set of *S. tatarica* enabled calculation of the strength of selection in different habitats replicated in time and space, and analysis of how plant density, habitat differences along the succession gradient and herbivory may shape plant fitness. Furthermore, the species is patchily distributed in space, and I therefore also tested whether group membership might influence the selection estimates for which I had no *a priori* expectations.

Because the landscape along the Oulanka River is dynamic, this can have profound effects on the population dynamics of *S. tatarica* both on the local scale of separate local populations (III) and on the regional scale over larger geographical areas (IV). When I started studies III and IV, I expected that river disturbances as well as succession towards closed vegetation are likely to cause local extinctions of *S. tatarica* populations. This would mean the species can not persist in riparian habitats if it can not successfully colonize new sites. This would in turn imply first that local populations would show rather divergent fates (III), and second that colonization-extinction dynamics are important for the persistence of the species on the regional scale (IV). My hypothesis was that the regional dynamics would be related to metapopulation dynamics in spite of the fact that the species is patchily distributed along the river in a rather continuous suitable habitat. In the beginning of the study, I was not sure if the dynamics satisfy all the other criteria that metapopulations are usually expected to exhibit at equilibrium conditions (III–IV). Because of the stochastic riparian environment, this assumption of equilibrium dynamics may fail in my study system (IV). Finally, I discuss possible consequences that this kind of colonization-extinction dynamics may have for the conservation of riparian plant species in dynamic landscapes.

2 Materials and methods

2.1 Species

S. tatarica is an endangered, long-lived perennial plant. In Finland it grows on slopes and along the shorelines of the Oulanka, Kitinen and Kemijoki Rivers, but its main distribution area is on the steppes of Europe, with rare occurrences in Hungary, Germany, Lithuania and northwest Russia (Ulvinen 1997). The river valley of Oulanka has been one of the main dispersal corridors of species to Finland (Cajander 1914) and it is probably that this species has arrived to the area during the period when the climate was suitable for steppe species. The Kitinen and Kemijoki Rivers do not have natural flood dynamics since they are regulated for electric power production, but the Oulanka River is in its natural state. In addition, some ruderal populations have been found along roadsides and the banks of railways. The species occurs in habitats ranging from very open to those with quite dense but low vegetation cover. Its habitat area is almost continuous with varying degrees of openness. It begins to flower in its third year. The species has no vegetative propagation and therefore new individuals and populations are established only by seeds. Numerous tiny seeds are dispersed by gravity and water and they germinate in the beginning of June. During spring flooding most individuals are dormant when submerged. Extensive soil sampling from riverside habitats showed no evidence of a permanent seed bank (Jäkäläniemi, unpublished).

2.2 Study areas

The area studied in I–IV is situated along the Oulanka River in Kuusamo, in northern Finland (66° N and 29° E). The Oulanka River is a meandering river with sandy and gravel riverbanks and shores. The roadside population studied is located 23 km SW of the riparian populations and it was established there about 15 years ago (I). The garden plants were grown approximately 30 km SW of the roadside site (I). In the riparian habitat, the sand burial of plants can be up to meters, but burial along the roadside and in the garden is likely to be only 0–2 cm.

2.3 Anatomical, morphological and physiological features

I collected plants for the study (I) from three sites: from a riverside with disturbance, from a roadside and from a garden without a disturbance regime. While the age of the riparian and roadside plants varied, the exact age of the garden plants was known. I collected the seeds for the garden plants from the riverside in 1998 and sowed them in 1999, and afterwards I used the plants for a resilience study and as an age reference in general.

In 2000 and 2002 I excavated 70 adult flowering individuals of the same size from the riparian habitat, 40 from the roadside habitat and 30 from the garden habitat for morphological and anatomical studies. Then I took samples 0.5–1 cm in length from roots and underground stems and split them longitudinally and prepared them for light microscopy. Afterwards, I counted the growth rings, i.e., the age of the plant from the cross sections. After preparing the samples I studied the surface structures of the roots, stems and seeds with a field emission scanning electron microscope (FESEM). To get an idea of the seedling growth, ten seeds were germinated in water in the lab. I analyzed the glucose, fructose, saccharose, and starch concentrations of the roots and underground stems from eight adult flowering individuals from the riverside and five from the roadside (I). Carbohydrates were quantified using an enzymatic method (Beutler *et al.* 1978) relative to standards obtained from the Boehringer Mannheim Company.

For a tensile strength test, I collected the roots of 20 individuals from each site (I) and took the samples from just below the root collar, which experience the highest velocity pull during flooding. I clamped a piece of root two cm in length with ten mm free length at its ends into the jaws of an Instron testing machine with a computer capable of simultaneously measuring applied force and displacement, and calculating the stress, the strain and the Young's modulus. Lower values of Young's modulus indicate higher resilience of the plant. Stress at maximum load is the tensile strength of the material, i.e., high values indicate resistance against straight pulling. Strain at maximum load indicates the ability of the material to sustain large relative elongation before breaking. Strain at maximum load is proportional to the maximum curvature to which the specimen can be bent without breaking. For more details on the parameters and calculations, see Beer and Johnston (1992).

2.4 Field work

For the demographic study (III), I randomly chose a total of fifteen populations from upstream and downstream parts of the river. The straight-line distance between the most upstream and the most downstream populations was eleven km and the distance along the river channel was seventeen km. In total, I monitored 4005 individually tagged plants from 1998 to 2003 (122–396 plants per population, depending on the population size). Because survival and reproduction of the species is connected to the size of the plants and the age of an individual more than three years old is difficult to determine reliably, I used the matrix population models with stage-based classification (Lefkovitch 1965) for studying demography. The five stages were based on the size and reproductive status of

the individuals: (1) juveniles with one vegetative shoot ≤ 1 cm in height, (2), small vegetative individuals, $1 \text{ cm} < \text{height} \leq 14 \text{ cm}$ with 1–3 vegetative shoots, (3) large vegetative individuals with more than three vegetative shoots and $> 14 \text{ cm}$ in height, (4) small fertile individuals with 1–5 fertile shoots, (5) large fertile individuals with more than 5 fertile shoots. I conducted the annual census from the peak of flowering to the time the seeds matured in August and marked all or a maximum of 30 new seedlings every year to obtain an estimate of their survival. In each census, individual plants were classified by stage and their reproductive output was recorded by counting their capsules and the number of seeds per capsule in one to three randomly chosen capsules/individual. I did the fecundity calculations by using the number of reproductive individuals and emerging seedlings in the whole sample area (in 1999, due to the small number of seedlings) or in areas of 2.5 to 9 m², depending on plant density. Then I projected the seedling production to the previous year's reproductive output of the individuals. When a marked individual was absent, I recorded it as a sign of mortality. The total population size was counted in 2001 and the numbers of vegetative and fertile individuals were separated. In 1999–2000 I measured and calculated the height and the number of flowering, vegetative and eaten shoots from each individual.

For the study of regional dynamics (IV), I surveyed altogether 43 km of the riverside annually in September 1999–2003. A narrow, potentially suitable habitat area along the river's shore was disrupted by 36 unsuitable habitat areas, which were 50–500 m long and densely covered by grasses and trees. In study IV a patch refers to a spatially distinct stand of individual plants, in which the distance between neighboring plants is less than 5 meters. Thus, later it was possible to extrapolate the patch structure for grouping distances of 10, 30, 50, 100 and 200 m. At the 200 m level all the identified patches were at least 200 m apart. In the first year I permanently marked all the patches found, measured their maximum length and width, and the distance between patches. The area of a patch (m²) was roughly estimated by multiplying its width by its length. In the subsequent years, I marked all new patches and surveyed the fate of old patches. An old patch may have survived without any change, survived and grown in size, divided into smaller patches, united together with other patches or became extinct. By using the age, the reproductive stage and the number of individuals, I determined five stage classes for patches: (1) newly colonized patches with only 1-year-old seedlings, (2) patches with only 2-year-old or older vegetative individuals, (3) small fertile patches with 1–5 flowering individuals, (4) medium-sized fertile patches with 6–20 flowering plants, and (5) large fertile patches with more than 20 flowering individuals. These five stage classes provide a representative life cycle of a patch from new colonization (stage 1) towards the establishment of a viable local stand (stages 2–3) and finally to a more mature, larger and possibly more permanent population (stages 4–5). In 2001, I counted the number of fertile and vegetative individuals in small patches (number of individuals < 300). For a few very large patches, I counted individuals along $1/3$ – $1/2$ of the length of the patch and calculated the total number of individuals for the total length of the patch.

To study the effect of habitat type, I estimated the surface coverage (%) of open ground (sand, gravel and humus) at the microhabitat level of individual plants from an area of 0.25 m² in each population in 1998–1999 ($N = 52$ – 258 /population). Open microhabitat consisted of over 80%, half-vegetated of 31–80% and closed below 30% of open ground. At the population level, an open habitat type was defined to have over 60%

of open microhabitats, and a closed habitat type to have over 60% of closed microhabitats. The remaining, half-vegetated populations, were included in the intermediate habitat type. In addition, I estimated the openness of the habitat of a patch by measuring the diameter of the biggest spot of bare ground between plants, using the classification: less than 0.1 m, 0.11–1 m and more than 1 m. The site morphology was classified as flat (frequently under water during floods), or slope (a high risk of erosion).

2.5 Selection analyses

The use of multivariate statistical techniques (see Brodie *et al.* 1995) for measuring the direction and magnitude of selection at the individual level has been widespread in field studies (Hoekstra *et al.* 2001, Kingsolver *et al.* 2001). In the second study (II) I used the data collected from the marked individuals in all fifteen populations in 1999 and 2000 (III), the latter year having harsher weather than the former year. In this study I used the group as a synonym for a patch or a stand of plants in spatially structured and subdivided populations. As a fitness indicator I used the number of capsules per plant, because it was highly correlated with seed production. This was related to the morphological characters of the height and the number of stems per plant. To allow comparisons across characters, the absolute fitness values were transformed to relative fitness values by dividing each absolute measure by the mean absolute fitness of the population (Lande & Arnold 1983). To compare the strength of selection I estimated the opportunity of selection (Wade & Arnold 1980), defined as the variance in relative fitness. The multivariate regression analysis between the morphological characters and the number of capsules involved calculations of two selection coefficients, which allow an estimation of directional phenotypic selection and selection of correlated characters at both the individual and group levels (Lande & Arnold 1983, Arnold & Wade 1984a, b). Selection differential is the difference between the mean value or variance of a trait before and after selection and it represents the total effect of selection. This total selection differential can be partitioned into selection differentials among and within patches (Price 1970).

