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Pollinators, Enemies, Drought, and the Evolution of Reproductive Traits in *Primula farinosa*

PER TORÄNG



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Abstract

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In this thesis, I combined comparative and experimental approaches to examine selection on reproductive traits and population differentiation in the insect-pollinated, self-incompatible, perennial herb *Primula farinosa*. More specifically, I (1) determined whether the effects of floral display and interactions with pollinators and seed predators, and plant reproductive success were frequency-dependent and affected by surrounding vegetation context, (2) examined the consequences of intermittent drought years on population dynamics using numerical simulations based on demographic data collected over seven years, (3) analyzed among-population differentiation in flowering phenology and reproductive allocation, and its relationship to soil-depth at the site of origin.

A field experiment suggested that conspicuous plants facilitate inconspicuous plants in terms of pollinator attraction, and that the facilitation effect is contingent on the height of the surrounding vegetation. Further experiments revealed that both mutualistic and antagonistic interactions can result in frequency-dependent selection on floral display. Among inconspicuous plants, both fruit initiation, and damage from seed predators increased with the proportion of the conspicuous morph. The relative strength of these effects, and therefore their net outcome on the relationship between morph ratio and seed production varied among years.

I combined information on vital rates and their relation to environmental conditions in simulations to predict future population viability in changing environments. Simulated stochastic population growth rate decreased with increasing frequency of drought years.

Reproductive allocation varied significantly among populations both in the field and in a common-garden experiment, but was correlated with soil depth at the site of origin only in the field. The results suggest that among-population variation in reproductive effort in the field mainly reflects plastic responses to environmental conditions, and that this plasticity may be adaptive. The common-garden experiment suggested that the study populations have diverged genetically in flowering time.

Keywords: Alternative reproductive strategies, climate change, facilitation, floral display, flowering phenology, frequency-dependent selection, genetic diversity, life-history strategies, local adaptation, pollination, predation, *Primula farinosa*, reproductive effort, soil disturbance, stochastic growth rate

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List of Papers

This thesis is based on the four papers listed below. They will be referred to by their Roman numerals.

- I Toräng, P., J. Ehrlén, and J. Ågren. 2006. Facilitation in an insect pollinated herb with a floral display dimorphism. *Ecology* 87:2113-2117.
- II Toräng, P., J. Ehrlén, and J. Ågren. Mutualists and antagonists mediate frequency-dependent selection on floral display. (Submitted manuscript)
- III Toräng, P., J. Ehrlén, and J. Ågren. Linking climate data and demography to predict future population viability of a perennial herb. (Manuscript)
- IV Toräng, P., J. Ehrlén, and J. Ågren. Site quality and among-population differentiation in flowering phenology and reproductive allocation in the perennial herb *Primula farinosa*. (Manuscript)

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Introduction

The reproductive organs and breeding systems of angiosperms exhibit greater diversity than those of any other group of organisms (Barrett 2002, Harder and Barrett 2006). A central problem in evolutionary biology is therefore to understand factors responsible for the origins and maintenance of this floral variation (Barrett 2002). This requires an understanding of the genetic background governing the expression of reproductive traits such as flower morphology (Bradshaw et al. 1995, Bradshaw et al. 1998, Broadhvest et al. 2000, Kelly 2005), or flowering time (Johanson et al. 2000, El-Assal et al. 2001, Simpson & Dean 2002, Michaels et al. 2003) but also the ecological factors responsible for the maintenance of genetic and phenotypic variation in floral traits in natural populations (Endler 1986, Silvertown and Charlesworth 2001, Conner and Hartl 2004, Hedrick 2006). One way to identify processes contributing to the maintenance of genetic variation in reproductive traits is to study temporal and spatial variation in the relative importance of ecological factors influencing reproductive success and natural selection on reproductive traits (Kingsolver et al 2001, Morgan 2006)

This thesis recognizes that there is an important and dynamic interplay between ecology and evolution within communities (Johnson and Stinchcombe 2007). Today, the understanding of the function of plant reproductive traits is substantial, and the evolutionary background of floral traits has received considerable attention. However, plants live in a setting dictated in part by the characteristics of the focal inflorescence, the morphology of their neighbours, the local abiotic environment, and the behaviour of mutualists and antagonists. Placing plant reproduction in this broader community context requires functional analyses of the relationships between individual traits, and biotic and abiotic interactions.

Plant reproduction

In contrast to free moving animals, most plants are sessile, at least in their mature life stages. As a result, plants have an obvious disadvantage when it comes to sexual reproduction and require intricate means to transfer male gametes (i.e. pollen) between mates. The angiosperms have an extraordinary structure to accomplish this – the flower. Flowers often contain both female (stigma) and male (stamens) parts. In addition, they are usually characterized

by conspicuous appearance and scent. The rationale behind their prominent features is that most flowering plants exploit animals, especially insects, to transport pollen between mates (Sprengel 1793, Faegri and van der Pijl 1966, Barrett and Harder 1996, Dodd et al. 1999). Plants have evolved floral traits to attract and manipulate the behaviour of pollinators so that they will efficiently transport pollen between mates of the same plant species (Darwin 1862, Stebbins 1970, Bronstein et al. 2006). Plant-pollinator interactions have been of critical significance for the evolution and radiation of angiosperms and their associated insects (Crane et al. 1995, Grimaldi and Engel 2005). Today, angiosperms dominate the biomes in most parts of the world and the insects make up by far the most diverse group of animals. Indeed, species interactions are thought to be of paramount importance in many speciation events (Thompson 1994, Waser and Ollerton 2006).

However, unfortunately for the plants, flowers do not only attract pollinators. Conspicuous flowers may also increase the susceptibility to fungal infection and disease (Elmqvist et al. 1993, Giles et al. 2006), or catch the attention of enemies (Gomez 2003, Irwin 2003, Adler and Bronstein 2004, Irwin 2006, McCall and Irwin 2006, Ashman and Penet 2007). Examples include florivores, nectar thieves, herbivores, and seed predators. If the antagonists reduce reproductive success, survival or other fitness traits, and if damage is correlated with one or several floral traits, the plants will be subject to natural selection mediated by both mutualistic and antagonistic flower visitors. Evidence that non-pollinator agents influence the evolution of plant reproductive traits is mounting (Herrera et al. 2002, Strauss and Whittall 2006).

