

Linking plant population dynamics to the local environment and forest succession

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Cover: Integral projection model of *Actaea spicata*
by Juliawati binti Azali

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Till Morfar.

Vad tjänar det till att ruta
in och göra skarpa gränser
i denna svala täta trängsel
av gröna gräs och blader.

- Harry Martinson, 1937.

Doctoral dissertation

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Abstract – Linking environmental variation to population dynamics is necessary to understand and predict how the environment influences species abundances and distributions. I used demographic, environmental and trait data of forest herbs to study effects of spatial variation in environmental factors on populations as well as environmental change in terms of effects of forest succession on field layer plants. The results show that abundances of field layer species during forest succession are correlated with their functional traits; species with high specific leaf area increased more in abundance. I also found that soil nutrients affect vegetative and flowering phenology of the forest herb *Actaea spicata*. The effect of nutrients shows that a wider range of environmental factors than usually assumed can influence plant phenology. Moreover, local environmental factors affected also the demography of *A. spicata* through effects on vital rates. An abiotic factor, soil potassium affecting individual growth rate, was more important for population growth rate than seed predation, the most conspicuous biotic interaction in this system. Density independent changes in soil potassium during forest succession, and to a lesser extent plant population size dependent seed predation, were predicted to alter population growth rate, and thereby the abundance, of *A. spicata* over time. Because these environmental factors had effects on population projections, they can potentially influence the occupancy pattern of this species along successional gradients. I conclude that including deterministic, as opposed to stochastic, environmental change in demographic models enables assessments of the effects of processes such as succession, altered land-use, and climate change on population dynamics. Models explicitly incorporating environmental factors are useful for studying population dynamics in a realistic context, and to guide management of threatened species in changing environments.

Key words: *Actaea spicata*, Forest herbs, Forest succession, Integral projection model, Plant demography, Plant phenology, Population dynamics, Pre-dispersal seed predation, Seed mass, Soil potassium, Specific leaf area

List of papers

The thesis is based on the following papers:

- I Dahlgren, J.P., O. Eriksson, K. Bolmgren, M. Strindell, & J. Ehrlén. 2006. Specific leaf area as a superior predictor of changes in field layer abundance during forest succession. *Journal of Vegetation Science* 17:577–582.
- II Dahlgren, J.P., H. von Zeipel, & J. Ehrlén. 2007. Variation in vegetative and flowering phenology in a forest herb caused by environmental heterogeneity. *American Journal of Botany* 94:1570–1576.
- III Dahlgren, J.P. & J. Ehrlén. Linking environmental variation to population dynamics of a forest herb. *Manuscript*.
- IV Dahlgren, J.P. & J. Ehrlén. A demographic model of a forest herb in a changing environment. *Manuscript*.

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Aim of the thesis

The main aim of the thesis is to assess effects of the local environment, and its temporal changes, on populations. A second aim is to develop methods used in ecological research and in conservation of threatened species, in particular to further develop demographic models and methods of population viability analyses. The contribution of the four papers is depicted in Fig. 1. I regard forest succession as a mechanism of environmental change for field-layer plants. In turn, the interaction between environment and species traits affects population growth rates and abundances of species via demography. Paper I is a study of how forest succession affects abundance changes of field-layer plants, and how species traits are connected to these changes. In paper II we assessed environmental effects on vegetative and reproductive phenology of a forest herb; traits that presumably affect demographic processes. In paper III we studied effects of environmental factors on vital rates, and the resulting effects on population growth rate. In paper IV we linked environmental change caused by forest succession with population dynamics, and predicted resulting abundance changes.

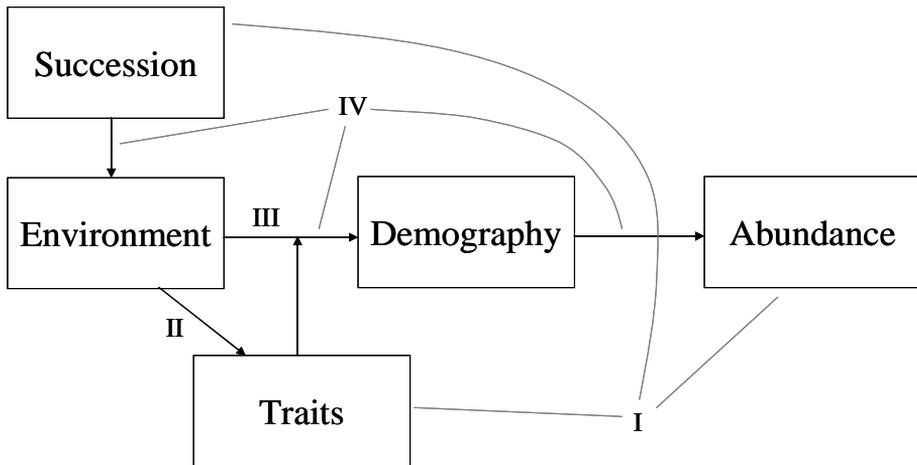


Figure 1. A visual model of how papers I–IV relate to the aim of describing environmental effects on populations.

Introduction

Understanding and predicting changes in species occurrences and abundances requires a more complete and mechanistic understanding of natural systems. Although the science of ecology has come a long way since the first true ecological studies at the end of the nineteenth century, many pieces of the puzzle are still missing. One missing piece is knowledge of the links between environmental variation and population dynamics. This is particularly true for abiotic interactions. Establishing the links between the environment and population dynamics is necessary to predict effects of temporal environmental changes due to succession, eutrophication, altered land-use and climate change, on populations and communities. Communities are affected by the environment via growth rates of the populations that constitute them. Population growth rate is the result of rates of demographic processes, or vital rates, determined by the interaction between traits of individual plants and the environment.