Selection gradients measure the direct effects of selection on each trait and show the target and the direction of selection, and allow the comparison of the magnitude of selection among different traits. Sometimes environmental factors may affect the characters and fitness and selection gradient analysis can be inaccurate, but the analysis can be improved by adding them as covariates in the model (Mitchell-Olds & Shaw 1987, Rausher 1992, Stinchcombe *et al.* 2002). Accordingly, I tested the possible effect of herbivory, but its intensity only marginally increased the power of the statistical model and it was not included in the final model. Because ANCOVA suggested that patch membership significantly affected variance in fitness, I estimated the selection gradients using contextual analysis (Fig. 2), as described in Heisler and Damuth (1987). This method attempts to identify the selection pressure on the characters that affect fitness both at the individual and group levels (Heisler & Damuth 1987, Stevens *et al.* 1995). When contextual analysis is used in the study of natural selection, it permits one to determine whether the group structure has an effect on individual fitness, but it also provides a method of identifying the particular group-level properties that are relevant for

fitness variation in spatially structured populations. The group-level traits may include “aggregate characters” such as the group means of the individual-level traits (e.g., plant height) as well as “global or emergent characters”, which are not measurable at the individual level (e.g., plant density) (Heisler & Damuth 1987). Two aggregate characters (the mean height and the mean number of stems per plant in population) and one global character (density) was used in the present analyses. To further analyze the differences of selective forces in different habitat types, I split the populations into three types (open, intermediate and closed) based on the percentage of vegetation cover.

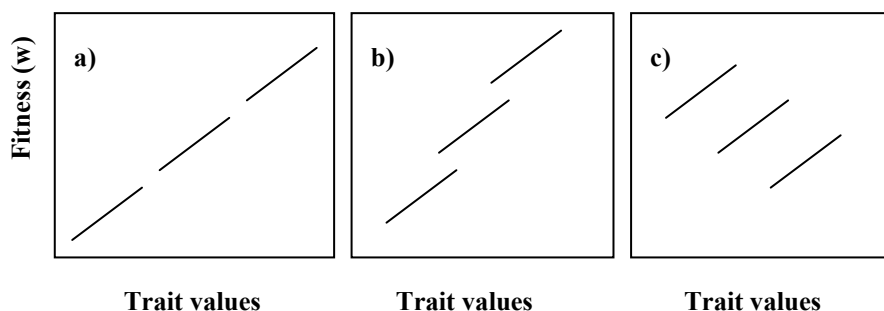


Fig. 2. Contribution of individual values (I) and group means (C) of a phenotypic trait on the fitness (w) of individual group members in a spatially structured population, which is subdivided into three groups or patches. The slope of the regression lines correspond to the selection gradient within the groups (β_I), which indicates directional selection for increasing the trait in all three cases a–b. a) The within-group regression lines have the same intercept and hence the group means of the trait do not make any independent contribution to fitness, i.e., the group-level coefficient $\beta_C = 0$. b) The intercept of the within-group regressions increases with the group mean indicating directional between-group selection ($\beta_C > 0$) of the trait. c) The intercept of within-group regressions decreases with the group mean, indicating opposite directions of within-group ($\beta_I > 0$) and between-group ($\beta_C < 0$) selection pressures.

2.6 Population and patch dynamics

I had four (1999–2003) to five (1998–2003) annual estimates of demographic transition probabilities from fifteen populations (III). A total of 64 transition matrices from different years and populations, four annual matrices (data pooled over populations, 1999–2000, 2000–2001, 2001–2002, and 2002–2003) and fifteen population matrices (data pooled over years) were formed. In addition, all observations of the transitions were pooled for a summary matrix (Horvitz *et al.* 1996). The theoretical framework and methods of the matrix population models and perturbation analyses used in this work are described in de Kroon *and colleagues* (1986), van Groenendael *and colleagues* (1988) and Caswell (2001).

I carried out the log-linear analysis to study the effects of population and year on the demographic fate of individuals (Caswell 2001 p. 326, III). To quantify the

spatiotemporal variation in transitions and the projected finite rates of increase (λ), I calculated the coefficients of variations (CV) among the sites for each year and within-sites among years. The reproductive values of the stages and the elasticities of each transition were calculated following Caswell (2001). In addition, I calculated the composite elasticities for growth (progression in stage), survival (stasis), retrogression (regression in stage) and fecundity (cf. Silvertown *et al.* 1993). Stasis refers to remaining in the same stage, and retrogression refers to shrinkage to a lower stage, as in Golubov *and colleagues* (1999).

In stochastic simulations (III) I assigned matrices representing each of four or five time intervals an equal probability of sampling, and populations were considered extinct if their size dropped below one individual. The initial population structure (number of individuals per stage) for a simulation was determined by extrapolating the observed proportions in various stages to the actual population size. I calculated the average annual population growth rates from 100 simulations per 10, 50, 100, 500 and 1000 years and used logistic regression to study the effect of the number of fertile individuals, habitat type and slope/flat morphology on site on the extinction probability of populations within 500 years. I used the fixed life table response experiment (LTRE; Caswell 2001) to find out the contribution of each transition to the variation in the projected population growth rates. A grand mean matrix was used as a reference matrix (see Horvitz *et al.* 1996). For LTRE analysis, a grand mean matrix was calculated as a mean of all matrices, and four annual mean matrices (mean over populations) and fifteen population matrices (mean over years) were formed. In the comparison of flats and slopes the mean of flat shores was used as the reference matrix. Those with large positive or negative contributions are the most important matrix entries (Horvitz *et al.* 1996). In this study I performed analyses of the fixed effects of site, habitat type, and flat/slope morphology. In addition, I used the random design of the LTRE analysis to analyze the contributions of transitions to the between-year variance of λ .

In the regional study (IV) I described the structure of the study populations in terms of the relative frequency of the different patch types, defined above, and the dynamics of the populations in terms of annual changes in the total number of patches in the study area (IV). First, I calculated the actual changes in the number of patches (N) from one year (t) to the next (t+1) as $\lambda_{t+1,t} = N_{t+1}/N_t$, analogously to the standard discrete-time model of population growth. Then I calculated the arithmetic and geometric means of the annual estimates of $\lambda_{t+1,t}$ for the entire study period. Second, in order to study the colonization-extinction dynamics, I applied the difference equation model where the balance between the relative rates of colonization and extinction indicates an increase (> 0) or a decrease in the number of patches (< 0) or a stationary state ($= 0$). Third, the dominant eigenvalue of the transition matrix provides an estimate of the finite rate of increase (λ) in the number of patches (IV). The first row of the transition matrix shows the average number of new colonizations that a fertile patch (types 3–5) was expected to produce annually. I estimated fecundities by allocating new colonizations among fertile patch types in proportion to (i) the annual frequencies of the patch types, and (ii) the number of flowering individuals in a given patch type in 2001. My primary interest was not to compare the elasticity values of single transitions (de Kroon *et al.* 1986, van Groenendael *et al.* 1988, Caswell 1989), but rather to study how the increase in the grouping distance from 5 to 200 m may influence the relative importance of colonization dynamics and

survival and growth of established patches. I therefore combined the transitions into four groups (composite elasticities), as stated above.

2.7 Statistical methods

I carried out the matrix calculations (III–IV) and stochastic simulations (III) using Microsoft Excel for matrix analysis KARISMA developed by Kari Lehtilä. I performed all the statistical analyses using SPSS for Windows 10.1.4, a statistical software application.

3 Results

3.1 Anatomical, morphological and physiological structures

The species has a long, deep penetrating tap root (I). During flooding, individuals in riparian habitats could be buried under sand, and after burial, the main stem began to ramify sympodially by growing a fleshy, vertical rhizome towards the ground surface and branching there into many new aerial shoots. The buried plants had mainly long internodes with regular bud formation in the axils of its scale leaves. The internodes in roadside and garden plants were much shorter than in the riparian plants. A common feature in all habitats was a huge number of axillary buds in the stem bases as a result of bud ramification. I did not find any significant differences in bud demography between the habitats. During aging, bud formation continued from the axils of the scales on the primary buds and then onto secondary buds until a whole group of buds was formed. Buds buried under sand could remain alive for many years as dormant short shoots.

The roots of riparian and roadside plants showed significantly higher resilience than did the roots of garden plants (i.e., Young's moduli was smaller), but there was no difference between riparian and roadside plants (I). The plants from all habitats could bend equally without breaking, i.e., there were no differences in relative elongation before breaking between the sites. However, the plants in the riparian and roadside habitats had less stress at maximum load than did those in the garden, i.e., they withstood a lower amount of straight pulling before breaking.

Most of the anatomical structures were similar between the sites and between root and rhizome (I). Early secondary growth was typical of both roots and rhizomes. In the annual rings of the secondary xylem, the vascular elements were asymmetrically interspersed with bands of unligified parenchyma forming a ring of porous wood with early and late wood.

Tracheids with helical thickenings were common in the primary xylem, and scalariform thickenings could be seen in the vascular elements in the peripheral areas of the secondary xylem. Lacunar collenchyma with intercellular spaces was a typical supporting tissue outside the phloem, and sclerenchyma was found only in aerial stems. Parenchyma cells around the thin-walled collenchyma cells separated the latter into

clusters just below the cork cambium. Surprisingly, storage material in both the underground stems and roots consisted of sugars, and the amount of saccharose was exceptionally high compared to most dicotyledons. Starch was absent.

The seeds were very tiny, having a reniform shape with a concave dorsal surface and a dorsal groove (I). The red-brown, dark brown or black seed coat was waxy and cutinized. Epidermal cells of the seed coat were air-filled and papillate. After immersion in water, the seeds started to swell and sink slowly to the bottom. The seeds were capable of germinating in water and when the cotyledons reached their final size, the seedlings rose again to the water surface.

3.2 Natural selection

When fitness variation was analyzed related to plant height and the number of stems at the individual and group levels (II), the analysis of covariance indicated that group membership significantly affected variance in fitness in both study years (1999 and 2000), and a higher density increased reproductive success. The selection differentials and gradients for plant height were positive at both levels. At the individual level, the higher mean number of stems was favored in opposition to the group level, where the number of stems was selected towards smaller values (Fig. 3).