Even though the importance of complex community structures for our understanding of natural selection mediated by species interactions has long been acknowledged, empirical studies examining the ecological and evolutionary consequences of multiple-species interactions are still few (Thompson 1999, Strauss and Irwin 2004). Plant reproduction occurs in a community of conspecific and heterospecific plants, as well as a diverse fauna of mutualistic and antagonistic animals and fungi. Studies of plant-animal interactions that omit community context may misinterpret causes and consequences of selection on reproductive traits (Strauss and Irwin 2004).

Local environmental conditions, which collectively make up the ecological context, will influence natural selection and evolutionary trajectories. Spatial variation in selection may result in population differentiation in appearance, behaviour or life-history traits, local adaptation and eventually to reproductive isolation between closely related populations (Stebbins 1970, Schemske and Bradshaw 1999). To understand biological diversity we need to study natural selection and local adaptation.

Selection on floral display – effects mediated by mutualists and antagonists

Pollinators

Most outcrossing plants often depend on pollinators for their reproduction, and their floral characteristics are crucial for fitness. Flowers should be characterised by traits that maximize visitation rates by efficient pollinators or traits that maximize efficient pollen transfer by frequent visitors (Stebbins 1970, Fenster et al. 2004).

Visual floral display is important for the attraction of pollinators (Chittka and Thomson 2001), and is a function of the number, size, and arrangement of flowers. For example, pollinator visitation rates (Peakall and Handel 1993, Donnelly et al. 1998), and pollen deposition (O’Connell and Johnston 1998, Lortie and Aarssen 1999) have been found to be dependent on plant stature in several species.

The morphological fit between flowers and their pollinators influence pollination efficiency, and should thus be crucial for plant reproductive success (Nilsson 1988, Johnson and Steiner 1997, Whittall and Hodges 2007). Pollen must be effectively deposited on the pollinator’s body and transferred to stigmas of conspecifics. Therefore, it is expected that flower morphology is adapted to the local pollinator fauna (Thompson 1994, Aigner 2006). The pollinator fauna is however not constant, and selection on floral morphology may therefore vary in spatially structured populations.

Optimal flowering time should also be dependent on the activity of mutualists. Within the limits set by the growing season, flowering phenology may therefore be tuned to maximize exposure to pollinators (Stiles 1977, Sandring 2007).

Enemies

Enemies may damage flowers and other parts of plants, and influence plant fitness via direct or indirect pathways (Mothershead and Marquis 2000, Galen and Cuba 2001, Strauss et al. 2001, Herrera et al. 2002, Gomez 2003, Ashman and Penet 2007). Direct pathways include damage to reproductive parts, i.e. anthers, stamens, ovaries, and developing seeds, and indirect pathways include damage to plant parts important for the attractiveness to pollinators such as petals and nectaries, or to plant parts important for the production and maintenance of flowers and inflorescences, such as leaves and roots.

Reproductive strategies and traits that increase attractiveness to pollinators may at the same time increase the risk of predation and parasitism. Stature, the number, size, colour, and arrangements of flowers, and nectar production can influence the risk of predation (Galen & Cuba 2001, Adler & Bronstein 2004, Cariveau et al. 2004, Frey 2004, Strauss & Irwin 2004), and fungal parasitism (Collin et al. 2002, Giles et al. 2006). Hence, antagonists

may mediate selection for fewer, smaller, or inconspicuous flowers. Optimal flowering time may also be dependent on the activity of antagonists and tuned to minimize exposure to enemies (Brody 1997, O'Neil 1999, Pilson 2000).

Ecological context

Selection on floral traits occurs in a community context and depends on environmental features not linked to focal floral traits (Herrera 1993). For example, plant-animal interactions and selection on inflorescence height may depend on the surrounding vegetation height (Cunningham 1995, Toräng et al. 2006).

The ecological context in which plants interact with pollinators and enemies may vary in space and time. The relative intensity, and therefore the outcome of context-dependent intraspecific interactions, may vary between years and populations (Maad and Alexandersson 2004, Moeller and Geber 2005, Price et al. 2005, Irwin 2006, Hersch and Roy 2007). As a result, the costs and benefits of different reproductive traits may vary accordingly.

Alternative reproductive strategies

Alternative reproductive strategies can broadly be categorized as risky or safe. Risky strategies imply that the appearance or behaviour of individuals are associated with high potential reproductive success, but also that the risk and cost of confronting antagonists can be higher. Safe strategies on the other hand, imply that individuals are less likely to face antagonists, but also that the attraction of pollinators or mates is constrained. For example, Boots and Knell (2002) modelled coexistence of risky and safe strategies in the presence of sexually transmitted diseases.

In many animals, alternative male mating strategies have been identified based on differences in mating behaviour and morphology (Andersson 1994, Zuk and Kolluru 1998). Different strategies can be favoured in different habitats, or exist in evolutionary equilibrium where negative frequency-dependent selection mediates coexistence in polymorphic populations (Gross 1996). For example, Cade (1979) described genetic variation in male mating behaviour in the field cricket *Gryllus integer*. Some males attract females by calling, but run at the same time a risk to catch the attention of parasitic flies. Other males, called 'satellites', sit silent near 'callers' and try to interfere females approaching a 'caller' (Cade 1979).

Similar to safe strategies in animals, plants adopting a safe strategy can avoid costs associated with reproduction by being less attractive than plants adopting a risky strategy. For example, by producing a conspicuous inflorescence, plants can increase their attractiveness to pollinators and thereby also their potential reproductive success. An inconspicuous inflorescence may on

the other hand experience fewer attacks by enemies. Because the floral display influences mutualistic and antagonistic interactions associated with reproduction, conspicuous and inconspicuous inflorescences can be regarded as two alternative reproductive strategies. Analogous to satellite male field crickets that choose to interfere females close to calling males, plants with inconspicuous inflorescences can have their reproductive success enhanced in the presence of conspicuous neighbours. However, in contrast to animals, plants cannot choose their location.