Forest herbs: their traits, life history strategies and light environment

In Grime's (1979) conceptual C-S-R triangle model, plant life history strategies are divided into ruderal, competitor, and stress-tolerator strategies. Forest herbs would typically fall into the stress-tolerator category due to their adaptations to tolerate the low light availability at forest floors. In accordance with this notion, many forest herbs are long-lived perennials that may live for decades, with associated slow growth, high survival and long regeneration time (Silvertown 1993, Ehrlén and Lehtilä 2002). The perhaps most striking features of forest herbs in relation to herbs in open environments are a range of traits that can be assumed to be adaptations to a light limited environment. Compared to grassland species, forest herbs typically have high seed masses, high leaf area to mass ratios (specific leaf area: SLA), and long shoots. A high seed mass may enable a larger provision of nutrients to the early growth of seedlings (Moles and Westoby 2004), a low transpiration rate may enable plants to invest less in leaf thickness (Wilson et al. 1999), and a greater height may allow greater success in competition for light in the herb layer (Hodgson et al. 1999). Of course, the advantages conferred by these traits come at a cost. A high SLA is associated with a high relative

growth rate and a high competitive ability, in terms of a high net photosynthetic capacity per unit leaf mass, but also with short leaf life span and low resistance to mechanical damage (Reich et al. 1997; Wright et al. 2004). The competitive advantage of tall species is countered by a greater sensitivity to disturbance (Westoby et al. 2002), and high seed mass is often associated with low seed number (Moles & Westoby 2004). Functional traits such as these should determine effects of changes in the light-environment on populations (Weiher et al. 1999).

Forest succession as environmental change

Succession has been studied throughout the entire twentieth century (Gleason 1917, 1926, Clements 1936, Pickett et al. 1987). The underlying mechanisms are, however, still not fully understood. Basically, succession is a process of individual replacement governed by chance (Gleason 1926). From a community perspective, there are still more or less likely outcomes of species replacements and abundance changes. Which species are replaced by which depends on site and species availability, and species trait compositions (Pickett et al. 1987).

A common and simple model of species replacement over succession is to regard community composition over time as a dynamic equilibrium of ruderal and competitor life history strategies (e.g. Stiling 2001). In this model, shorter species with small seeds and high SLA should be more common early in succession (see above). However, species replacement over succession can also result from facilitation and inhibition, i.e. environmental change caused by non-competing species. Species replacement in forest field layers is to a large extent caused by overstory succession, even though the field layer may also have an effect on tree establishment (Royo and Carson 2006). In succession from open land to forest, reduction in light availability is the most important change in abiotic conditions for field layer composition (Hart and Chen 2006). Thus, during succession from open land to forest, traits associated with shade tolerance, e.g. high SLA, should become increasingly beneficial for field layer species. In later forest succession, other environmental factors, such as soil nutrient concentrations and water content, may be more important (Schwendenmann 2000). Also intensity of biotic interactions can be expected to change over succession, both in response to changes in community composition and as a result of responses to population densities (e.g. Fagan and Bishop 2000, Crist et al. 2006). One interaction that may be density dependent is the one between plants and specialist seed predators. Such interactions could either dampen or accelerate effects of forest succession on individual field layer species.

Taken together, this suggests that environmental change over forest succession is an important mechanism of changes in field-layer composition.

Phenology: a result of past and present environment

Yearly timing of development in plants can be part of optimal strategies that depend on the environment. For example, in deciduous forests many plants benefit from taking advantage of the time period between thawing and the development of the tree canopy (Schemske et al. 1978). Therefore, species adapted to this environment should be expected to start vegetative development early in the season. Flowering may occur early in plants adapted to deciduous forests as a result of a correlation with vegetative phenology (Diggle 1999), or if also pollination is affected by tree leaf development (Heinrich 1976). Moreover, yearly plant development is often initiated by environmental cues (e.g. Diekmann 1996), and it may be dependent on plant resource state (Wang 1960). These proximate causes entail that phenology may be influenced by recent variation in environmental factors.

The most studied aspect of plant phenology is flowering time (e.g. Rathcke and Lacey 1985). Flowering time can affect plant fitness (e.g. Schemske et al. 1978, Marquis 1988, Mahoro 2002), and temporal variation in availability of pollinators, seed dispersers, and herbivores may impose strong selection on flowering phenology (Augspurger 1981, Evans et al. 1989, Brody 1997, but see Ollerton and Lack 1992). Abiotic environmental factors shown to influence flowering time include temperature, photoperiod, and moisture (Rathcke and Lacey 1985). However, relatively little is known of the role of other environmental factors, such as soil properties (Schnelle 1955). Detailed understanding of environmental effects on phenology is particularly important for models predicting consequences of climate change, because changes in plant phenology can have large ecosystem consequences due to other organisms' dependency on plants (Fitter and Fitter 2002).

Demography in relation to the environment

Knowledge of how environmental factors affect a given trait, such as the effect of light availability on flowering time, is not sufficient to answer questions regarding population-level consequences of changes in this factor. To understand the overall importance of an environmental factor for population growth, both its effect on other traits and the overall importance of all affected traits to population growth rate have to be assessed. This assessment can be performed using demographic models explicitly incorporating environmental factors. Such models are needed because effects of abiotic and biotic environmental factors on population dynamics are poorly known.

Several studies have analyzed effects of biotic interactions on population growth rates and found results suggesting that herbivores can restrict plant distributions, although the generality of this is still questioned (Maron and Crone 2006, Kolb et al. 2007). Regarding abiotic factors, results from studies

specifying different matrix models for different environments suggest that they can have substantial effects on population dynamics (e.g. Gotelli and Ellison 2002, Colling and Matthies 2006). However, abiotic interactions have rarely been explicitly incorporated in demographic models, and to my knowledge, no demographic models have been published that incorporate both biotic and abiotic factors, enabling assessment of their relative effects.

The possibility of analysis of environmental effects on population dynamics has been greatly enhanced by methodological advances ever since the seminal paper by Leslie (1945). Leslie introduced the technique of using matrix algebra to model dynamics of age structured populations. Since then, techniques of modeling structured populations have grown to encompass stage and size structured populations, and the incorporation of stochastic effects in the models (Lefkovitch 1965, Caswell 2001). Sensitivity analyses can be used to investigate effects of single or groups of class transitions on population properties, such as growth rate (e.g. De Kroon et al. 1986). The idea behind matrix modeling is to convert a life cycle graph into algebra. The matrix in the model describes all possible transitions between life cycle stages, or classes. The transitions are composed of survival and growth probabilities, and average reproductive outputs of the different classes. A typical matrix model can be expressed as

$$\mathbf{n}(t + 1) = \mathbf{A} \mathbf{n}(t),$$

where \mathbf{n} represents the population vector containing population densities in each class the population is divided into. \mathbf{A} is the transition matrix.