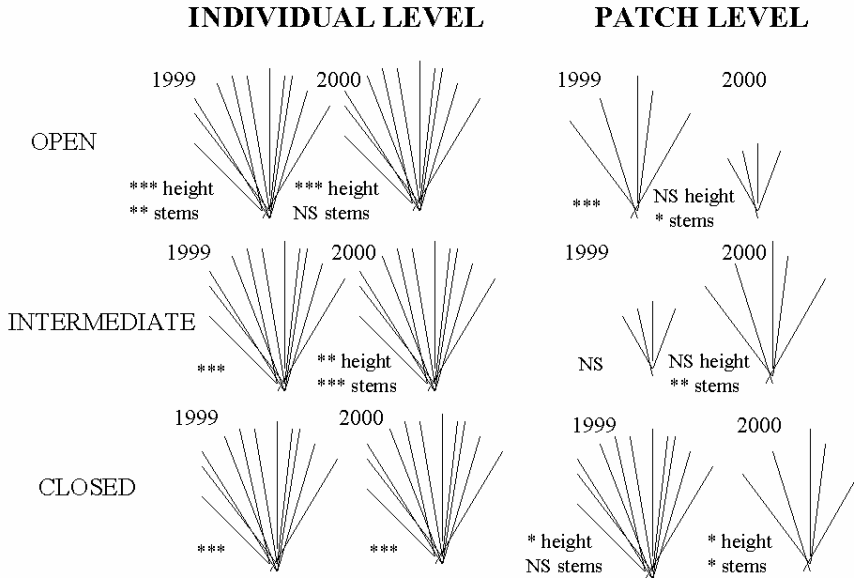


Fig. 3. Direction and the strength of selection gradients in *Silene tatarica* at the individual, patch and habitat levels. The schematic diagram of plants describe the direction of selection in plant height and the number of stems. The significance level is the same for both traits if only one level is shown. * $p < 0.001$, ** $p > 0.01$, * $p < 0.05$, NS = not significant.**

Herbivory was more intense in 2000 and greatest in open habitat (II). Because of this difference, the herbivory was added into the model as a covariate and it increased the explanatory power of the model in each habitat type. In contrast to the individual-level selection gradients, the gradients at the group level were different between the habitat types in both study years, with the selection forces being highest in the closed habitat with low exposure to river disturbance (Fig. 3). In individual-level selection, high plants with many stems were favored in all habitats. Patch-level selection generally favored plants with fewer stems, except in intermediate and closed habitats in 1999. Higher plants had the best reproductive success in open habitats in 1999 and in closed habitats in both years (Fig. 3).

In this study with a large sample size, the estimates of selection had rather high values in both years (II). But when the data was split into three parts with respect to the habitat types, the magnitude of the selection gradient increased further. Consequently, higher estimates of selection gradients were obtained with smaller and more homogeneous data sets.

3.3 Local population dynamics

In the study of fifteen local populations (III), stasis (i.e., staying in the same stage) was the most common transition among all stages in the pooled data over populations and years, except in juveniles, which often grew to small vegetative individuals. In addition, the average fecundity of large fertile individuals was many times higher than that of small fertile individuals. The reproductive value also increased towards large fertile individuals, the steepest increase occurring between small and large fertile individuals. The expected stable stage and observed distributions were significantly different in all years. According to both observed and expected distributions, the populations mostly consisted of juvenile and small vegetative individuals. The high seedling production in the beginning of the study period was later seen as the increasing amount of small and large vegetative individuals in the end of the study period. According to the log-linear model, the transition probabilities varied significantly among populations and years. Temporal variation was generally lower than spatial variation among populations, the variation being highest among juvenile individuals.

The finite growth rate (λ) varied significantly between the populations and years (III). The lowest value of λ was 0.348 and the highest was 1.938. The overall best period was 1999–2000, and the 2002–2003 period was the worst. The growth rate from the grand mean matrix over years and populations was 1.161. The geometric mean of population growth rates over the years 1998–2003 showed that six of fifteen populations had increasing population size. In decreasing populations, λ either fluctuated (five populations) or was quite constant (four populations) between the years. Only one population showed an increasing trend every year, while there were six populations with a decreasing trend all the time. Stochastic simulations resulted in three different groups of populations: increasing (six), slowly decreasing (five) and rapidly decreasing (four populations). The five slowly decreasing populations were estimated to become extinct within 500 years, and the four rapidly decreasing populations within 100 years. In one of the latter populations, the decrease was so rapid that it was predicted to disappear within fifteen years. The extinction probability within 500 years was significantly higher on flat shores as compared to slopes.

In the summary matrix over populations (III), elasticity concentrated to growth in three study periods (1999–2002) and to stasis in one study period (2002–2003). Among growth transitions, the highest elasticity was found in growth from juvenile to small vegetative individuals. In 2002–2003, the highest elasticity was in the stasis of large fertile individuals. When comparing populations, elasticity components correlated closely with the mean population growth rate. Correlations were positive in the case of growth and fecundity, and negative in the case of stasis and regression.

The LTRE analyses quantify the contributions of the matrix entries to the difference in the population growth rate as compared to the reference matrix (grand mean over sites and years) (III). The growth transitions and especially the transition from juvenile to small vegetative individuals were the most influential in the temporal variation in λ . Among the sites, three populations had higher and twelve populations had lower growth rates than the grand mean matrix. These differences were mainly due to two transitions:

survival and growth from juvenile to small vegetative individuals, and the fecundity of large fertile individuals.

The populations in intermediate habitats had a higher growth rate than the reference matrix, opposite to closed and open habitats (III). In closed habitats, λ was reduced due to the lower probability of surviving and growing from juvenile to small vegetative individuals. In open habitats, λ remained low because of the lower fecundity of large fertile individuals. Accordingly, in intermediate habitats both juvenile and large fertile individuals performed well and, hence, the average population growth rates were higher.

When comparing slopes and flat shores, higher fecundity improves λ on slopes, while growth had the greatest negative effect (III). The fecundity of large fertile individuals was the most important transition in shaping the difference in λ between slopes and flat shores.

3.4 Regional population dynamics

In the regional study (IV), the colonization rate (0.2–12%) was higher than the extinction rate (0.7–5%) in the beginning of the study period, whereas the reverse was true in the end of the study period. However, the mean difference between colonizations and extinctions over the years was positive. Recolonization of patches that had previously become extinct was very rare (0.4% of all colonizations). New sites were colonized by a few individuals and the mean distance from new patches to the closest old patch was 46.0 ± 39.9 m (median = 36 m). Extinctions were most common among new, vegetative and small fertile patches, and no extinctions were found among medium and large fertile patches. When compared with the habitat distribution of all patches, colonizations were more frequent in open habitats, whereas extinctions were not specifically associated with open habitats. According to the logistic regression analysis, an increase in patch area decreased extinction probability.

The realized and projected finite rate of increase in the number of patches varied only slightly from year to year, being around one, and both growth rates indicated a slight increase in the number of patches. The matrix models indicated a period of increase followed by a period of decrease, which is consistent with the actual changes in the number of patches. Stasis (staying in the same stage from one year to the next) was the most common stage transition among both vegetative and fertile patches. The mean of the observed distributions did not differ from the stable distribution of the mean matrix. According to the matrix analysis, the large fertile patches had the highest reproductive value and stasis had the highest elasticity value, followed by growth and fecundity (production of new patches).

With increasing scale from 5 metres to 200 metres, the balance between colonizations and extinctions approaches zero. As a consequence, increasing scale led to slower patch dynamics, and stasis achieved greater dominance among patch transitions. Stable stage distributions differed from observed distributions in most years and scales, whereas mean distributions differed only at the 200 m scale. The elasticity analysis seems to be qualitatively robust, as the increasing scale did not change the ranking of the importance of the transitions.

4 Discussion

4.1 Adaptations to river disturbance

Several anatomical, morphological and physiological features of *S. tatarica* make the species well adapted to physical stress on the riverside. Typical phenomena of these annually flooded habitats are submerging, sand burial, strong currents and mechanical damages by ice plates and dead trees carried by water. Besides flooding, the species is subject to summer drought, a long freezing period during winter, and mammalian herbivory.

After sand burial the species begins to grow an underground stem to reach light (I). This has also been recorded in seagrasses in marine waters (e.g., Wallén 1980, Disraeli 1984, Marbà & Duarte 1994, 1997, Marbà *et al.* 1994, Terrados 1997) and a few sand dune species (e.g., Maun & Lapierre 1984, Zhang & Maun 1992). Some of the buds in the former growing point stayed alive, which can be useful after sand erosion (I). Sand accretion may stimulate the formation of large bud families by bud ramification, which is a formerly unknown feature among herbs, but more common in trees (Chattaway 1958, Blake & Carrodus 1970, Kauppi *et al.* 1987, 1988, 1991, Johansson 1992). In addition, a large number of basal buds can also buffer against mammalian browsers as new shoots are initiated from the buds following apical damage (e.g., Paige & Whitham 1987, Strauss & Agrawal 1999). Although I do not have comparative morphological data from other geographical regions, the structures described in the present study may well present adaptations to ground disturbance in the steppes, such as wind-carried loess, which often causes plants to be buried. In this sense, *S. tatarica* could have become “preadapted” to the disturbance dynamics of the Oulanka River.

A low rigidity of roots and rhizomes and responses to velocity pull are crucial elements for the species survival under flooding water and herbivory pressure (I). In general, the resilience of *S. tatarica* was many times higher than that of other terrestrial plants, and it showed almost similar rigidity as aquatic species that is typical for fast-flowing rivers (Usherwood *et al.* 1997). This study revealed that rigidity was not connected to the age of the plant. Instead, a mixture of these primitive and developed anatomical structures was typical for *S. tatarica*. Enhancing the low rigidity for these

primitive anatomical structures (see Esau 1965, Fahn 1990, Ennos 1993, Usherwood *et al.* 1997) were (i) an abundance of tracheids and parenchymatous cells in the xylem, (ii) the presence of helical and scalariform thickenings of the vascular elements even in secondary wood and, (iii) the presence and location of collenchyma instead of sclerenchyma in the cortex area. In addition to resilience, the deeply penetrating tap root increases anchorage strength during a flood.

Furthermore, the long tap root of the species enables the plant to get water from deep layers of soil, which enhances survival during drought periods (I). The tap root is typical also for *Silene regia* (Menges & Dolan 1998) and *Lithospermum carolinense* (Weller 1985) in dry prairie and sand habitats, respectively. The wood of *S. tatarica* was strongly xeromorphic. The helical thickenings of the tracheary elements allow water, which is needed in conditions of increased evapotranspiration, to pass through quickly (Mauseth 1998). Furthermore, tracheids reinforce the conductive system when the vessels embolize during drought and freezing periods (Carlquist 1999) and in a very dry season stronger scalariform thickenings are needed to keep the tracheary elements open (Mauseth 1998). Sugars as a storage material allow the plants to start their growth earlier in spring (Crawley 1997) and to accumulate resources over brief warm periods in autumn. In addition, they can also increase cold-resistance and could be utilized during submergence (De Simone *et al.* 2003).

Plants from ruderal sites differ slightly from riparian plants, indicating the presence of phenotypic plasticity of individuals (I). Flooding can form an important selection pressure on plants, and variation in flooding duration can induce intraspecific specialization even within populations (Lenssen *et al.* 2004). Natural selection is predicted to favor traits that increase plant fitness. Since the number of flowers and fruits is often a function of meristem availability (Geber 1990), plant reproductive success often correlates positively with plant height and ramification. Indeed, in *S. tatarica*, selection gradients were positive for both characteristics (II). This can be associated with pollination, since taller and larger plants often attract more pollinators (e.g., Heinrich 1983, Peakall & Handel 1994, Donnelly *et al.* 1998, Lortie & Aarsen 1999). In addition to a multivariate statistical technique, sensitivity analyses can be used to predict trait combinations that should be favored by selection (Caswell 1989, 2001). Sensitivity analysis of transition matrices (III; data not shown) also showed strong selection towards bigger size, i.e., taller plants and a higher number of stems, which is in concordance with the results of the multivariate analysis.