Frequency-dependent selection

Not only the individual reproductive traits but also those of neighbours may influence reproductive success in focal plants. Neighbouring plants may either compete for, or facilitate each other, in terms pollinator services (Callaway 1995). Empirical studies have documented both negative (Chittka and Shürkens 2001, Brown et al. 2002) and positive (Thomson 1978, Lavery 1992, Alexandersson and Ågren 1996, Johnson et al. 2003, Moeller 2004) interspecific interactions. Studies of intraspecific interactions have often focused on effects of population size and density (Sih and Baltus 1987, Ågren 1996, Kunin 1997, Ehlers et al. 2002, Waites and Ågren 2004, Campbell and Husband 2007), or mating system (McCauley et al. 2000) on reproductive success, while studies considering phenotypic characteristics of neighbouring plants and population composition are scarce (but see Gigord et al. 2001 for an example of frequency-dependent selection on flower colour mediated by pollinators). However, both within and between species, tall conspicuous plants could act as beacons (Fægri and van der Pijl 1979) that attract pollinators and seed predators, and thus influence the reproductive success of shorter less conspicuous neighbours.

Theory predicts that both mutualistic and antagonistic interactions can result in frequency-dependent selection on traits affecting mating success (Gross 1996, Brockmann 2001). In a species dimorphic for a display trait, the probability that an inconspicuous morph is detected by an interactor can be expected to increase with the local frequency of the conspicuous morph. If the fitness of the inconspicuous morph is limited by the intensity of the mutualistic interaction, this may lead to negative frequency-dependent selection. On the other hand, if variation in fitness is mainly governed by an antagonistic interaction, this may result in positive frequency-dependent selection. Because the relative strength of mutualistic and antagonistic interactions may vary spatially and temporally, so may their joint effect on selection on display. However, empirical studies linking frequency-dependent selection and multispecies interactions are still few (Sinervo and Calsbeek 2006).

Life-history traits

Life history traits directly determine the reproduction and survival, and hence the fitness, of individuals. In general, life-history traits can be expected to vary among populations in a clinal fashion along latitudinal and altitudinal gradients because of associated variation in the length of the growing season (Kalisz & Wardle 1994, Li et al. 1998). Within the constraints set by climatic conditions, life-history traits subjected to selection mediated by both local abiotic conditions (e.g. soil characteristics), and biotic interactions (e.g. with pollinators) not related to latitudinal or altitudinal gradients, can be expected to vary among populations in a more mosaic fashion (Macnair 1993, Brody 1997, O'Neil 1999, Pilon 2000, Miller et al. 2006). Information on population differentiation in putatively adaptive traits may provide valuable insights into the mechanisms underlying population differentiation.

Population differentiation

Age or size at first reproduction and reproductive effort are key life-history traits in most organisms and strongly influence fitness (Stearns 1992). Iteroparous organisms are faced with a trade-off between the benefits of starting to reproduce early and the costs this may have in terms of reduced future survival and reproduction. Life-history theory predicts that a short juvenile period and high reproductive effort should be favoured in adverse or stochastic environments where adult life span is unpredictable and mortality age- and size-independent (Stearns & Koella 1986, Kozłowski & Wiegert 1987, Kozłowski 1992, Silvertown et al. 2001). In contrast, delayed reproduction and low reproductive effort should be favoured in more stable environments where mortality is age- or size-dependent. Both biotic and abiotic environmental factors have been shown to influence population differentiation of life-history traits in some other iteroparous species (Kalisz & Wardle 1994, Prati & Schmid 2000, Kittelson & Maron 2001, Pluess & Stöcklin 2005, Miller et al. 2006). For example, van Kleunen (2007) reported considerable population differentiation in life-history traits in *Mimulus guttatus* in relation to variation in water availability. Populations growing under temporarily wet conditions had an annual life cycle with high allocation to reproductive structures, whereas populations growing under permanently wet conditions had a perennial life cycle and lower allocation to reproduction. However, empirical data on among-population variation in age at first flowering and reproductive effort in iteroparous plants are still rare.

Global change and future population dynamics

Because of changes in the environment induced by human activities, many species are declining and risk going extinct. A main challenge facing ecologists is to identify the factors governing population dynamics and to develop methods to forecast the effect of environmental change on population viability. Many of the most serious threats to biodiversity are associated with directional change in environmental conditions. In recent years, the threat of global warming to rare species has become a growing concern (McCarty 2001). In spite of the important role of environmental change, traditional approaches to determine and predict population viability are applicable only to constant or stochastic environments. As a consequence, very few studies have predicted the effects of environmental change and global warming on populations of rare species.

In recent years, powerful tools have been developed to explore how temporal variability in environmental conditions affects vital rates and population dynamics (Tuljapurkar et al. 2003, Horvitz et al. 2005). They consider both the effects of disturbance and successional stage, and stochastic variation in vital rates within similar environmental states (Horvitz et al. 2005, Morris et al. 2006). For example, seed germination may vary among years both because of successional change and because of stochastic variation in environmental conditions.

By combining information about disturbance regime and rates of recovery after disturbance with data on the correlation between vital rates and environmental state, the effects of stochastic variation and directional change in environmental conditions can be explored by simulation models. This approach involves three steps: (1) Associations between environmental conditions and vital rates are documented through detailed demographic studies. (2) Historical information on among-year variation in environmental conditions, e.g. weather data is used to assess patterns of environmental variation over a larger period of time. (3) Population dynamics under current environmental conditions, and effects of future environmental variation, on population dynamics and viability are explored with simulations. Such analyses are particularly useful for asserting the effects of global change on future population dynamics and viability (Morris et al. 2006).

Aims of this thesis

The general objective of this thesis is to explore the ecological and evolutionary consequences of plant-animal interactions, and mechanisms by which biotic and abiotic agents influence population dynamics and differentiation in reproductive and life-history traits. I have studied the self-incompatible herb *Primula farinosa*, which is dimorphic for scape-length and occurs in a short-scaped and long-scaped morph.

I address the following questions:

1. Do interactions with mutualistic pollinators and antagonistic seed-predators depend on local scape-morph ratio? More specifically, do fruit initiation, seed set, and seed predation increase with the local relative frequency of the conspicuous long-scaped morph (I, II)? If so, do these effects depend on the height of the surrounding vegetation (I)?
2. Are the effects of local scape-morph ratio stronger in the inconspicuous short-scaped morph than in the conspicuous long-scaped morph, resulting in frequency-dependent selection on scape morph (II)?
3. How does the frequency of intermittent drought years influence population dynamics and the relative importance of survival, growth and regeneration for overall fitness of *P. farinosa* in different habitats (III)?
4. Does the length of the juvenile period, reproductive effort, or flowering phenology vary among populations or scape-morphs, and is among-population variation related to soil depth (IV)?