In recent years, integral projection models (IPMs) have been introduced to ecologists (Easterling et al. 2000). IPMs resemble matrix models, but have the advantage of being able to incorporate continuous state variables. As a consequence, IPMs do not require a division of populations into arbitrary classes in the cases where no obvious class divisions exist. Continuous projection kernels replace matrices, and density functions are used instead of population vectors. A typical integral projection model can be expressed as

$$n(y, t + 1) = \int_L^U F(x, y) P(x, y) n(x, t) dx,$$

where x is state year t , y is state year $t + 1$, n is the population density function and L and U describe the range of possible states. Probability density functions of fecundity, $F(x, y)$, and state transition, $P(x, y)$, constitute the kernel.

For plants, where size is typically a better predictor variable than age, integral projection models are more realistic than classic matrix models. It has also been found that although population growth rates calculated by matrix models are similar to those produced by IPMs, sensitivity and elasticity values are dependent on the number of classes in the matrix models (Easterling

et al. 2000). Another advantage of IPMs is that it is possible to directly incorporate regression models into the kernel, making parameterization easier and the connection with statistical tests more direct. The use of regression models for parameterization also entails that fewer observations are needed, facilitating incorporation of several state variables in the same model (Ellner and Rees 2006). The incorporation of multiple variables in structured population models creates an opportunity to further increase their use in ecological research. For example, environmental factors, as well as changes in these factors over time, may be included explicitly in the models.

Population models are also of fundamental importance in a conservation context due to their use in population viability analysis (PVA). PVA encompasses “a broad suite of population modeling and data-fitting methods for assessing extinction risk and guiding the management of rare and threatened species” (Morris and Doak 2002). Many PVAs have been based on matrix projection models. Matrix models can be used to answer such questions as what the risk of extinction is over a given time period, and the most important life cycle transitions of populations can be determined using sensitivity analyses. The same questions can be answered, but with greater accuracy, using IPMs. PVAs to date have focused on environmental and demographic stochasticity as causes of decline and extinction of populations (Menges 2000, Morris and Doak 2002). However, extinctions may also commonly be the result of deterministic changes of the environment, e.g. succession (e.g. Menges 1990, Lehtilä et al. 2006). Demographic models including changing environmental factors could be used to analyze such processes. In addition, the inclusion of environmental factors in the models makes PVAs more mechanistic and useful for guiding management. Thus, apart from putting studies of population dynamics in more realistic contexts, models incorporating environmental factors can be used to enhance accuracy of population viability analysis.

Data mining and cause-and-effect

Relatively simple statistical models are in many cases sufficient for testing predictions of ecological hypotheses. The difficulty instead often lies in the formulation of experiments (cf. Ruxton and Colegrave 2003). However, in this thesis I investigate which out of several candidate environmental factors affect populations, and study these effects. Thus, the thesis does not deal with many clear-cut, testable hypotheses, or true experiments. Rather, I have employed statistical models for the sake of data mining and made inferences based on the assumption that the best-fitting models, e.g. with the highest likelihood values, are the most probable. Although sometimes met with doubt, I believe these types of study will to an increasingly greater extent, contribute to the field of ecology. Data mining procedures can be valuable to generate hypotheses when much data is available. For example, statistical

tests of correlations can be used for variable selection, if used with the understanding that conclusions about causal relationships can not always be drawn solely on these results. However, as Shipley (2002) states, correlation does in fact imply causation at some stage. Disregarding mere chance, two correlated variables must be causally connected, either directly or indirectly through other variables (e.g. they share a common “causal ancestor”). In accordance, statistical procedures capable of answering questions about causality utilizing observational data, such as structural equation modeling (SEM) and the closely related Bayesian networks, are now available.

A classical SEM is constituted by a structural part describing causal connections between unmeasurable latent variables, and a measurement model that is made up of measurable indicator variables of the latent variables. Path analysis can be viewed as a special case of structural equation modeling, with only a structural model of measured variables (Grace 2006). Through theoretical and software development, most notably in the Tetrad project, the use of SEMs has evolved from being only hypothesis testing (Spirtes et al. 2005). In the Tetrad software, SEMs are the outcome of search algorithms that decide causality between factors given their correlations along with correlations and causal connections with other factors. The theory behind this is referred to as d-separation (Shipley 2002). Although there are no search algorithms for this in Tetrad as of yet, structural equation models can even provide estimations of models including “non-recursive” interactions such as circular causality (e.g. the “chicken and egg” dilemma) (Kline 1998). In my view, the use of advanced data mining techniques, such as the search functions in Tetrad, will further the understanding of nature through their use in many areas of science.

Methods

Study species

The main study species in this thesis was *Actaea spicata*. Paper I was based on inventories of *A. spicata* and 45 additional field-layer species in a deciduous forest. The species included in paper I were chosen by Måns Ryberg (1971) with the intent to cover as wide a gradient of ecological strategies as possible. Most species are typical of forests and all are iterocarpic except *Cardamine impatiens*, *Geranium robertianum*, and *Lapsana communis* (Mossberg & Stenberg 2003).

Baneberry (*Actaea spicata* L. Ranunculaceae) is distributed over most of Europe and parts of Asia (Germplasm Resources Information Network, <http://www.ars-grin.gov/>). In northern Europe it occurs in shady, well-drained habitats in rich deciduous and mixed deciduous and coniferous forests, often on limestone (Pellmyr 1984). Accordingly, in paper I *Actaea spicata* was found to increase sharply in abundance over succession from open land to forest, and to have a relatively high SLA value. The estimated mean life span of individuals surviving to reproduction is 20.2 yr (J. Ehrlén and J.P. Dahlgren, unpublished data). The growth form is typical for an early summer flowering forest herb, i.e. it has a greater height than spring ephemerals and has an umbrella-like leaf structure (cf. Givnish 1987). In the study area, aerial parts usually become visible in the beginning of May. Vegetative growth stops and flowering starts around three weeks after shoot emergence. Individuals usually produce one or two, but sometimes up to five shoots in the study area. Single shoots sometimes produce up to four inflorescences (Eriksson 1995), each having 1-30 white flowers. The fruit is a black berry, usually containing 8-16 seeds, that matures in August (von Zeipel 2007). Vegetative propagation has never been recorded, and new individuals originate from seeds (J. P. Dahlgren, unpublished data). *Actaea spicata* seeds germinate producing a radicle, usually one year after release, while cotyledons emerge one year after germination (Ehrlén and Eriksson 2000; Fröborg and Eriksson 2003).