Selection detected at the group level also favored taller plants (II). Dense groups with taller plants may be more visible to pollinators than sparse groups with shorter plants (e.g., Heisler & Damuth 1987, van Treuren *et al.* 1994, Roll *et al.* 1997, Kunin 1997, Kéry *et al.* 2000). In general, there was a group-level selection against a large number of stems, and this was most evident in the open habitats. This may suggest an association with mammal herbivory, which was more severe in open habitats. Groups with a large number of stems may have been more attractive to the herbivores and thus a small number of stems were favored. In closed habitats, competition with other plants can lead to the selection of higher plants.

A large number of selection studies in natural environments reviewed by Kingsolver *and colleagues* (2001) pointed out that most of the selection differentials and gradients had rather low values. Large ones were associated with a small sample size. Moreover,

selection estimates were seldom replicated in time or space. In this study with a large sample size, the estimates of selection had high values in both years (II), but when the data was split into three parts with respect to the habitat types, the magnitude of the selection gradient increased. This may be true in a more general context, too, since large samples may be collected from more heterogeneous environments than small samples, and the heterogeneity may lower the estimates of selection in larger pooled data sets.

Consequently, the heterogeneity of habitat as well as the spatial structure of *S. tatarica* populations are important in shaping the strength of selection (see also Stevens *et al.* 1995, Stinchcombe *et al.* 2002). In this species, the relatedness within patches is likely to be high, since new patches are established by a few founding individuals (IV) and the average dispersal distance of seeds within local populations is rather short (< 10 m; Tero *et al.* 2005).

4.2 Population and patch dynamics

Environmental stochasticity is often more important than demographic stochasticity for the fate of local populations (Caughley 1994). In *S. tatarica*, spatial variation in transitions, especially among juvenile individuals, and in population growth rates was much higher than temporal variation (III). These observations emphasize the importance of local conditions and environmental heterogeneity in shaping the demography and the dynamics of populations (e.g., Moloney 1988, Stratton 1992).

The seedling and juvenile dynamics explained most of the variation in the growth rates of *S. tatarica* populations (III). This was supported by both the elasticity and LTRE analyses. Moreover, these results are consistent with my unpublished data where the annual mean growth rates correlated positively with juvenile survival, but not with the survival of fertile individuals (Jäkäläniemi *et al.*, unpublished). Adults of this species were quite well equipped to survive flood disturbances (I). In some sites seedlings can establish every year, but in other sites only in good years (IV). Annual floods remove litter, which with competition can inhibit seedling establishment and survival, especially in closed habitats. In addition, extinctions were common in young patches (IV) and therefore suitable and safe seedling habitats are crucial for new populations to survive. This suggests that there is large spatial and temporal variation in the location of suitable seedling and adult habitats, depending on the local weather conditions and disturbance intensity. In a common garden experiment, the emergence of seedlings of *S. tatarica* was greatest from a sand surface (Marttila 2004), but for example in sand dune species *L. caroliniense*, it was from the depth of 1–4 cm (Weller 1985). In sand dunes, sand at depth of 10–15 cm tended to be moister than at the surface (Weller 1985), therefore the rapid production of a tap root increases the likelihood of surviving droughts.

The projected and simulated growth rates showed similar trends in population growth. Some populations increased, some decreased and a few of them were projected to become extinct in the near future (III). The habitat properties and its physical morphology can explain a part of this variation. First, flat shores were expected to be subject to frequent and widespread flood disturbances with more detrimental consequences for young than mature plants, whereas populations on steep slopes are more likely to be

subject to more harsh but smaller spread erosion disturbances, which could destroy young as well as mature plants (III). Although, the difference in λ in favor of the slopes was small, the probability of extinction was significantly lower on slopes than on flat shores. According to LTRE, higher fecundity improved λ on slopes and the fecundity of large fertile individuals was the most important transition in shaping the difference in population growth rates. Second habitat type along the succession gradient did not affect the probability of extinction (III). However, the average population growth rate indicated an increasing trend in intermediate habitats, whereas most populations in open and closed habitats showed a declining trend. The low average growth rate in closed habitats was mainly affected by the lower probability to survive and grow from juvenile to small vegetative individuals. In open habitats, on the other hand, low population growth was associated with the lower fecundity of large fertile individuals. This can be connected to the greater amount of herbivory in open habitats (II). The plants performed better in intermediate habitats because of weaker river disturbance and competition than in open or closed habitats, respectively.

Oostermeijer *and colleagues* (1994) have classified the populations of perennial *Gentiana pneumonanthe* as invasive or ‘dynamic’, normal or ‘stable’ and regressive or ‘senile’ populations. Invasive populations consisted mainly of seedlings and juveniles, normal populations of adult stages with a low number of seedlings and juveniles and regressive populations of only adult individuals. In *S. tatarica*, invasive populations were typical in open, normal populations in intermediate and regressive populations in closed habitats. However, this division of populations did not completely follow Oostermeijer *and colleagues* (1994) because, for example, the survival of juvenile individuals was significantly lower than that of adults in all habitat types (III–IV).

The extinction-colonization and patch dynamics revealed that the rate of colonization was quite high (0.2–12%) compared with the 2.8% rate of *Pedicularis furbishae* (Menges 1990), but 5–6 times lower than that of *Silene alba* (Antonovics *et al.* 1994). The ability to germinate and float in water (I) enhance the establishment of new populations, which typically consist of a few seedlings (IV). According to my observations, in most cases, the seedlings were situated in open habitats near the flood water line. Variation in seed color (I) may affect germination ability and seed predation in different habitat types. For example, on sand shores the predation of light brown seeds is expected to be lower than that of black seeds. On the other hand black seeds accumulate solar radiation better than brown seeds and therefore they can germinate earlier in the summer. Later germination of brown seeds may ensure seedling production even if seedlings from black seeds die during cold weather. The brown color can be an adaptation to the northern conditions since in the steppes the black seeds should be favored because of a short wet season and the dark color of the surface. However, the effects of seed color variation on predation probability and germination were not examined in this study.

The rate of extinction of *S. tatarica* was quite low (1–5%) compared with the 36% rate of the annual *Eichhornia paniculata* (Husband & Barrett 1998), the 9–30% rate of *S. alba* (Antonovics *et al.* 1994) and the 2–12% rate of *P. furbishae* (Menges 1990) (III). These comparisons are, however, somewhat biased in favor of annual plants, since they do not take into account the longer generation time of perennial species (see Whittaker 1998: 141). Population size in stochastic environments can be unconnected to the extinction rate (Hanson & Tuckwell 1978, 1981, Lande 2002). Because the risk of extinction in *S.*

tatarica was more strongly associated with patch area (IV) than with population size, environmental stochasticity may be more important than demographic stochasticity in determining the persistence of small populations (e.g., Lande 1988b, 1993, Wiens 1997). Considerable annual variation in both colonization and extinction rates further support this view. Basically, the extinction of newborn patches can be due to river dynamics as well as unfavorable weather conditions, whereas the extinction of large patches of mature plants requires large-scale erosion or a sufficiently large and thick accumulation of eroded sand.

The balance between the extinction and colonization rates may be largely a matter of flood intensity. A low flood water level is profitable for colonizations, because disturbance by ice plates and dead trees creates much open areas for seedlings. At the high flood water levels extinctions are common because of the water erosion and thick accumulation of sand. However, the seeds might disperse longer than during the low flooding, but it is expected that most of the seeds disappear because of moving sand and gravel. During high floods the water level rises to the forest line and provides an opportunity for late successional sites to be disturbed and consequently, improves the survival of seedlings there. After colonization, moist weather is needed for successful seedling establishment of *S. tatarica*. The combination of high flood and dry weather in early summer creates the opportunity for a year with a high extinction rate. The difference in the colonization and extinction rates in this study were positive in the first two years and then negative, but the mean over the study period was positive (IV) suggesting that the regional population is viable in spite of annual fluctuations between good and bad years.

4.3 Metapopulation concept and regional dynamics

In the long run, all patches of *S. tatarica* can be expected to have some risk of extinction because of deterministic causes related to succession and environmental stochasticity related to river disturbances (III, IV). The dynamics of local populations was asynchronous (III), and there is also evidence of rare long-distance dispersal between the populations (Tero *et al.* 2003). Consequently, this species shows many features of metapopulation dynamics and the metapopulation perspective has helped in understanding the spatial dynamics of this species.

Because the extinction of plant populations is a result of rather slow processes, the persistence of *S. tatarica* in time scale of years or decades largely depends upon local processes, as suggested by Freckleton and Watkinson (2002, 2003). The dynamics of *S. tatarica* do not satisfy two features of plant metapopulations (*sensu* Freckleton & Watkinson 2002); high rates of recolonization and plant distribution to discrete habitat patches. In the classification of Freckleton and Watkinson (2002) the low recolonization rate of *S. tatarica* points toward regional ensembles or spatially extended populations (Table 1), although the rates of extinction and colonization are probably higher and long-term dispersal more common than expected (IV). There is much suitable habitat along the Oulanka River for *S. tatarica* to colonize, and consequently recolonizations are rare. The

low rate of recolonization has been suggested to be very common in plants (Freckleton & Watkinson 2002).

The fact that populations are subdivided into many scales means the delimitation of local populations is often subjective (Hanski & Gilpin 1991). Ehrlén and Eriksson (2003) suggested that metapopulation dynamics are largely a matter of spatiotemporal scale and depending on the scale, and different researchers can classify the same system differently. In *S. tatarica* the turnover rate decreased and the growth rate converged near one when the scale was increased from 5 to 200 meters. In this sense the scale of research matters, since the dynamics of species become slower (IV). However, the elasticity analysis of patch demography in *S. tatarica* showed that the spatial scale did not have any significant effect on the importance rank of transitions with respect to their contribution to the growth rate of regional population

In this study the regional network of potentially suitable habitats includes both occupied and unoccupied habitat areas (IV). This regional population consists of local patch networks or local populations, each of which includes one or more patches of plants occupying an area of potentially suitable habitat. A short-distance dispersal refers to local dispersal within a single local network, either within a patch or between patches, whereas long-distance dispersal refers to either dispersal between distant patches within a local network or between separate local networks. A molecular genetic study of *S. tatarica* indicated relatively short local dispersal distances, less than 10 m (Tero *et al.* 2005), and the patchy appearance may well result in part from limited local dispersal. Because new colonizations were found at an average distance of 46 m from the closest old patch, colonization is not only influenced by short-distance dispersal, but to a great extent also by long-distance dispersal, either within or between local patch networks. Furthermore, the elasticity analysis strongly supported the importance of local within-patch processes, since the stasis of local patches clearly made a higher contribution than did the production of new patches. As local networks are occasionally destroyed, the long-term persistence of the species will more or less inevitably require that new colonizations occur and that they further lead to the establishment of new viable local populations. When new potential colonization sites are created and old networks and patches are destroyed by extrinsic forces, the abundance and distribution of the species will, in the long run, track the availability of the habitat (see also Thomas 1994, Harrison & Taylor 1997, Keymer *et al.* 2000, Snäll *et al.* 2003). The survival of *S. tatarica* in habitat-tracking regional population depends on two processes: the rate of creation of new habitats and the rate of colonization of such empty habitats, and it is not possible to distinguish between the two in this study.