Material and Methods

Study species

The studies were performed on the perennial plant *Primula farinosa* L. (Primulaceae). It is a hermaphroditic, self-incompatible herb occurring throughout Europe (Hamblen and Dixon 2003). Flowering individuals typically produce a single inflorescence which develops from the leaf rosette. The flowers are arranged in an umbel. Like many other *Primula* species, it is distylous, i.e. flowers are either long-styled (pin morph) or short-styled (thrum morph). On the islands Öland and Gotland, off the southeast Swedish coast, it occurs as two distinct scape-morphs (Lagerberg 1948, Fig. 1).



Figure 1. The study plant *Primula farinosa*. To the left is the common conspicuous long-scaped morph, and to the right is the inconspicuous short-scaped morph, which is found on the islands Öland and Gotland.

Individual plants produce either a regular 2-25 cm long scape, with the flowers presented well above the soil surface, or a markedly thicker and striate 0-6 cm short scape, with the flowers presented very close to the ground. Because scape morph influences mutualistic and antagonistic interactions asso-

ciated with reproduction, the morphs can be regarded as two alternative reproductive strategies. The frequency of the short-scaped morph varies from 0 to 70 % among natural populations and even more among patches within populations (J. Ågren, J. Ehrlén, P. Toräng, and D. Vanhoenacker, unpublished data). Controlled crossings suggest that scape-morph is determined by a single locus with a dominant allele for short-scape (J. Ågren and J. Ehrlén, unpublished data). *P. farinosa* occurs in moist meadow vegetation on calcareous ground and its persistence at a given site is favoured by grazing (Sterner 1986, Lindborg and Ehrlén 2002). Flowering takes place in May. The fruit is a multi-seeded capsule, which matures in July. Seeds germinate early in the spring or remain dormant in the seed bank (unpublished data). Seedlings form a small leaf rosette in the first year.

Pollinators

In the study area, butterflies (especially *Pyrgus malvae*) and solitary bees (especially *Osmia bicolor*) are the main pollinators. Pollen limitation is higher in the short-scaped than in the long-scaped morph (Ehrlén et al. 2002, Ågren et al. 2006, Vanhoenacker et al. 2006), suggesting that pollinating insects locate and visit long-scaped plants more frequently than short-scaped plants. Differences in fruit initiation between the two morphs may however be dependent on surrounding vegetation height (Ehrlén et al. 2002, Toräng et al. 2006), so that both short- and long-scaped plants are easy to detect in low vegetation whereas in tall vegetation, short-scaped plants are more difficult to locate than long-scaped plants.

Enemies

Initiated fruits are often attacked by larvae of the small tortricid moth, *Fal-seuncaria ruficiliana*, and the entire inflorescence is sometimes eaten by domesticated grazers (cattle, sheep and horses). Flowers and fruits can furthermore be damaged by molluscs, or be infected by the smut fungus *Urocystis primulicola*. Long-scaped plants are more often attacked by the moth larvae than short-scaped plants, probably because they are easier to locate (Toräng et al. 2006). The relative intensity of interactions with enemies may also be dependent on vegetation height.

Study populations and site descriptions

Studies in natural populations were performed on the Baltic island Öland, off the Swedish southeast coast. All populations, except G, were located on the Great Alvar in the southern part of the island (Fig. 2). The Alvar areas are semi-natural calcareous grasslands characterised by shallow soils on sedimentary limestone bedrock and is very flat, which results in a mosaic of more or less permanent wetlands in a very dry matrix. *Primula farinosa* typi-

cally grow in distinct moist patches near temporal marshes or ponds. Growing conditions vary both spatially and temporally. Some populations are located on very thin soils which are usually flooded in early May but then become very dry later in the season. Vegetation is usually sparse and mainly restricted to rock fissures in a matrix of bare weathering soils. Disturbance is intense due to repeated flooding and drought, freezing and thawing. Other populations are located on somewhat deeper soils with a closed vegetation cover and an expected more stable water availability. Since the soil has a low capacity to keep water, there may be a high risk of drought damage in years with low precipitation and warm weather. Almost the entire region is grazed by cattle, sheep, or horses, although the intensity and timing of grazing differs between areas.

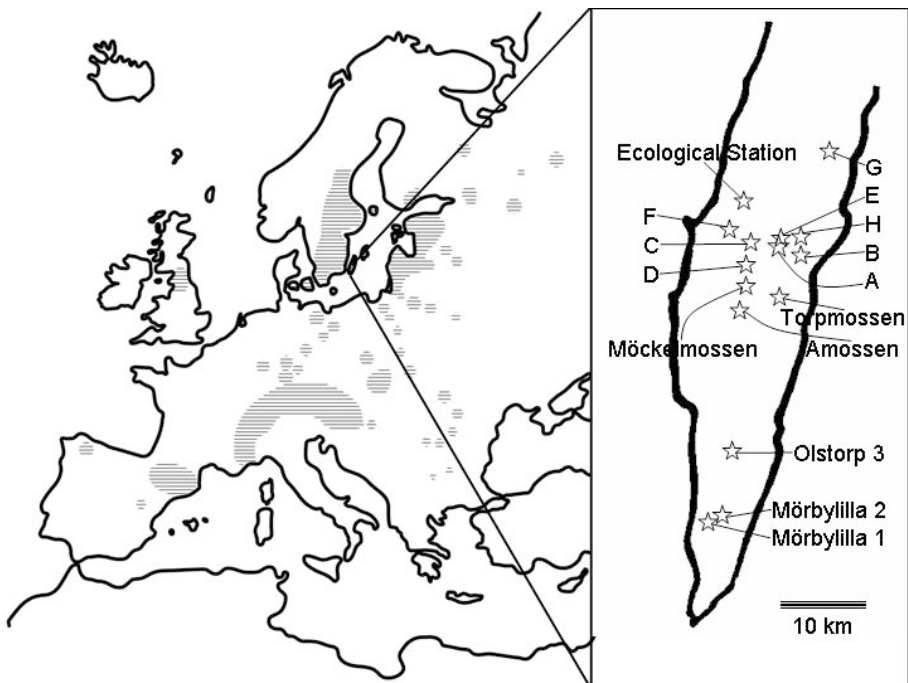


Figure 2. Distribution of *P. farinosa* in Europe. Southern Öland is enlarged and study populations and experimental sites are marked. Experiments were conducted at the Ecological Station (paper I), and in Amossen (paper II). Field surveys were conducted in the Möckelmossen, Torpmissen, Olstorp 3, Mörbylilla 1 and 2 populations (paper II), and in the A, C, and E populations (paper III). Populations A-G were examined in paper IV.