In the study area, the most conspicuous biotic interaction for *Actaea spicata* is the one with the specialist pre-dispersal seed predator, *Eupithecia immundata* (Geometridae). Observed predation rates in patches in the study area range from 0 to 100% of fruits in primary infructescences (von Zeipel

2007). Oviposition occurs during a short period from mid-June to early July, almost exclusively affecting primary infructescences (Eriksson 1995). Typically, one larva is developed per fruit. After consuming most of the seeds, the larva eats its way out in mid-July to August, leaving an exit hole. Seed predation intensity is curvilinearly related to host plant population size, with medium sized populations experiencing the highest predation rates (von Zeipel 2007). The entire plant is toxic and the only other known herbivores are the specialized *Eupithecia actaeata* feeding on the leaves late in the season, generalist rodents feeding on dispersed seeds, and molluscs feeding on seedlings (J. Ehrlén and J.P. Dahlgren, personal observation, Fröborg 2001). Potential pollinators include several insect orders, but most reported visitors belong to Coleoptera and Diptera (Pellmyr 1984). *Actaea spicata* is either self-incompatible, but facultatively apomictic, or able to self-pollinate, in either case leading to close to 100% seed set (Pellmyr 1984; Eriksson 1995).

Study area

All field studies were conducted in Tullgarn natural reserve in SE Sweden, 45 km SSW of Stockholm (58°6' N, 17 °4' E). The forests range from pure deciduous stands to coniferous stands dominated by Norway spruce (*Picea abies*). Forest patches are interspersed with agricultural land and contain, for the area, high amounts of deciduous tree species. Historically the majority of the forest patches, including Näset peninsula – the study site in paper I, were used as wooded meadows, containing many deciduous tree species valuable for agriculture (Ryberg 1971). After abandonment forest succession has entailed that most parts of the forests are now dominated by spruce. Grazing at Näset peninsula ceased in 1945.

Data collection and analysis

Species abundance changes over forest succession (Paper I)

The aim in paper I was to determine how forest succession affects abundances of field layer species, and to investigate what species traits are connected with abundance changes over time. The study was based on inventories of species frequencies in the deciduous forest at Näset peninsula. Permanent plots were established in 1961 by Måns Ryberg (1971), and the presence of 46 vascular plant species was recorded then and in 1970. We reinventoried these plots in 2003 and abundance changes were calculated for species included in the first inventories, as differences in the natural logarithm of number of occupied plots. In 2004, we collected leaf samples as well as literature and herbarium information in order to assign functional trait values and measures of habitat preference to each species. The traits considered were SLA (specific leaf area: leaf area to mass ratio), seed mass,

height, and flowering phenology in terms of start date, length and end of the flowering period. The measures of habitat preference were a four-graded scale of increasing forest preference based on a local flora (Mossberg and Stenberg 2003), and the Ellenberg indicator values of light, nitrogen, moisture and calcium (Ellenberg et al. 1992). Regression analyses were performed to assess the association of abundance change with functional traits and habitat preference measures.

The environment and phenology of Actaea spicata (Paper II)

Papers II–IV were based on data from four patches of *Actaea spicata* that were censused from 2004 and onwards. The aim of paper II was to unravel how the local environment affects vegetative and flowering phenology of *Actaea spicata*. In 2004, five to seven 5 m × 5 m plots were laid out (25 plots in total), and two hundred established individuals were marked per patch. Environmental factors were measured in 2004 or in 2005. Seven environmental factors were measured at the location of each individual: slope, soil depth, litter depth, interspecific density, intraspecific density, May canopy openness, and July canopy openness. Nine additional environmental factors were measured in each plot quadrant: soil temperature, soil water content, soil pH, and soil concentrations of calcium, potassium, magnesium, phosphorus, carbon, and nitrogen. A unique value of the latter factors were assigned to each individual based on the weighted distance to the center of each plot quadrant. In 2005, vegetative and flowering phenology were measured for each individual, in terms of timing of shoot emergence and start of flowering, respectively. Shoot emergence was defined as the ratio of height May 6th over the height of the fully developed shoot. Flowering time was defined as the Julian day when 50% of the flowers of the first inflorescences had started flowering.

Statistical analyses were performed on both individual and plot levels to assess effects of the environment on shoot emergence and flowering time. Simple regressions were used in a first step to exclude uncorrelated variables. Out of the retained variables, multiple regression analyses with all combinations of predictor variables were formulated, and the models with the lowest AIC (Akaike's An Information Criterion) were chosen as the optimal models. Since some environmental variables for individuals were interpolations and thus not independent observations, tests of statistical significance were carried out by performing the same analyses using data from plot quadrants. Finally, structural equation models (SEM) were used to test path models of environmental effects on phenology, in order to include indirect effects on flowering phenology through vegetative phenology. In paper II, SEMs were formulated in accordance with the regression analyses. When preparing this summary I used the latest version of the software Tetrad IV (Spirtes et al. 2005) to search for the most plausible causal connections between variables based on their covariances. I included only the variables

retained after the first model building step, above. The resulting path models were the same as the ones in paper II.

Demography of Actaea spicata in relation to the environment (Paper III)

The aim of paper III was to estimate effects of local environmental factors on survival, individual growth and reproduction of *A. spicata*, and to model the resulting effect on population growth rate. In 2004-2007, detailed demographic data was collected for all individuals included in the plots used in paper II. Presence, shoot diameters, plant height, and total fruit number were recorded for all individuals each year in June-July. Size was defined as the natural logarithm of the sum of squared shoot diameters multiplied by plant height. Individual growth was defined as the difference of the size measure between years. An individual was considered dead if it was missing at two consecutive censuses. Fruit predation was recorded each year as number of fruits with exit holes from larvae. Fecundity was calculated by multiplying fruit number, that was counted each year, with seed number per fruit. Seed number per fruit was determined separately for preyed and non-preyed fruits in 2005. All seedlings were counted as they emerged, and up to 50 marked per site and year. Each surviving seedling was marked the following year. Pre-dispersal seed predation and ten of the environmental factors described above were used to characterize the environment of individuals. The environmental factors were: canopy cover before and after tree leafing, soil concentrations of phosphorus and potassium, soil temperature, soil depth, soil water content, ground slope, inter- and intraspecific density.