Consequently, my study system full fills some but not all of the requirements of metapopulations, as stated by Hanski (1999, pp. 17–19) and Freckleton and Watkinson (2002). This concerns mainly the discreteness of patches. However, habitats are heterogenous in many scales and patch boundaries may in real landscapes be indistinct gradients rather than sharp discontinuities (Wiens 1997, Hanski 1999, Freckleton & Watkinson 2002). The distinction between one population occupying a number of different patches and a metapopulation consisting of populations in discrete habitat patches is not always clear (Stacey *et al.* 1997). The perception of metapopulations in terms of the species' occupancy in a network of discrete habitat patches may well be a most useful approximation, but perhaps it should not be adopted as the generative model

for defining metapopulations (for a discussion, see Baguette 2004, Hanski 2004), at least not in plant population biology. Some genetic studies have adopted a more liberal perspective (Tero *et al.* 2003, Pannell & Obbard 2003) and, furthermore, metapopulation dynamics can also be modeled as a set of populations interconnected by migration without any explicit reference to the habitat structure (for examples, see Hanski 1997). Thus, the main question does not seem to be habitat structure as such but rather whether migration or colonization-extinction dynamics have any significant impact on the persistence of the species in addition to the local “within-patch” dynamics. In the case of *S. tatarica* the answer is likely to be positive, since the local populations showed highly divergent fates (III), and hence the colonization-extinction dynamics will most probably be crucial for the long-term persistence of this species (IV).

4.4 Long-term persistence in transient environments

The classical view of metapopulations emphasizes a balance between extinctions and recolonizations of local populations that facilitates long-term persistence of metapopulations (Levins 1969, Hanski 1999). Environmental stochasticity and deterministic threats are the most likely ultimate causes of natural local extinctions. Deterministic local extinctions are more common than stochastic in many species (Hanski & Simberloff 1997) and also in real metapopulations (Thomas 1994), which is considered to violate the assumptions of the classical metapopulation model (Harrison & Taylor 1997). In deterministic extinctions the local patch may remain unsuitable after extinction occurs, and the persistence of regional population depends on how well the organisms can track the shifting spatial locations of new suitable habitat patches (Thomas 1994, Wiens 1997). In this sense it is possible that patch disappearance or unsuitability leads to a non-equilibrium situation in colonization-extinction dynamics, especially if the species has a long life span (see Thomas 1994, Harrison & Taylor 1997). Regional equilibrium is possible when the habitats are quite permanent in relation to the generation time of the species and to the frequency and intensity of external disturbances. In the non-equilibrium case of habitat tracking species (Table 1), the survival of regional scales depends on the rate of new colonizations compared to the rate of local extinctions, and a positive colonization-extinction balance requires the creation of a certain amount of suitable habitats related to the rate of habitat destruction and deterioration (IV).

An environmental mosaic perspective shifts the emphasis to transient dynamics and away from the equilibrium concept of metapopulation dynamics, for which there is said to be little evidence in nature (Thomas 1994, Whittaker 1998, Baguette 2004; but see Hanski 2004). In recent years, several attempts have been made to replace “equilibrium assumptions” with spatial and temporal variability driven by “non-equilibrium processes” (Wiens 1995, Whittaker 1998). Some authors (e.g., DeAngelis & Waterhouse 1987, Harrison 1991, 1994, Thomas (1994) have even questioned whether it is valid to define the existence of an equilibrium state at all, and they have suggested that this is a property that can emerge asymptotically from extrapolation to sufficiently large spatial scales. My results partly support this view. The rates of colonizations and extinctions of *S. tatarica*, varied among the study years, but with increasing scale the colonization-extinction

balance as well as the finite rate of patch number approached an “apparent equilibrium state”, i.e., colonizations – extinctions = 0 or $\lambda = 1$, respectively (IV). However, this equilibrium can be also seen as an artefact, since only a few colonization and extinction events occurred on the largest scales of 100–200 m (IV).

To some extent, most disturbance regimes in real landscapes will impose a spatiotemporal correlation on the dynamics of a suitable habitat (Stelter *et al.* 1997). On the regional scale the dynamics of *S. tatarica* resembles the dynamics of the grasshopper *Bryodema tuberculata* (Stelter *et al.* 1997), in which extinctions due to succession or flood events are compensated by colonization of newly created gravel bars. A similar situation has also been found in the *P. furbishae* plant (Menges 1990), in which new habitat is created by floods, and in the *Euphydryas gillettii* butterfly (Debinski 1994) by fire and beaver activity, and the *Trimerotropis saxatilis* grasshopper (Gerber & Templeton 1996) by fire. In addition, the persistence of simulated populations of the riparian gravel shore plant *Aster kantoensis*, is dependent on flood frequency and the time until perennial invasion (Shimada & Ishihama 2000). Also another riparian plant *Boltonia decurrens*, requires regular flooding for suitable habitat creation and seed dispersal along the river (DeWoody *et al.* 2004). A perennial species with wind dispersed seeds, *Erigeron acer* subsp. *decoloratus* (Asteraceae), shows very similar dynamics to *S. tatarica* (IV; unpublished data in 1999–2003) along the Oulanka River. In plants this could be seen as “passive habitat selection”, in which local populations grow in areas to which they are well adapted and decline in areas where they are poorly adapted (Lande 2002) and then disperse to a new open patch to escape from succession. For habitat tracking species long-distance seed dispersal is the mechanism by which a suitable habitat is colonized, thereby enabling the regional population to persist despite the fact that individual populations are doomed (Cain *et al.* 2000, Keymer *et al.* 2000, Johnst *et al.* 2002).

Spatial variation in the projected and stochastic growth rates of populations as such (III) tends to suggest that the present case of *S. tatarica* can be largely consistent with the habitat tracking model of regional dynamics (see Thomas 1994, Harrison & Taylor 1997, Snäll *et al.* 2003). Because four of fifteen populations included in this study are estimated to become extinct within 15–60 years, the long-term persistence of the species will more or less inevitably require that new colonizations occur and that they lead to new viable local populations (see also Ehrlén & Eriksson 2003). Consequently, the observed colonization-extinction dynamics (IV), the divergent fates of local populations (III, IV), habitat dependence (IV) and the ability for long distance dispersal in *S. tatarica* (Tero *et al.* 2003) support the view that the regional dynamics of the species could be consistent with the non-equilibrium dynamics of the habitat tracking model. While this kind of dynamics may in some respect differ from the classical metapopulation model in static landscapes (Fig. 4), both of them presume that colonization-extinction dynamics are important for the persistence of the species on regional scales.

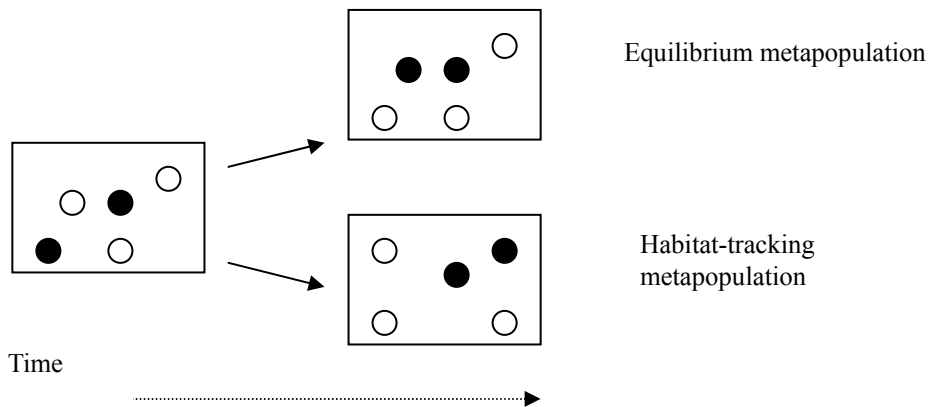


Fig. 4. Schematic view of dynamics in a plant metapopulations in static landscapes (equilibrium metapopulation, Table 1) and in a habitat-tracking species living in a dynamic landscape where suitable habitat patches are destroyed and new ones created by external disturbances and vegetation changes in the course of succession. Open and closed circles denote unoccupied and occupied suitable habitat patches, respectively.

4.5 Conservation implications

In a conservation sense, it is most profitable to recognize that all populations are spatially structured (Fahrig & Merriam 1994). A long-term conservation goal is to maintain genetic variation in a regional population, which may be composed of multiple subpopulations that are connected by some gene flow (Mills & Allendorf 1996, Allendorf & Ryman 2002). According to Wright's theories (1931, 1940, 1943) evolution might proceed rapidly in spatially structured populations, especially if there are local extinctions and recolonizations. In species with frequent turnover in natural environments, genetic stochasticity is expected to affect persistence relatively little, and Lande (1988b) and Sjögren (1991) have shown that it increases the risk of extinction in populations that have recently declined in size and that lack histories of severe fluctuations. Extinction-colonization dynamics in a regional population need not affect both the demography and the genetic structure of species to the same extent (Pannell & Obbard 2003). For example, in plant species distributed via hydrochory, dispersal patterns may better explain the genetic structure among populations than do extinction-colonization processes (DeWoody *et al.* 2004).

Local populations of *S. tatarica* have been shown to have clear subpopulation differentiation with an intermediate level of intrapopulation genetic diversity, a low level of gene flow and few long-distance dispersal events and migrants ($N_m = 0.333$) between patches (Tero *et al.* 2003). Several studies have suggested (e.g., Kimura & Crow 1963, Mills & Allendorf 1996) that occasional migration (1–10 migrants/generation) between small local populations can maintain genetic variation better than would a single large population, essentially because drift is likely to fix different alleles in different populations. Inbreeding has been shown to be very rare in *S. tatarica* (Tero *et al.* 2005).