Studied traits

Morphological, phenological and life-history traits assumed to be important for plant fitness were studied in surveys of natural populations, in experimental arrays, and in a common-garden experiment. Measurements of scape-length and flower number were used to quantify floral display. Rosette area was used as a measure of vegetative size. First day of flowering was recorded to describe flowering phenology in the common garden experiment (IV). Age at first flowering was recorded in the demographic study (III) and in the common garden experiment (IV). Life span and vegetative propagation was recorded in the demographic study (III). Style-morph was noted in all studies. In mid-July, when fruits were almost fully developed, the entire inflorescence was harvested and brought to the laboratory for estimation of female reproductive success. For each plant, the number of mature fruits, the number of fruits damaged by seed predators, the number of ovules not initiated, and total seed production was recorded. In the demographic study (III), fruits were not collected and seed production was estimated as the number of mature, undamaged fruits multiplied by fifty, which corresponds to observed seed production per fruit in the field (personal observation).

Floral display and frequency-dependent selection (I, II)

To examine the effect of scape-morph ratio on fruit initiation, seed set, and seed predation, experimental arrays were established; each consisting of eight plants. The style-morph ratio was kept even among both short-scaped and long-scaped plants. Arrays were distributed randomly at nodes in a rectangular grid containing 100 nodes separated by 30 m. Arrays mimicked the size and density of small patches within natural populations of *P. farinosa*.

In a first experiment, scape-morph composition and surrounding vegetation height was manipulated in a factorial design. Arrays were either monomorphic, and consisted of eight short-scaped plants, or polymorphic, and consisted of four short-scaped plants plus four long-scaped plants. In half of the arrays, the surrounding vegetation was kept low throughout the experiment and in half of the arrays vegetation was left intact. Each treatment combination (array composition \times vegetation height) was replicated ten times.

In a second experiment, scape-morph frequency was manipulated in six separate treatments but surrounding vegetation was left intact in all arrays. This experiment was repeated in two years. In 2005, each array consisted of eight plants of which either zero (0 %), two (25 %), four (50 %), or six (75 %) were long-scaped. In 2006, arrays of the same size, but in which one (12.5 %) or eight (100 %) of the plants were long-scaped, were also in-

cluded. Each scape-morph ratio treatment was replicated eleven times in 2005 and nine times in 2006.

To determine whether effects observed in experimental arrays could be detected also in natural populations, the effect of local scape-morph ratio on plant reproductive success in five large natural populations was examined. Focal plants were chosen haphazardly throughout the population with the restriction that each focal plant should be located more than 80 cm from the closest other focal plant. Neighbouring conspecific plants within a radius of 40 cm were classified according to scape-morph (short vs. long) and style-morph (same as the focal plant vs. different). The floral neighbourhood within an area of similar size as the experimental arrays was thus determined.

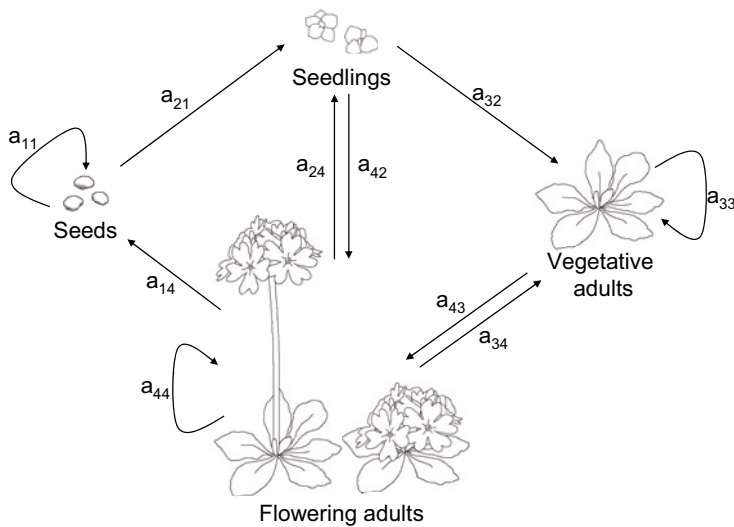


Figure 3. Life cycle graph of *Primula farinosa*. Four stage classes were recognized in the models: seeds (stage 1), seedlings (stage 2), vegetative adults (stage 3), and flowering adults (stage 4). Arrows represent possible transitions between stages, and letter codes with subscripts depict corresponding matrix entries.

Population dynamics (III)

Demographic data were collected in three populations varying in disturbance regime and therefore expected life-span, and the relationship between vital rates and environmental conditions were examined. Over seven years, 2000 – 2006, 8911 seedlings, vegetative adults and flowering adults were followed in permanent quadrats. Each year, the emergence of new seedlings,

survival, flowering status (vegetative or flowering), and reproductive output among all plants were recorded. With these data I was able to construct life-history transition matrices, in which the elements (a_{ij}) describe the probabilities of individuals to transition from one stage class j in year $t-1$ to stage class i in year t (Caswell 2001). *P. farinosa* had four stage classes in the models: seeds, seedlings, vegetative rosettes, and flowering rosettes (Fig. 3). The transition probabilities of seeds were inferred from data on occurrence of new seedlings. Each year was considered as a unique habitat state and categorized as drought, recovery, or mature state (Fig. 4.). Each habitat state determined a particular life-history transition matrix A_{α} .

To model stochastic population dynamics, I used adjusted MATLAB-scripts provided by C.C. Horvitz and followed the methods described in Tuljapurkar et al. (2003) and Horvitz et al. (2005). Stochastic population growth rate, λ_s , is an approximation of random variables which depends on the sequence of previous habitat transition states, and is obtained from numerical simulations. It is an analogue of deterministic elasticity that takes into account the probability rules given by the habitat state transition matrix. The effects of perturbations of life-history rates on the stochastic growth rate may vary among habitat states (Tuljapurkar et al. 2003) as described by the matrices of habitat-stage elasticities, E^S_{β} , where β is a state of the habitat. As a consequence, the effect of variation in a transition rate on population dynamics will depend on the state of the habitat.