In order to assess effects of the environment on the demography of *Actaea spicata*, we carried out analyses in two steps. First, we determined how properties of the local environment influence the plant vital rates; survival, growth, and fertility (divided into probability of flowering, number of fruits per flowering individual, and number of seeds per fruit). For this we used a model selection procedure analogous to the one in paper II. Growth, fruit number and seed number were modeled with linear regressions, and survival and flowering probabilities were modeled with logistic regressions.

As a second step, we incorporated the effects of soil potassium concentration on individual growth and pre-dispersal seed predation on seed number, which were the two aspects of the environment identified as the most important in the first step, into size structured integral projection models. We then estimated population growth rates in environments corresponding to different levels of these two environmental variables. The code used for the computer implementation of the model was based on the one provided in Ellner and Rees (2006). Our model was formulated as the following three coupled equations (cf. Rees et al. 2006):

$$n(y, z, t + 1) = p_s p_d(y) S_2(t) + \int_L^U s(x) g(y, x, z) n(x, z, t) dx; \quad (1)$$

$$S_2(t + 1) = p_e S_1(t); \quad (2)$$

$$S_1(t + 1) = L \int_L^U p_f(x) f_n(x) f_s n(x, t) dx, \quad (3)$$

where n is a distribution function describing the adult population, S_2 is the number of seedlings, and S_1 is the number of seeds. x is size year t and y is size year $t + 1$. L and U are minimum and maximum possible sizes, respectively. In (1), p_s is seedling survival probability, $p_d(y)$ is the size distribution of surviving seedlings, $s(x)$ is the survival function, and $g(y, x, z)$ is the normal probability density function of growth, dependent on size and potassium concentration, z . In (2), p_e is the probability of seed survival and seedling establishment. In (3), $p_f(x)$ is the probability of flowering, $f_n(x)$ is number of fruits produced, and f_s is the number of seeds per fruit after pre-dispersal seed predation, given by

$$f_s = m_{pred} p_{pred} + m_{int}(1 - p_{pred}), \quad (4)$$

where p_{pred} is proportion of fruits attacked by seed predators, m_{pred} is mean number of intact seeds in attacked fruits, and m_{int} is mean seed number in intact fruits.

Demography of Actaea spicata over forest succession (Paper IV)

In paper IV we asked how the local environment changes over forest succession and what effect this has on population growth of *A. spicata*. In 2008, we measured soil potassium concentration and deciduous tree proportion at one hundred sites in the study area. Soil potassium was measured with the AL extraction method on a pooled sample of nine field samples per site. Deciduous tree proportion was defined as ratio of deciduous to spruce tree basal areas and was estimated visually. Four of the sites were the *Actaea spicata* patches used to parameterize the demographic model. In addition, 96 sites in a 3 km \times 4.5 km area containing these four patches were sampled. We used the data from these 100 sites as a chronosequence to determine how soil potassium changes during the succession from deciduous to spruce forest in the study area. We included temporal change in potassium in an integral projection model analogous to the one used in paper III, with the exception that we had one more year of demographic data (the 2006-2007 interval could be included because deaths could be confirmed in 2008). We also included environmental stochasticity by randomly drawing a projection kernel each simulated year. We modeled population growth in a scenario where succession from deciduous to spruce forest took 120 years, and soil potassium changed with the rate of spruce increase. In addition, we specified the model without seed predation to study its effect, and we incorporated a curvilinear relationship between plant population size and seed predation (von Zeipel

2007), in order to study how a density dependent biotic factor can modify effects of deterministic change in an abiotic factor on population dynamics.

Unless stated, all statistical analyses and demographic models presented in this thesis were run in the free software R, versions 2.2.1-2.7.2 (R Development Core Team, 2007).

Results and discussion

Paper I - Species abundance changes over forest succession

Species with larger abundance increases over the 42 years of forest succession had larger specific leaf areas (SLA) (Fig. 2). This result is in accordance with the hypothesis that species with larger thinner leaves are more shade tolerant. The result illustrates that easily measured plant traits can be used to predict responses to environmental change. Correlations of Ellenberg light indicator value with both abundance change and SLA support the hypothesis that a decrease in light availability over succession favors high-SLA species. In contrast to earlier studies, finding high seed masses to be advantageous in the forests field layer, there was a weak negative correlation between abundance change and seed mass. The fact that SLA, but not seed mass, was a good predictor of herb species response to forest succession suggests that interactions during the established life-cycle phase are more important than interactions during the recruitment phase.

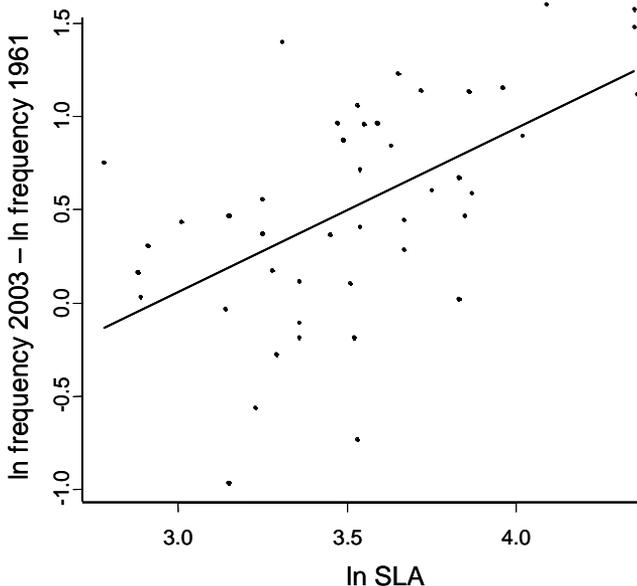


Figure 2. Relationship between specific leaf area (SLA) and abundance change of 45 herb layer species over 42 years of forest succession.