The genetic studies of *S. tatarica* also suggested recent population bottlenecks (Tero *et al.* 2003), which are probably due to the founder effect, since the populations are established by a few individuals (IV). Genetic differentiation within a metapopulation can be dependent on the origin of the dispersers (McCauley 1991). Slatkin (1977) defined two modes of colony formation; in the migrant pool mode genes are drawn individually and at random from all possible source populations and in the propagule pool mode all the individuals are from one of the possible source populations. It has been suggested that *S. tatarica* shows a colonization structure that is a mix of these two models (Tero *et al.* 2003). *S. tatarica* has arrived to the Oulanka River just after the last Ice Age and survived from there on without signs of genetic erosion. Therefore, it is expected that ecological factors are more important than genetic ones in the conservation of the species.

Models of extinction by demographic stochasticity predict that subdivision of a habitat should decrease the mean time to extinction, while environmental stochasticity models predict that subdivision may increase the mean time of extinction (Quinn & Hastings 1987). However, Akcakaya and Baur (1996) found that, in animal populations, subdivision may act as a way to decrease the effects of environmental fluctuations and catastrophes, if such threats are distributed unevenly over the landscape. Fahrig (1992) showed in a simulation study that in a dynamic landscape the rate of change in landscape structure is more important than the degree of patch isolation in determining population survival and abundance. As long as the dispersal behavior can track the rate of change in the landscape's spatial structure, it is possible for the species to survive in the changing landscape (Fahrig & Merriam 1994). If the landscape structure change at a rate higher than this, the species will be unable to compensate for local extinctions in terms of new colonizations at a sufficient rate and the regional population will become extinct (Fahrig & Merriam 1994). Consequently, for habitat tracking species to persist in a dynamic landscape, conservation must focus on maintaining habitat continuity (Thomas 1994). Lande (1987, 2002) found that some species cannot persist if the proportion of suitable habitat drops below a certain level. Below the threshold value, the effects of patch isolation begin to be important for regional dynamics (Wiens 1997, Hanski & Ovaskainen 2002). Consequently, questions arise; how large a geographical area is needed for a species to persist, how much suitable habitats are needed and what is the temporal and spatial suitability of a habitat?

In *S. tatarica*, the river forms an appropriate vector of dispersal, and most seedlings and new patches were found at the flood water level, where most open areas exist. In Finland, the species is also distributed along regulated rivers, where new locations suitable for colonization are not created by natural processes. There most local populations occur on constructed riverbanks of accumulated sand and gravel. In addition, the species has dispersed to secondary habitats along roads and railways, where I have found a few new populations (I). In this ruderal habitat, the species seems to thrive the best in locations with an open or half-open habitat with sand-gravel ground.

According to the above outline, conservation of *S. tatarica* requires (1) the creation of new suitable open sites for colonization, (2) a dispersal process leading to successful colonizations, and (3) favorable conditions for survival of the colonizers to reproductively mature stages. These conditions can be maintained either by natural processes or by active conservation management. In Oulanka, the river channel forms a corridor for seeds to disperse and the natural dynamics of the river creates opportunities

for new colonizations and early successional areas for older populations to survive. In regulated rivers, the river corridor enables the seeds to disperse, but the establishment of new populations requires the creation of suitable open habitats. In ruderal habitats, management activities such as sowing or transplanting populations to open habitats may well ensure the persistence of the species on the regional scale.

5 Conclusions

The most critical life-history phase in *S. tatarica* is colonization. Although seed production is high, most of the seeds may be lost during a flood. Seedling survival is low, and hence only a few new populations reach reproductively mature stages. However, after the bottleneck in establishment, the survival of reproductively mature plants is quite high, because they obey several adaptive structures for tolerating both stress and disturbances. In addition, large populations have a low risk of sudden extinction.

While environmental stochasticity can increase the probability of extinction in single local populations, divergent fates of populations and habitat heterogeneity may, on the other hand, improve the long-term persistence of the species over larger regional scales. In *S. tatarica*, the duration and availability of suitable habitat, dispersal by water and asynchronous dynamics of local populations are connected to river disturbance. The survival probability of the species is most probable on the level of intermediate disturbance, because weaker disturbance can not create enough open areas for colonization and more extensive disturbance destroys most of the populations. In this sense, habitat tracking is the most important phenomenon in shaping the dynamics of *S. tatarica*. When the species slowly tracks the availability of suitable habitat, its long-term persistence depends on a positive balance between new colonizations and local extinctions that occur as result of environmental changes associated with succession and/or flood disturbances. The results of this study could be indicative for entire species groups growing in transient successional habitats.

The study at the regional level gave information on the habitat properties of new populations, habitat configuration and the extent of colonization- extinction dynamics. Consequently, the dynamics of the present species and its response to the disturbance regime can not be fully understood by studying the local processes alone. Furthermore, metapopulations have often been modeled in a static landscape, where the physical location of patches cannot change over the years. The future development of regional models is likely to expand towards dynamic landscape models, which put more emphasis on the transient dynamics of metapopulations and which may incorporate the dynamics of habitat patches in patch occupancy models. Such dynamic landscape approaches may give additional information on the minimum area needed to preserve a species with a

habitat tracking strategy and to maintain a suitable amount of natural disturbance in a transient environment.

References

- Aarssen LW (1995) Hypotheses for the evolution of apical dominance in plants: implications for the interpretation of overcompensation. *Oikos* 74:149–256.
- Aarssen LW & Irwin DL (1991) What selection: herbivory or competition. *Oikos* 60: 261–262.
- Akcakaya HR & Baur B (1996) Effects of population subdivision and catastrophes on the persistence of a land snail metapopulation. *Oecologia* 105: 475–483.
- Akcakaya HR & Sjögren-Gulve P (2000) Population viability analysis in conservation planning: an overview. *Ecological Bulletins* 48: 9–21.
- Allendorf FW & Ryman N (2002) The role of genetics in PVA. In: Beissinger SR & McCullough DR (eds) *Population viability analysis*. The University of Chicago Press, Chicago, 50–85.
- Amarasekare P & Possingham H (2001) Patch dynamics and metapopulation theory: the case of successional species. *Journal of Theoretical Biology* 209: 333–344.
- Antonovics J, Thrall P, Jarosz A & Stratton D (1994) Ecological genetics of metapopulations: the *Silene-Ustilago* plant-pathogen system. In: Real A (ed) *Ecological genetics*. Princeton University Press, Princeton, New Jersey, 146–170.
- Arnold SJ & Wade MJ (1984a) On the measurement of natural and sexual selection: theory. *Evolution* 38: 709–719.
- Arnold SJ & Wade MJ (1984b) On the measurement of natural and sexual selection: applications. *Evolution* 38: 720–734.
- Baguette M (2004) The classical metapopulation theory and the real, natural world: a critical appraisal. *Basic and Applied Ecology* 5:213–224.
- Beer FP & Johnston ER (1992) *Mechanics of materials*. 2nd edition in SI units. McGraw-Hill Book Company, London, UK.
- Bell TJ, Bowles, ML & McEachern AK (2003) Projecting the success of plant population restoration with viability analysis. *Ecological Studies* 165: 313–348.
- Beutler HO, Michal G & Beinstingl G (1978) Enzymatische Analyse von komplexen Kohlenhydratchemischen. *Deutsche Lebensmittel Rundschau* 74: 431–434.
- Blake TJ & Carrodus BB (1970) Studies on the lignotubers of *Eucalyptus obliqua* L'heri. II. Endogenous inhibitor levels correlated with apical dominance. *New Phytology* 69: 1073–1079.
- Blom CWPM & Voesenek LACJ (1996) Flooding: the survival strategies of plants. *Trends in Ecology and Evolution* 11: 290–295.
- Boorman SA & Levitt PR (1973) Group selection on the boundary of a stable population. *Theoretical Population Biology* 4: 85–128.
- Brodie ED III, Moore A J & Janzen F (1995) Visualizing and quantifying natural selection. *Trends in Ecology and Evolution* 10: 313–318.
- Bullock JM, Moy IL, Pywell RF, Coulson SS, Nolan AM & Caswell H (2002) Plant dispersal and colonization processes at local and landscape scales. In: Bullock JM, Kenward RE & Hails RS (eds) *Dispersal Ecology*. Blackwell Publishing, Oxford, 279–302.

- Cain ML, Milligan BG & Strand AE (2000) Long-distance seed dispersal in plant populations. *American Journal of Botany* 87: 1217–1227.
- Cajander AK (1914) Kasvien vaellusteistä Suomeen. *Lännetar*, Uusi jakso II: 12–45.
- Carlquist S (1999) Wood and stem anatomy of *Stegnosperma* (Caryophyllales); phylogenetic relationships; nature of lateral meristems and successive cambial activity. *IAWA Journal* 20: 149–163.
- Caswell H (1989) *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Sunderland, Massachusetts, USA
- Caswell H (2001) *Matrix population models. Construction, analysis, and interpretation*. 2nd edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Caughley G (1994) Directions in conservation biology. *Journal of Animal Ecology* 63: 215–244.
- Chattaway MM (1958) Bud development and lignotuber formation in eucalypts. *Australian Journal of Botany* 6: 103–115.
- Crawley M (1997) *Plant ecology*. 2nd edition. Blackwell Science, Oxford, UK.
- DeAngelis DL & Waterhouse JC (1987) Equilibrium and non-equilibrium concepts in ecological models. *Ecological Monographs* 57: 1–21.
- Debinski DM (1994) Genetic diversity assessment in a metapopulation of the butterfly *Euphydryas gillettii*. *Biological Conservation* 70: 25–31
- Delmotte F, Bucheli E & Shykoff JA (1999) Host and parasite population structure in a natural plant-pathogen system. *Heredity* 82: 300–308.
- De Simone O, Junk WJ & Schmidt W (2003) Central Amazon floodplain forests: root adaptations to prolonged flooding. *Russian Journal of Plant Physiology* 50: 943–951.
- DeWoody J, Nason JD & Smith M (2004) Inferring demographic processes from the genetic structure of a metapopulation of *Boltonia decurrens* (Asteraceae). *Conservation Genetics* 5: 603–617.
- Disraeli DJ (1984) The effects of sand deposits on the growth and morphology of *Ammophila breviligulata*. *Journal of Ecology* 72: 145–154.
- Donnelly SE, Lortie CJ & Aarssen LW (1998) Pollination in *Verbascum thapsus* (Scrophulariaceae): the advantage of being tall. *American Journal of Botany* 85: 1618–1625.
- Ehrlén J & Eriksson O (2003) Large-scale spatial dynamics of plants: a response to Freckleton & Watkinson. *Journal of Ecology* 91: 316–320.
- Ennos AR (1993) The mechanics of the flower stem of the sedge *Carex acutiformis*. *Annals of Botany* 72: 123–127.
- Eriksson O (1996) Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos* 77: 248–258.
- Esau K (1965) *Plant anatomy*. 2nd ed. John Wiley & Sons Inc., New York, USA.
- Fahn A (1990) *Plant anatomy*. 4th ed. BPCC Wheatons Ltd, Exeter, UK.
- Fahrig L (1992) Relative importance of spatial and temporal scales in a patchy environment. *Theoretical Population Biology* 41: 300–314.
- Fahrig L & Merriam G (1994) Conservation of Fragmented Populations. *Conservation biology* 8: 50–59.
- Falk DA (1992) From conservation biology to conservation practice: strategies for protecting plant diversity. In: Fiedler PL & Jain SK (eds) *Conservation Biology. The theory and practice of nature conservation preservation and management*. Chapman and Hall, London, 397–431.
- Fleishman E, Ray C, Sjögren-Gulve P, Boggs CL & Murphy DD (2001) Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. *Conservation Biology* 16: 706–716.
- Freckleton RP & Watkinson AR (2002) Large-scale spatial dynamics of plants: metapopulations, regional ensembles and patchy populations. *Journal of Ecology* 90: 419–434.
- Freckleton RP & Watkinson AR (2003) Are all plant populations metapopulations? *Journal of Ecology* 91: 321–324.
- Geber MA (1990) The cost of meristem limitation in *Polygonum arenastrum*: Negative genetic correlations between fecundity and growth. *Evolution* 44: 799–819.
- Gerber AS & Templeton AR (1996) Population sizes and within-deme movement of *Trimerotropis saxatilis* (Acrididae), a grasshopper with a fragmented distribution. *Oecologia* 105: 343–350.