To assess the effect of weather-induced environmental conditions on variation in vital rates, we correlated plant survival with seasonal records of precipitation and mean temperatures. During the study years, survival of established *P. farinosa* plants dropped to zero in the year with the lowest precipitation in all examined populations. The frequency of similarly severe drought years was estimated to be 0.16 using 56 years of weather data. To model the effect of intermittent drought years, I hence used habitat transition matrices where the state transition probability from all other habitat stages to the drought state was 0.16. Scenarios of global warming indicate that the frequency of drought years is likely to increase in northern Europe (Kjellström et al. 2005, Rowell 2005). To simulate possible historical and future frequencies of intermittent drought years, I simulated the effect of halved and doubled frequency of that obtained during the last 56 years. The remaining habitat state transition probabilities, $c_{\beta\alpha}$, were given by the observed sequence of states after the drought year and were hence specific for each examined population.

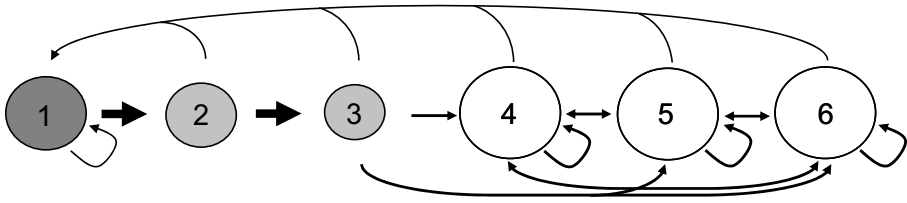


Figure 4. Example of a habitat state transition graph representing the habitat state transition matrix for population E in paper III. Each circle represents a habitat state and the size of the circle depicts the relative frequency of the habitat state in the temporal sequence. Each habitat state determines a particular life-history transition matrix. Shading denotes which phase in the temporal sequence the habitat belongs to (i.e. catastrophic, recovery, or mature states). Circle 1 represents a catastrophic drought state with a standing probability of 0.16 to occur. Circles 2 and 3 represents recovery habitat states, and circles 4 – 6 represents mature habitat states. Arrows and their sizes depict possible habitat transition steps and their relative probability. Transition probabilities were based on an estimate of the occurrence of drought years and the observed sequence of habitat states after a drought year in 2002. Each time step, the habitat state transition matrix performs one of three tasks: (1) with a probability of 0.16 a new drought disturbance occurs (habitat state 1); (2) if no drought occurs and the previous state was a drought or recovery state, it advances to the next post-disturbance state; (3) if no drought occurs and the previous state was a mature state, one matrix is chosen at random from among the set of life-history matrices corresponding to mature habitats (Morris et al. 2006).

Common-garden experiment (IV)

To quantify population differentiation in the length of the juvenile period, investment in vegetative and reproductive structures, and start of flowering, I conducted a common-garden experiment and a field survey in eight populations that differed in soil depth and therefore in vegetation cover, frost-induced soil movement in winter, and water-holding capacity. 186 maternal families collected in the field were grown from seeds and monitored for five years. I tested the predictions that populations from thin soil habitats would flower at an earlier age, have a higher allocation of resources to reproductive structures, and start to flower earlier in the season, than plants from deep soil habitats.

Results and Discussion

Floral display and frequency-dependent selection (I, II)

Context-dependent reproductive success (I)

I have demonstrated experimentally that female reproductive success in the insect-pollinated plant *Primula farinosa* is affected by individual floral display, the floral display of neighbours, and the height of the surrounding vegetation. In tall vegetation, the fruit initiation and seed production of short-scaped *P. farinosa* is higher in polymorphic than in monomorphic arrays (Fig. 5), suggesting that tall plants facilitate short plants in terms of pollinator attraction. In contrast, in low vegetation, array composition did not affect fruit or seed production of short-scaped plants. The presence of long-scaped plants should thus promote the persistence of short-scaped plants in ungrazed areas, where litter accumulates and vegetation grows tall.

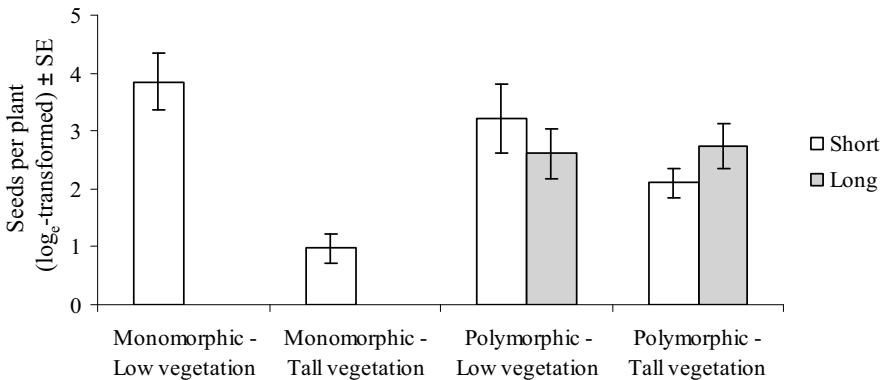


Figure 5. Effects of vegetation height and array composition on the number of seeds produced by short-scaped (open bars) and long-scaped (filled bars) plants in experimental arrays consisting of eight plants. Means and standard errors are based on array means ($N = 9 - 10$).

Frequency-dependent reproductive success (II)

The second study demonstrated that both mutualistic and antagonistic interactions can result in frequency-dependent selection on floral display in this species. Among short-scaped plants, both fruit and seed initiation, and dam-

age from seed predators increased with the proportion of the long-scaped morph. The relative strength of these effects, and therefore their net outcome on the relationship between scape morph ratio and seed production of the short-scaped plants varied among years. In polymorphic arrays, the relative seed output of the short-scaped morph increased with increasing frequency of long-scaped plants in 2006 (Fig. 6), whereas in 2005, effects mediated by pollinators and seed predators were balanced, and the relative seed output was uncoupled from the local morph ratio this year. In the natural populations, seed output among short-scaped plants was positively correlated with the local proportion of long-scaped plants in two populations in 2005. Among long-scaped plants, fruit initiation, fruit survival, and number of seeds were not related to local scape-morph ratio.

The results suggest that interactions with mutualists can lead to negative frequency-dependent selection on display traits, whereas interactions with antagonists may lead to positive frequency-dependence. Hence, frequency-dependence may vary from negative to positive depending on the relative strength of these interactions.