Abundance change was not significantly correlated with plant height or start, peak and length of the flowering period. The lack of effect of plant height suggests that competition for light among field layer plants is less important for forest floor herbs than other factors. This is probably due to the low density of forest herbs under the closed tree canopy. To maximize light uptake, other traits are probably more important, e.g. SLA. The fact that there was no consistent effect of plant height and seed mass on abundance change also suggests that a trade-off between ruderal and competitor strategies is not relevant in this system. The lack of relationship between flowering phenology and changes in abundance was in contrast to our predictions, assuming that typical deciduous forest species have adapted their phenology to take advantage of the available light before the development of the tree canopy. There can be several explanations for this, but it may simply be that other traits are more important than phenology.

Paper II - The environment and phenology of *Actaea spicata*

The results support the view that flowering time of temperate forest herbs is constrained by several environmental factors acting indirectly through effects on shoot emergence time. Among plots, soil temperature and canopy cover explained 63% of the variation in shoot emergence, while soil temperature, slope and canopy cover together explained 83% of the variation in flowering time. Within plots, small plants on steep south facing slopes with high soil potassium concentrations emerged earlier in the year, and individuals that emerged earlier flowered earlier (Fig. 3). These results support earlier findings that temperature is the most important environmental cue for flowering. This is particularly true because we expect the slope parameter, which is a combination of inclination and "southwardness" of the slope of the ground, to also convey mainly temperature differences. The results also show that factors other temperature, photoperiod, and moisture affect flowering phenology. The indirect effect of individual environment on flowering time through shoot emergence indicates that evolutionary explanations of flowering phenology must include also selection acting on vegetative phenology. Still, only around 10% of the variation in flowering time within plots was explained by vegetative phenology on the within-plot level, suggesting that differences in genetics, individual history, or unmeasured small-scale environmental heterogeneity also influence flowering time. We conclude that soil nutrients affecting plant phenology are potential and largely overlooked sources of spatial heterogeneity in plant–animal interactions, and that effects of soil nutrients should be taken into account in detailed studies, e.g. of effects of climate change, on phenology.

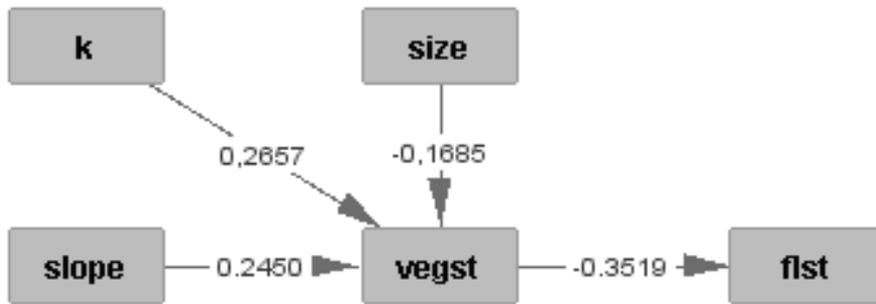


Figure 3. Path model of effects of environmental factors on vegetative and flowering phenology. Output from Tetrad 4.3.9. Values are SEM estimates. *Note: k = soil potassium concentration, size = plant size, slope = inclination and 'southwardness' of the slope of the ground, vegst = start of vegetative development (ratio of height 6 May to height of the fully developed plant), flst = Julian date at start of flowering*

Paper III - Demography of *Actaea spicata* in relation to the environment

Soil potassium was positively correlated with individual growth of *Actaea spicata* and pre-dispersal seed predation reduced seed production considerably. At the population level, realistic changes in either of these two factors could reverse population growth rate from positive to negative (Fig. 4). The correlation with potassium is particularly interesting since the connection between abiotic environmental factors and population dynamics is a “missing link” in ecology. The effect of seed predation on population growth rate in conjunction with an apparent lack of compensating mechanisms suggest that plant population growth rate, and therefore habitat range, can be restricted by seed predators.

To my knowledge, this demographic study is the first that has incorporated both an abiotic and a biotic interaction. Overall the results suggest that abiotic interactions may be more important than biotic interactions for population growth rate in the study system, because seed predation is likely the most important biotic interaction for *Actaea spicata* (see Study species). The smaller relative effect of potassium on individual growth had a larger effect on population growth rate than the larger relative effect of seed predation on seed number. This result stresses the need to integrate information about environmental effects on fitness components with information about species life histories when assessing environmental effects on populations.

In a spatial context, models including environmental factors can be used in combination with presence-absence based habitat range models to delimit suitable habitats for a species. Such models could also be used in population viability analyses, in particular when there are strong reasons to suspect particular environmental factors to have large effects. Additional studies incor-

porating demographic approaches such as this one would help establish the links between environmental variation and dynamics of populations and communities.