- Giles BE & Goudet J (1997) Genetic differentiation in *Silene dioica* metapopulations: estimation of spatiotemporal effects in a successional plant species. *The American Naturalist* 149: 507–526.
- Gilpin M & Hanski I (eds) (1991) *Metapopulation dynamics: empirical and theoretical investigations*. Academic Press, London.
- Golubov J, Mandujano MC, Franco M, Montana C, Eguiarte LE & Lopez-Portillo J (1999) Demography of the invasive woody perennial *Prosopis glandulosa* (honey mesquite). *Journal of Ecology* 87: 955–962.
- Goodman LA (1971) On the sensitivity of the intrinsic growth rate to changes in the age-specific birth and death rates. *Theoretical Population Biology* 2: 339–354.
- van Groenendael J, de Kroon H & Caswell H (1988) Projection matrices in population biology. *Trends in Ecology and Evolution* 3: 264–269.
- Hanski I (1991) Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of Linnean Society* 41: 17–38.
- Hanski I (1994) Patch-occupancy dynamics in fragmented landscapes. *Trends in Ecology and Evolution* 9: 131–135.
- Hanski I (1997) Metapopulation dynamics. From concepts and observations to predictive models. In: Hanski I & Gilpin ME (eds) *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, California, USA, 69–91.
- Hanski I (1999) *Metapopulation Ecology*. Oxford University Press, Great Britain.
- Hanski I (2004) Metapopulation theory, its use and misuse. *Basic and Applied Ecology* 5: 225–229.
- Hanski I & Gilpin M (1991) Metapopulation dynamics: Brief history and conceptual domain. In: Hanski I & Gilpin ME (eds) *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, California, USA, 3–16.
- Hanski I, Moilanen A & Gyllenberg M (1996) Minimum viable metapopulation size. *The American Naturalist* 147: 527–541.
- Hanski I. & Simberloff D (1997) The metapopulation approach, its history, conceptual domain, and application to conservation. In: Hanski I & Gilpin ME (eds) *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, California, USA, 5–26.
- Hanski I & Ovaskainen O (2002) Extinction debt at extinction threshold. *Conservation Biology* 16: 666–673.
- Hanson FB & Tuckwell HC (1978) Persistence times of populations with random fluctuations. *Theoretical Population Biology* 14: 46–61.
- Hanson FB & Tuckwell HC (1981) Logistic growth with random density independent disasters. *Theoretical Population Biology* 19: 1–18.
- Harrison S (1991) Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of Linnean Society* 42: 73–88.
- Harrison S (1994) Metapopulations and conservation. In: Edwards PJ, May RM & Webb NR (eds) *Large-scale ecology and conservation biology*. Blackwell Scientific Press, Oxford, 111–128.
- Harrison S & Taylor AD (1997) Empirical evidence for metapopulation dynamics. In: Hanski I & Gilpin ME (eds) *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, California, USA, 27–42.
- Hastings A (2003) Metapopulation persistence with age-dependent disturbance or succession. *Science* 301: 1525–1526.
- Heinrich B (1983) Insect foraging energetics. In: Jones EC & Little JR (eds). *Handbook of experimental pollination biology*. Van Nostrand Reinhold Company, New York, 187–214.
- Heisler IL & Damuth J (1987) A method for analyzing selection in hierarchically structured populations. *The American Naturalist* 130: 582–602.
- Hellström K (2004) Variation in grazing tolerance and restoration of meadow plant communities. Ph.D. thesis. *Acta Universitatis Ouluensis, Ser A 423*, Oulu University Press, Finland.
- Hess GR (1996) Linking extinction to connectivity and habitat destruction in metapopulation models. *The American Naturalist* 148: 226–236.
- Hoekstra HE., Hoekstra JM, Berrigan D, Vignieri SN, Hoang, A, Hill CE, Beerli P & Kingsolver JG (2001) Strength and tempo of directional selection in the wild. *Proceedings of National Academy of Sciences USA* 98: 9157–9160.

- Horvitz C, Schemske W & Caswell H (1996) The relative “importance” of life-history stages to population growth: prospective and retrospective analyses. In: Tuljapurkar S & Caswell H (eds). Structured population models in marine, terrestrial and freshwater systems. Chapman and Hall, New York, USA, Pages 247–271.
- Huhta A-P (2001) Restorative mowing on semi-natural grasslands: community-level changes and species-level responses. Ph.D. thesis. Acta Universitatis Ouluensis. Ser A 365, Oulu University Press, Finland.
- Husband BC & Barrett SCH (1996) A metapopulation perspective in plant population biology. *Journal of Ecology* 84: 461–469.
- Husband BC & Barrett SCH (1998) Spatial and temporal variation in population size of *Eichornia paniculata* in ephemeral habitats: implications for metapopulation dynamics. *Journal of Ecology* 86: 1021–1031.
- Ingvansson PK & Giles BE (1999) Kin-structured colonization and small-scale genetic differentiation in *Silene dioica*. *Evolution* 53: 605–611.
- Johansson T (1992) Sprouting of 2- to 5-year-old birches (*Betula pubescens* Ehrh. and *Betula pendula* Roth) in relation to stump height and felling time. *Forest Ecology and Management* 53: 263–281.
- Johnst K, Brandl R & Eber S (2002) Metapopulation persistence in dynamic landscapes: the role of dispersal distance. *Oikos* 98: 263–270.
- Kauppi A, Rinne P & Ferm A (1987) Initiation, structure and sprouting of dormant basal buds in *Betula pubescens*. *Flora* 179: 55–83.
- Kauppi A, Kiviniitty M & Ferm A (1988) Growth habits and crown architecture of *Betula pubescens* Ehrh. Of seed and sprout origin. *Canadian Journal of Forest Research* 18: 1603–1613.
- Kauppi A, Paukkonen K & Rinne P (1991) Sprouting ability of aerial and underground dormant basal buds of *Betula pendula*. *Canadian Journal of Forest Research* 21: 528–533.
- Kéry M, Matthies D & Spillmann HH (2000) Reduced fecundity and offspring performance in small populations of the declining grassland plants *Primula veris* and *Gentiana lutea*. *Journal of Ecology* 88: 17–30.
- Keymer JE, Marquet PA, Velasco-Hernández JX. & Levin SA (2000) Extinction thresholds and metapopulation persistence in dynamic landscapes. *The American Naturalist* 156: 478–494.
- Kimura M & Crow JF (1963) On the maximum avoidance of inbreeding. *Genetic Research* 4: 399–415.
- Kingsolver JG, Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hill CE, Hoang A, Gibert P & Beerli P (2001) The strength of phenotypic selection in natural populations. *American Naturalist* 157: 245–261.
- Koutaniemi L (1984) The role of ground frost, snow cover, ice break-up and flooding in the fluvial processes of the Oulanka river, NE Finland. *Fennia* 162: 127–161.
- de Kroon H, Plaisier A, van Groenendael J & Caswell H (1986) Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67: 1427–1431.
- Kunin WE (1997) Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. *Journal of Ecology* 85: 225–234.
- Lande R (1987) Extinction thresholds in demographic models of territorial populations. *The American Naturalist* 130: 624–635.
- Lande R (1988a) Demographic models of the northern spotted owl (*Strix occidentalis caurica*). *Oecologia* 75: 601–607.
- Lande R (1988b) Genetics and demography in biological conservation. *Science* 241: 1455–1460.
- Lande R (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist* 142: 911–927.
- Lande R (2002) Incorporating stochasticity in population viability analysis. In: Beissinger SR & McCullough DR (eds). Population viability analysis. The University Chicago Press, Chicago, 18–40.
- Lande R & Arnold S J (1983) The measurement of selection on correlated characters. *Evolution* 37: 1210–1226.