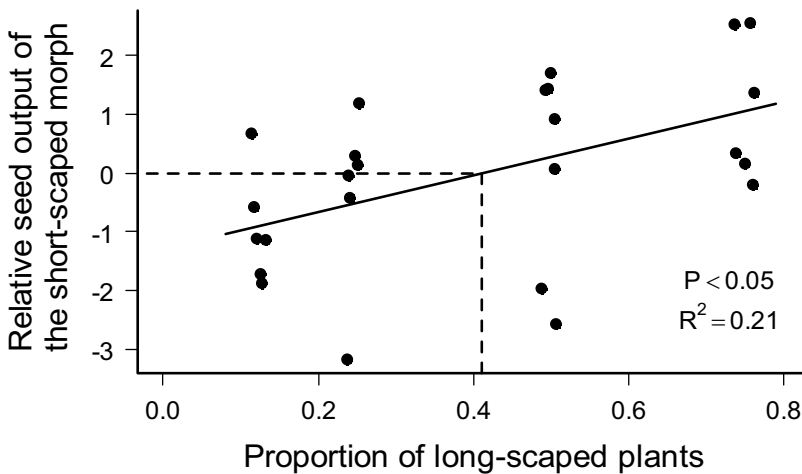


Figure 6. Relative seed output of short-scaped *P. farinosa* as a function of scape-morph ratio in experimental arrays consisting of eight plants. For each array, relative seed output of the short-scaped morph was calculated as $\log_e(\text{seed output of the short-scaped morph} / \text{seed output of the long-scaped morph})$. P and R^2 values from linear regression analysis are indicated. Broken lines indicate the scape-morph ratio at which short-scaped and long-scaped plants produce equal numbers of seeds.

Population dynamics (III)

The seven-year demographic study demonstrated how information about variation in vital rates and environmental conditions summarized in life-history stage and habitat-state transition matrices can be combined to explore and simulate population dynamics in varying and changing environments. Simulation models suggested that an increase in the frequency of drought disturbance will result in a much lower population growth rate and will make regeneration from seeds even more important for population dynamics.

The results indicate that seed dynamics (formation, survival and germination of seeds) is more important than survival of seedlings and adult plants for population growth of *P. farinosa* at the examined sites, and that seed production thus strongly contributes to plant fitness. This is important when we infer the effects of various ecological factors on plant fitness, estimated as the relative change they impose on specific components of plant performance (e.g. seed output), because these measures may be poor predictors of their relative importance as selective agents (Ehrlén 2003).

Contrary to expectation, no obvious differences in the effects of drought on vital rates between thin soil, represented by the A and C populations, and deep soil, represented by the E population were found. Apparently, differences in local environmental conditions did not result in detectable differences in response to drought during the study period. The examined populations in the present study showed very large among-year variation in vital rates (Table 2). By comparison, in a four-year study conducted in populations on the Swedish mainland, Lindborg & Ehrlén (2002) found only small among-year variation in habitat quality measured as deterministic population growth rate. It is possible that that the relative stable population dynamics found in that area in part was due to lower among-year variation in water availability.

Common-garden experiment (IV)

The results from the common-garden experiment suggest that among-population variation in reproductive effort observed in the field mainly reflects plastic responses to environmental conditions, and that their plasticity may be adaptive. In the field, reproductive effort varied considerably among *P. farinosa* populations, and was negatively related to soil depth as predicted assuming that a size- and age-independent mortality is more important on thin than on deep soils. The common-garden experiment further indicated significant genetic differentiation in life-history traits among *P. farinosa* populations and scape-morphs. However, in the common-garden, age at first flowering, reproductive effort and flowering phenology was not related to soil depth in the population of origin.

The small population differences detected in the common garden could either reflect adaptive population differentiation related to some other factor than soil depth or be a result of genetic drift. Population differences were not related to the geographic distance between populations suggesting that the observed population differences are not a simple function of drift and limited gene flow. Among-family variation indicated the presence of within-population genetic variation in rosette area, flower production, reproductive effort and flowering time.

Conclusions

In this thesis, I have explored how biotic and abiotic factors influence the reproductive ecology of *Primula farinosa*, and evaluated how context-dependent variation in selection on reproductive traits may influence evolutionary trajectories. The results demonstrate how variation in interactions with both the biotic and abiotic environment may contribute to the maintenance of genetic and phenotypic variation in plant reproductive traits.

I have demonstrated experimentally that the reproductive success of a focal plant may be a function of its floral display, the floral display of conspecific neighbours, and vegetation structure. In recent years there has been an increasing awareness that community context can affect the direction and strength of selection (Johnson & Stinchcombe 2007). The results of my experiments illustrate how the genetic structure of a population can influence the outcome of mutualistic and antagonistic interactions to determine trait selection. They make clear that an understanding of local selection, as well as geographic selection mosaics, may require that both population composition and community context are considered.

The demographic study illustrates how demographic and environmental data can be combined to analyze population viability under environmental change. I examined population viability under current climatic conditions and explored the effects of an increased frequency of drought years. The simulations indicated that population size would decline, and the importance of seed dynamics increase, if climate change results in an increase in drought year frequency. The approach taken in the current study provides a powerful tool to predict population viability not only in constant or stochastically varying environments, but also in environments that undergo directional change.

I have documented limited but statistically significant among-population variation in age at first reproduction, rosette area, flower production and reproductive effort. However, in the common-garden, population differences tended to be smaller than in the field, and were not related to soil depth at the site of origin. Phenotypic plasticity rather than genetic differentiation could be an alternative path of matching genotypes to the local environment

(Schlichting 1986), and may be important for the seemingly adaptive differences in reproductive effort between *P. farinosa* populations on soils of different depth. Data on current selection, additive genetic variance and gene flow among populations would be valuable to assess the role of selection and drift for population differentiation in life-history traits in this system.

Taken together, the findings suggest that variation in reproductive strategies can evolve and be maintained in response to divergent selection pressures mediated by pollinators, enemies and the abiotic environment, and that spatial variation in these interactions can maintain population differentiation for floral traits. My results further indicate that positive interactions may promote coexistence of alternative reproductive strategies, a notion that may be important in many systems with both discrete and continuous trait variation.

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Sist men allra mest tackar jag Anna som gör att solen skiner nästan varje dag.