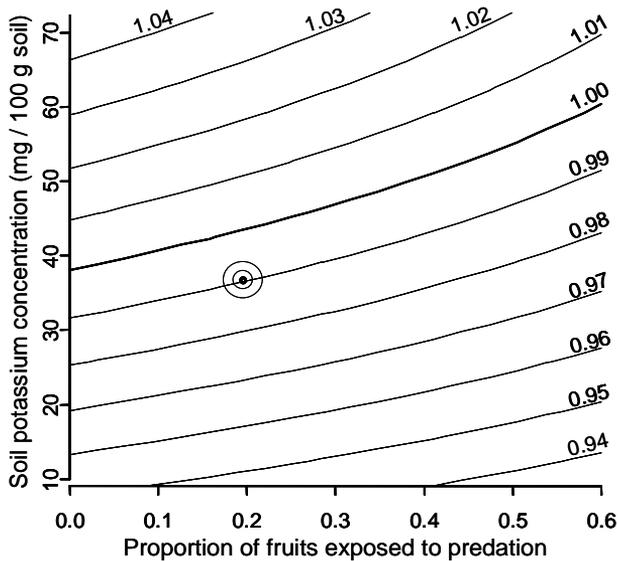


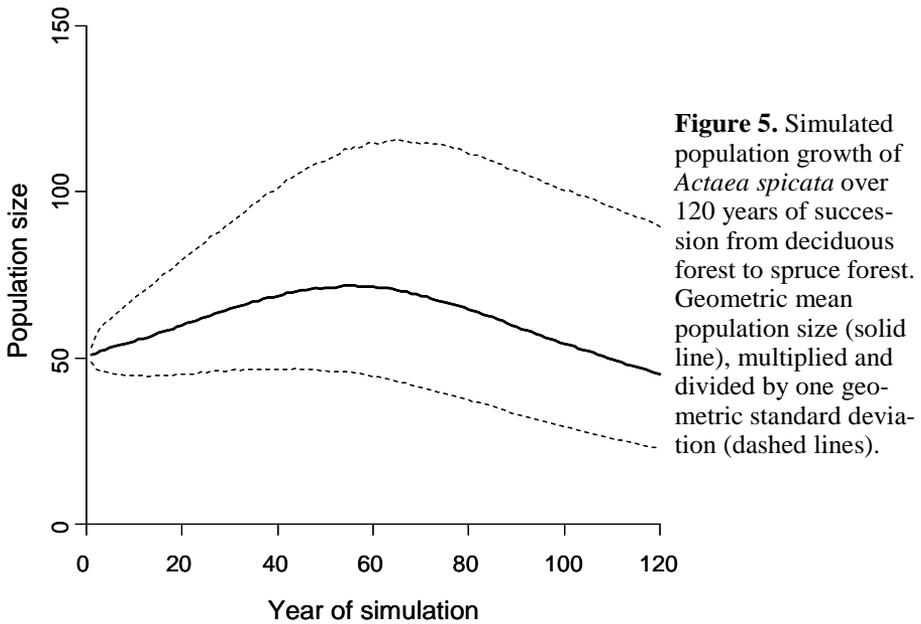
Figure 4. Population growth rate of *Actaea spicata* as a function of soil potassium concentration and seed predation intensity. The observed mean growth rate of two transition intervals is marked.

Paper IV - Demography of *Actaea spicata* over forest succession

In the integral projection models, temporal changes in the deterministic extrinsic factor soil potassium, and the plant population-size dependent intrinsic factor seed predation, both affected *Actaea spicata* population growth over forest succession. Soil potassium concentration increased with increasing proportion of deciduous trees in the studied forest patches. Thus, a potassium decrease over succession from deciduous to spruce forest was incorporated in the model. Average simulated *Actaea spicata* populations increased until 51% of trees were spruce (Fig. 5). After that a decrease in size followed, as a result of the decrease in soil potassium. Stochastic population growth rate changed from 1.01 to 0.99 over succession. This result suggests that a decrease in soil potassium concentration during succession constitutes one reason why *A. spicata* is rarely found in forests where deciduous trees have completely given way to spruce.

The results of the simulations also suggest that seed predation modifies the effect of changing soil potassium concentration over succession. Excluding seed predation in the model resulted in growth rates that never decreased to below unity. In contrast, plant population size dependent changes in seed predation had only a limited effect on population trajectories. Because of the curvilinear relationship between population size and seed predation, the di-

rection of the effect depended on the initial population size in the model. For small initial populations, incorporating dynamic seed predation resulted in final population sizes being lowered by 6%. For large initial populations, the negative effect of plant population size on seed predation intensity slightly ameliorated the negative effect of decreasing soil potassium on population growth, and final population sizes were 9% larger than in models with constant predation.



The results in paper IV show how population trajectories over time can be substantially altered by incorporating realistic environmental change into demographic models. The results also show that a relatively small change in a factor that has a relatively small effect on individual performance, may influence patterns of species occupancy along a successional gradient. Including deterministic, as opposed to stochastic, environmental change in demographic models is ideal for studying effects on populations of processes such as succession, eutrophication, altered land-use and climate change on population dynamics. Such models should also prove useful in population viability analyses, since many threatened species occur in changing environments.

Conclusions

The main results of the four papers included in the thesis point to these conclusions: (I) Field layer species are affected by forest succession in accordance with their functional traits. (II) Soil nutrients affect vegetative and flowering phenology, showing that a wide range of environmental factors, including previously overlooked factors, can influence traits related to plant fitness. (III) Local environmental factors affecting vital rates have substantial effects on plant population dynamics. Abiotic factors may sometimes be the most important and need to be incorporated in realistic demographic models along with biotic interactions. Finally, (IV) environmental factors affecting vital rates of field layer plants change as a result of forest succession. This alters population growth rates and thereby causes abundance changes in field layer plants over time. In addition, the methods of population modeling presented in papers III and IV can be useful in population viability analyses (PVA). The results in the thesis suggest that the explicit incorporation of environmental factors, and changes in these factors over time, can substantially alter predictions of PVAs.

I suggest that environmental conditions should to a greater extent be incorporated into models of population and community dynamics. In many cases “environmental effects” are indirectly measured as between year or between site differences. Indeed, this is what I did in paper I. However, if the links between environment and population dynamics are to be established, the explicit inclusion of environmental factors is needed. Naturally, it is often difficult to know beforehand what factors are important. In this case, applying data mining procedures such as the model selection procedures used here is a useful approach.

An interesting conclusion from this thesis is that relatively small environmental effects on individuals can have large population level consequences. If such effects are common, then their seemingly limited importance in studies not estimating effects on entire populations may be one reason why niches have seemed so elusive *in vivo*. Density dependent relationships, such as the one between seed predation and plant population growth shown here, may be another reason. More detailed demographic studies are needed to firmly establish the links connecting population and community dynamics with environmental variation. The incorporation of density dependent models of resource use would also take us further towards this aim. In addition, due to the ease of including more than one state variable in

population projection models, models with more measures of individual vitality or quality than only size or age are plausible and useful. Moreover, linking vital rates to individual traits is necessary in order to develop more mechanistic models. For example, it would be useful to see how (and if) reproductive phenology affects fecundity, possibly at the expense of other vital rates.

In conclusion, linking environmental variation to population dynamics can contribute to answering some of the fundamental questions in ecology.

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Sammanfattning

Avhandlingen bygger på fyra studier av hur miljön och dess förändringar över tid påverkar populationer av växter. Fastställandet av länken mellan miljöfaktorer och populationsdynamik är nödvändigt för att kunna förstå hur miljön påverkar arters populationsstorlekar och utbredningar, d.v.s. för att svara på en av kärnfrågorna inom ekologin. Det finns flera angreppsvinklar eller perspektiv när det gäller att studera den här länken och i avhandlingen studerar jag frågan på tre huvudsakliga sätt; (i artikel I) genom att jämföra förändringar i populationer av arter i samma miljö men med olika egenskaper, (i artikel II) genom att studera hur miljön påverkar en viss egenskap, fenologi, och (i artiklar III & IV) genom att länka miljön till demografiska processer och populationstillväxttakt.