- Lefkovich LP (1965) The study of population growth in organisms grouped by stages. *Biometrics* 21: 1–18.
- Lenssen JP, Van Kleunen M, Fischer M & De Kroon H (2004) Local adaptation of the clonal plant *Ranunculus reptans* to flooding along a small-scale gradient. *Journal of Ecology* 92: 696–706.
- Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15: 237–240.
- Lortie CJ & Aarssen LW (1999) The advantage of being tall: Higher flowers receive more pollen in *Verbascum thapsus* L. (Scrophulariaceae). *Ecoscience* 6: 68–71.
- Lytle DA & Poff NL (2004) Adaptation to natural flow regimes. *Trends in Ecology and Evolution* 19: 94–100.
- Marbà N & Duarte CM (1994) Growth response of the seagrass *Cymodocea nodosa* to experimental burial and erosion. *Marine Ecology Progress Series* 107: 307–311.
- Marbà N & Duarte CM (1997) Interannual changes in seagrass (*Posidonia oceanica*) growth and environmental change in the Spanish Mediterranean littoral zone. *Limnology and Oceanography* 42: 800–810.
- Marbà N, Cebrián J, Enríquez S & Duarte CM (1994) Migration of large-scale subaqueous bedforms measured with seagrasses (*Cymodocea nodosa*) as tracers. *Limnology and Oceanography* 39: 126–133.
- Marttila S (2004) Tatarikohokin (*Silene tatarica*) taimettumis- ja kolonisaatiodynamiikka häiriönalaisilla jokirannoilla. Master thesis, Department of biology, University of Oulu. [In Finnish]
- Maun MA & Lapierre J (1984) The effects of burial by sand on *Ammophila breviligulata*. *Journal of Ecology* 72: 827–839.
- Mauseth JD (1998) Botany, an introduction to plant biology. Jones and Bartlett Publishers, Sudbury, Massachusetts, USA.
- McCauley DE (1991) Genetic consequences of local population extinction and recolonization. *Trends in Ecology and Evolution* 6: 5–8.
- McCauley DE, Raveill J & Antonovics J (1995) Local founding events as determinants of genetic structure in a plant metapopulation. *Heredity* 75: 630–636.
- Menges ES (1990) Population Viability Analysis for an Endangered Plant. *Conservation biology* 4: 41–62.
- Menges ES (1992) Stochastic modelling of extinction in plant populations. In: Fiedler PL & Jain SK (eds) *Conservation biology*. Chapman and Hall, London, 253–275.
- Menges ES (2000) Population viability analyses in plants: challenges and opportunities. *Trends in Ecology and Evolution* 15: 51–56.
- Menges ES & Dolan RW (1998) Demographic viability of populations of *Silene regia* in midwestern prairies: relationship with fire management, genetic variation, geographic location, population size and isolation. *Journal of Ecology* 86: 63–78.
- Menges ES & Quintana-Ascencio PF (2003) Modelling the effects of disturbance, spatial variation, and environmental heterogeneity on population viability of plants. *Ecological Studies* 165: 289–311.
- Mills LS & Allendorf FW (1996) The one-migrant-per-generation rule in conservation and management. *Conservation Biology* 10: 1509–1518.
- Mitchell-Olds T & Shaw RG (1987) Regression analysis of natural selection: statistical interferences and biological interpretations. *Evolution* 41: 1149–1161.
- Moloney KA (1988) Fine-scale spatial and temporal variation in the demography of a perennial bunchgrass. *Ecology* 69: 1588–1598.
- Oostermeijer G, van't Veer R & den Nijs M (1994) Population structure of the rare, long-lives perennial *Gentiana pneumonanthe* in relation to vegetation and management in The Netherlands. *Journal of Applied Ecology* 31: 428–438.
- Ouborg, NJ & Eriksson O (2004) Toward a metapopulation concept for plants. In: Hanski I & Gaggiotti, OE (eds) *Ecology, genetics and evolution of metapopulations*. Elsevier Academic Press, Burlington, 447–469.
- Overton J McC (1994) Dispersal and infection in mistletoe metapopulations. *Journal of Ecology* 82: 711–723.

- Paige KN & Whitham TG (1987) Overcompensation in response to mammalian herbivory. The advantage to be eaten. *The American Naturalist* 129: 407–416.
- Pannell JR & Obbard DJ (2003) Probing the primacy of the patch: what makes a metapopulation? *Journal of Ecology* 91: 485–488.
- Peakall R & Handel SN (1994) Pollinators discriminate among floral heights of a sexually deceptive orchid: Implications for selection. *Evolution* 47: 1681–1687.
- Pease CM, Lande R & Bull JJ (1989) A model of population growth, dispersal and evolution in a changing environment. *Ecology* 70: 1657–1664.
- Pickett STA & White PS (1985) *The ecology of natural disturbance and patch dynamics*. Academic Press, London.
- Price GR (1970) Selection and covariance. *Nature* 227: 520–521.
- Pulliam HR (1988) Sources, sinks, and population regulation. *American Naturalist* 132: 652–661.
- Quinn JF & Hastings A (1987) Extinction in subdivided habitats. *Conservation Biology* 1: 198–208.
- Quintana-Ascencio PS & Menges ES (1996) Inferring metapopulation dynamics from patch-level incidence of Florida scrub plants. *Conservation Biology* 10: 1210–1219.
- Rassi P, Kaipainen H, Mannerkoski I & Ståhl G (1992) Uhanalaisten eläinten ja kasvien seurantatoimikunnan mietintö. Komiteamietintö 1991: 30. [in Finnish]
- Rassi P, Alanen A, Kanerva T & Mannerkoski I (2001) Suomen lajien uhanalaisuus 2000. Ympäristöministeriö & Suomen Ympäristökeskus, Helsinki, Finland. [in Finnish]
- Rausher MD (1992) The measurement of selection on quantitative traits: Biases due to environmental covariances between traits and fitness. *Evolution* 46: 616–626.
- Rautiainen P, Laine AL, Aikio S, Aspi J, Siira J & Hyvärinen M (2004) Seashore disturbance and management of the clonal *Arctophila fulva*; Modelling patch dynamics. *Applied Vegetation Science* 7: 221–228.
- Reed JM, Mills LS, Dunning jr JB, Menges ES, McKelvey KS, Frye R, Beissinger SR, Anstett M-C & Miller P (2002) Emerging issues in population viability analysis. *Conservation biology* 16: 7–19.
- Roll J, Mitchell RJ, Cabin RJ & Marshall DL (1997) Reproductive success increases with local density of conspecifics in a desert mustard (*Lesquerella fendleri*). *Conservation biology* 11: 738–746.
- Schemske DW, Husband BC, Ruckelshaus MH, Goodville C, Parker IM & Bishop JG (1994) Evaluating approaches to the conservation of rare and endangered plants. *Ecology* 75: 584–606.
- Shaffer ML (1981) Minimum population sizes for species conservation. *Bioscience* 31: 131–134.
- Shimada M & Ishihama F (2000) Asynchronization of local population dynamics and persistence of a metapopulation: a lesson from an endangered composite plant, *Aster kantoensis*. *Population Ecology* 42: 63–72.
- Silvertown J, Franco M, Pisanty I & Mendoza A (1993) Comparative plant demography - relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology* 81: 465–476.
- Sjögren P (1991) Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). *Biological Journal of Linnean Society* 42: 135–147.
- Snäll T, Ribeiro Jr PJ & Rydin H (2003) Spatial occurrence and colonisations in patch-tracking metapopulation: conditions versus dispersal. *Oikos* 103: 566–578
- Slatkin M (1977) Gene flow and genetic drift in a species subject to frequent local extinctions. *Theoretical Population Biology* 12: 253–262.
- Sousa WP (1984) The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15: 353–391.
- Stacey PB, Johnson VA & Taper ML (1997) Migration within Metapopulations. The Impact upon Local Population Dynamics. In: Hanski I & Gilpin ME (eds) *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, California, USA, 267–291.
- Stelter C, Reich M, Grimm V & Wissel C (1997) Modelling persistence in dynamic landscapes: lessons from a metapopulation of the grasshopper *Bryodema tuberculata*. *Journal of Animal Ecology* 66: 508–518.

- Stevens L, Goodnight C J & Kalisz S (1995) Multilevel selection in natural populations of *Impatiens capensis*. *The American Naturalist* 145: 513–526.
- Stinchcombe JR, Rutter MT, Burdick DS, Tiffin P, Rausher MD & Mauricio R (2002) Testing for environmentally induced bias in phenotypic estimates of natural selection: theory and practice. *The American Naturalist* 169: 511–523.
- Stratton DA (1992) Life-cycle components of selection in *Erigeron annuus*: II Phenotypic selection. *Evolution* 46: 92–106.
- Strauss SY & Agrawal AA (1999) The ecology and evolution of plant tolerance to herbivory. *Trends Ecology and Evolution* 14: 179–185.
- Taylor DR, Trimble S & McCauley DE (1999) Ecological genetics of gynodioecy in *Silene vulgaris*: relative fitness of females and hermaphrodites during the colonization process. *Evolution* 53: 745–751.
- Tero N, Aspi J, Siikamäki P, Jäkäläniemi A & Tuomi J (2003) Genetic structure and gene flow in a metapopulation of an endangered plant species, *Silene tatarica*. *Molecular Ecology* 12: 2073–2085.
- Tero N, Aspi J, Siikamäki P & Jäkäläniemi A (2005) Local genetic population structure in an endangered plant species, *Silene tatarica* (Caryophyllaceae). *Heredity* 94: 478–487.
- Terrados J (1997) Is light involved in the vertical growth response of seagrasses when buried by sand? *Marine Ecology Progress Series* 152: 295–299.
- Thomas CD (1994) Extinction, colonization, and metapopulations: environmental tracking by rare species. *Conservation Biology* 8: 373–378.
- Tilman D, May RM, Lehman CL & Nowak MA (1994) Habitat destruction and the extinction debt. *Nature* 371: 65–66.
- Travis JMJ & Dytham C (1999) Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society of London B* 266: 723–728.
- van Treuren RM, Bijlsma R, Ouborg NJ & Kwak MM (1994) Relationships between plant density, outcrossing rates and seed set in natural and experimental populations of *Scabiosa columbaria*. *Journal of Evolutionary Biology* 7: 287–302.
- Tuljapurkar S (1989) An uncertain life: demography in random environments. *Theoretical Population Biology* 35: 227–294.
- Tuljapurkar S (1990) Delayed reproduction and fitness in variable environments. *Proceedings of the National Academy of Sciences USA* 87: 1139–1143.
- Ulvinen T (1997) Tataarikoehokki- ryssglim. In: Rytteri T & Kettunen T (eds) *Uhanalaiset kasvimme*. Kirjayhtymä Oy, Helsinki. [in Finnish]
- Usherwood JR, Ennos AR & Ball DJ (1997) Mechanical and anatomical adaptations in terrestrial and aquatic buttercups to their respective environments. *Journal of Experimental Botany* 48: 1469–1475.
- Verheyen K, Vellend M, Van Calster H, Peterken G & Hermy M (2004) Metapopulation dynamics in changing landscapes: a new spatially realistic model for forest plants. *Ecology* 85: 3302–3312.
- Wade MJ & Arnold SJ (1980) The intensity of sexual selection in relation to male sexual behavior, female choice and sperm precedence. *Animal Behaviour* 28: 446–461.
- Wallén B (1980) Changes in structure and function of *Ammophila* during primary succession. *Oikos* 24: 227–238.
- Watkinson AR, Freckleton RP & Forrester L (2000) Population dynamics of *Vulpia ciliata*: regional, patch and local dynamics. *Journal of Ecology* 88: 1012–1029.
- Weller SG (1985) The life history of *Lithospermum carolinense*, a long-lived herbaceous sand dune species. *Ecological Monographs* 55: 49–67.
- Whittaker RJ (1998) *Island biogeography*. Ecology, Evolution, and Conservation. Oxford University Press, Oxford.
- Wiens JA (1995) Landscape mosaics and ecological theory. In: Hansson L, Fahrig L & Merriam G (eds) *Mosaic landscapes and ecological processes*. Chapman & Hall, London, 1–26.
- Wiens JA (1997) Metapopulation Dynamics and Landscape Ecology. In: Hanski I & Gilpin ME (eds) *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, California, USA, 43–62.

- Wright S (1931) Evolution in Mendelian populations. *Genetics* 16: 97–169.
- Wright S (1940) Breeding structure of populations in relation to speciation. *The American Naturalist* 74: 232–248.
- Wright S (1943) Isolation by distance. *Genetics* 38: 114–138.
- Zhang J & Maun MA (1992) Effects of sand burial on seed germination, seedling emergence, survival, and growth of *Agropyron psammophilum*. *Canadian Journal of Botany* 68: 304–310.