I den första artikeln undersöker jag hur skogssuccession, d.v.s. förändringar i trädfloran över tid, påverkar växter som växer på marken, i fältskiktet. Jag ställer frågan vilka egenskaper hos fältskiktsarter som bäst kan förklara förändringar i populationsstorlek över tid. Jag använder tidigare inventeringar av ett antal fältskiktsväxter i ädellövträdsskogen på Tullgarnsnäs i Södermanland för att se hur deras populationsstorlekar har förändrats över tid. Den första inventeringen utfördes 1961 när miljön fortfarande var att betrakta som en löväng. Sedan dess har området växt igen. I avhandlingen undersöker jag om det finns några statistiskt signifikanta korrelationer mellan förändringar i populationsstorlek och ett antal egenskaper hos växterna, nämligen ett mått på bladtjocklek (SLA), fröviktt, skotthöjd och blomningstid samt vad som tidigare är känt gällande i vilken miljö växterna återfinns. Jag kom fram till att SLA var den karaktär som bäst stämde överens med populationsstorleksförändringar och att arter med stora tunna blad (högt SLA) var de som ökade mest (se Figur 2). Jag drar slutsatsen att det här sambandet beror på att ljustillgången successivt har minskat i fältskiktet. Inga av de andra växtegenskaperna var signifikant korrelerade med populationsstorleksförändringar och detta är också ett intressant resultat. Framförallt fröviktt är en egenskap som tidigare ansetts viktig när det gäller ekologin hos skogsväxter och jag förväntade mig att arter med tyngre frön skulle öka mer än arter med lättare frön. Dessa resultat kan betyda att egenskaper hos etablerade växter är viktigare under skogssuccessionen och att egenskaper som påverkar reproduktiv framgång är mindre viktiga. Korrelationen med SLA är även intressant eftersom en så stor del av variationen i populationsstorleksförändring kunde förklaras av denna enkelt mätbara egenskap.

I den andra artikeln undersöker jag vilka miljöfaktorer som påverkar tiden på året då trolldruva (*Actaea spicata*) påbörjar sin vegetativa tillväxt och när blomningen sker. Det här gör jag genom att använda mätningar jag gjort i skogarna i Tullgarn av vegetativ- och blomningsfenologi (fenologi \approx läran om tidpunkten för olika återkommande fenomen i naturen) samt av miljöfaktorer invid samma individer. Genom att undersöka hur fenologin överensstämde med olika miljöfaktorer kunde jag styrka tidigare studier där man funnit att temperatur är den viktigaste bestämmande miljöfaktorn i klimat motsvarande det svenska. Jag kom dessutom fram till att flera miljöfaktorer påverkar vegetativ fenologi som i sin tur påverkar blomningsfenologi och att tidigare förbisedda miljöfaktorer, nämligen markens näringsinnehåll, verkade kunna påverka växters fenologi (se Figur 3). Att förstå vilka miljöfaktorer som påverkar växters fenologi är viktigt eftersom många djur är anpassade till växternas periodicitet och därför att denna kan komma att påverkas av framtida klimatförändringar.

I den tredje artikeln undersökte jag hur olika miljöfaktorer kan påverka växters populationsdynamik. Det här är något som inte studerats i stor utsträckning, men är nödvändigt för att förstå vad som styr arters utbredning. Under åren 2004 till 2008 följde jag samma fyra trolldruvepopulationer och varje år mättes alla individers storlek, överlevnad och fröproduktion. I den här artikeln använde jag dessutom de mätningar av miljöfaktorer som användes i den andra studien samt mått på andelen av frukter som blivit angripna av en fjärilslarv som äter trolldruvans frön. I avhandlingen korrelerar jag miljöfaktorer med individuell tillväxt, överlevnad och fröproduktion för att se vad som påverkar dessa faser i trolldruvans livscykel, som i sin tur bestämmer populationernas tillväxt. När jag kommit fram till vilka miljöfaktorer som är de viktigaste inkluderar jag dessa i en så kallad "integral projection model" (IPM). En IPM är en typ av strukturerad populationstillväxtmodell som jag använder för att särskilja individer med avseende på deras storlek och deras påverkan på populationens tillväxt. Resultaten visade att kaliumhalten i marken påverkade individers tillväxttakt och att fröpredationen hade stor påverkan på antalet frön som producerades (se Figur 4). Båda dessa faktorer påverkade dessutom populationstillväxttakten, men kaliumhalten hade en större effekt. Jag drar slutsatsen att genom att inkludera miljöfaktorer i populationstillväxtmodeller, som vi gjorde i artikeln, kan man både studera populationsdynamik i ett realistiskt sammanhang och dessutom kan denna metod bidra till mer pålitliga analyser av populationers tillstånd och utdöenderisk.

I artikel fyra undersökte jag hur miljöförändringar över tid kan påverka populationsdynamiken. Jag undersökte först hur kaliumhalten i marken förändras över det naturliga successionsförloppet när lövskog utvecklas till granskog. Sedan inkluderade jag kaliumförändringen över tid samt en dynamisk fröpredationsgrad som berodde på trolldruvepopulationens storlek i en IPM. Denna IPM inkluderade dessutom slumpmässiga skillnader i miljön

mellan år. Modelleringsresultaten visade att skillnaden i kalium som orsakas av skogssuccession gör att trolldruvepopulationer växer i tidig, men minskar i sen succession (se Figur 5). Förändringen i kalium kan därför vara en av anledningarna till att trolldruva vanligtvis inte återfinns i sena successionsstadier. Modellen visade också att effekten av fysiska miljöförändringar över tid till vis del kunde påverkas av växt-djur-interaktioner eftersom fröpredatorn kunde påverka effekten av minskat kalium. Det mest intressanta resultatet av artiklarna III och IV var att små effekter av miljöfaktorer på individnivå kan få stora konsekvenser på populationsnivån. Artikel IV är dessutom ett exempel på hur effekten av miljöförändringar kan inkorporeras i populationsmodeller.

Sammanfattningsvis visar avhandlingen hur länkar mellan miljö och populationsdynamik kan fastställas för att besvara grundläggande ekologiska frågor om arters utbredning.

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