Summary in Swedish

Halvan behöver helan hos öländska majvivor

Samspelet mellan växter, djur och den lokala miljön påverkar evolutionen av reproduktiva egenskaper hos majviva

Varför finns det så många olika sorters blommor? Solrosen skyltar ogenerat med stora blommor högt upp i vädret medan penningbladet presenterar sina små blommor helt nära marken. Blommorna fyller hos praktiskt taget alla växter samma funktion – att producera frö genom sexuell befruktning – ändå kan de se så olika ut. För att bättre förstå varför olika sorters blommor kan utvecklas för att lösa samma grundläggande problem åkte jag till Öland. Där har jag ägnat flera vårar åt att studera majvivor.

På Öland finns det två sorters majvivor, dels de vanliga majvivorna med blommorna i toppen av lång stjälk, dels de mer svårupptäckta, kortstjälkade majvivorna som i Sverige bara finns på Öland och Gotland. De båda sorterna tillhör samma art och kan korsa sig med varandra. Eftersom de växer tillsammans insåg jag att de utgör ett synnerligen lämpligt studieobjekt om man vill undersöka olika typer av blommor och deras för- och nackdelar. Framför allt har jag försökt ta reda på om förutsättningarna för en framgångsrik reproduktion skiljer sig mellan korta och långa majvivor. Eller med andra ord, hur det naturliga urvalet påverkar de två olika sätten att klara av den sexuella reproduktionen.

Långstjälkade majvivor är lätta att upptäcka för pollinerande insekter men också för en liten nattfjäril som lägger sina ägg i blommorna. Ur äggen kläcks larver som lever inuti majvivans frukter och äter upp dess frön. Kortstjälkade plantor däremot lyckas ofta undvika fjärilslarverna men har samtidigt svårt att locka till sig pollinatörer.

Skillnaderna mellan de två sorterna påverkas av omgivningen. I välbetade marker med kort växtlighet är både kort- och långstjälkade plantor lätta att upptäcka. I högre vegetation blir skillnaderna däremot genast tydliga eftersom de korta plantorna lätt göms under fjolårsgräset. De två varianterna växer tillsammans på det öländska alvaret men proportionerna varierar mellan olika lokaler.

Konsten att utnyttja sina grannar

Med två experiment har jag visat att den reproduktiva framgången (hur många frön de sätter) hos de två olika typerna av majvivor inte bara beror på den enskilda plantans stjämlängd, utan också på hur dess grannar ser ut. Har kortstjälkade plantor turen att växa bredvid långstjälkade grannar ökar deras reproduktiva framgång jämfört med om de skulle råka växa i en miljö med bara kortstjälkade släktingar.

Detta beror sannolikt på att de långstjälkade plantorna lockar till sig pollinatörer som lättare kan upptäcka även de korta plantorna när de flugit helt nära dem. Men på samma sätt kan också fiender lättare upptäcka de korta plantorna. Sammantaget är framgången hos de två varianterna beroende av beteendet hos besökande djur, omgivande växtlighet och den lokala frekvensen av lång- och kortstjälkade majvivor. Den positiva effekten av att växa bredvid långa grannar har sannolikt bidragit till att den kortstjälkade majvivan har överlevt i området.

Varför finns blommor?

Sexuell fortplantning är en viktig del av livscykeln hos många växter. Inga andra organismer uppvisar så stor variation i sina reproduktiva organ och sexuella strategier som blomväxterna. För att kunna förstå denna variation måste vi studera hur det naturliga urvalet och de lokala anpassningarna fungerar hos växterna i deras naturliga miljö.

Djuren kan vanligtvis förflytta sig långa sträckor för att finna sina partners, medan växterna däremot har den uppenbara nackdelen att de sitter fast där de en gång slagit rot.

Men blomväxterna har ett trumf på hand – blomman. Blommorna är fantastiska organ. De rymmer som regel både hanliga ståndare med pollen och honliga pistiller med främnen. Dessutom har de ofta vackra kronblad och kan utsöndra både doftämnen och nektar. Med hjälp av sina snillrika blommor har de flesta växter hittat ett bra sätt att ordna sin fortplantning.

Många blomväxter utnyttjar djur, ofta insekter, för att överföra pollen från planta till planta. Växternas blommor har utvecklats genom naturligt urval för att på olika sätt attrahera och manipulera pollinatörer så att de effektivt ska transportera pollen mellan individer. Eftersom pollinatörerna är viktiga för växterna kan vi förvänta oss att pollinatörernas egenskaper är avgörande för hur det naturliga urvalet styr evolutionen av blommornas utseende och funktion.

Tråkigt nog för växterna attraheras inte bara pollinatörer av blommor. Andra djur äter blommor, pollen, frön eller nektar utan att bidra till pollinationen. Dessa fiender lockas sannolikt av samma egenskaper hos blommorna som pollinatörerna. Fiendernas negativa inverkan borde också påverka evolutionen av växternas reproduktiva egenskaper.

Enskilda växter och deras besökare samverkar i ekosystem som de delar med många andra arter och individer och som dessutom påverkas av yttre faktorer som väder och jordmån. Lokal variation i den omgivande miljön bör ha konsekvenser för vilka egenskaper hos en växt som gynnas av det naturliga urvalet. Följaktligen kommer de egenskaper och reproduktiva strategier som gynnas att variera mellan år och mellan olika platser. Sådan variation kan upprätthålla den genetiska variationen inom en art och kan i förlängningen leda till att nya arter bildas. Det har skett många gånger under de 130 miljoner år som blomväxterna har interagerat med vänner, fiender, grannar och sin fysiska omgivning.

Majvivans reproduktiva strategier

Man kan säga att majvivans två varianter representerar två olika sexuella strategier. Långstjälkade plantor har en riskfylld strategi: chansen är stor att pollinatörer besöker blommorna, men samtidigt är risken stor att de skadas av frätande predatorer. Kortstjälkade majvivor har en försiktigare strategi: risken för skador är mindre, men chansen att upptäckas av pollinatörer också lägre. Lite tillspetsat kan man säga att det är en fråga om att antingen ha mycket men riskfylld sex eller säker sex mer sällan.

Dessutom uppvisar majvivorna en lite mer svårupptäckt variation som också är kopplad till reproduktionen. Det öländska alvaret kännetecknas av en mosaik av mer eller mindre permanenta våtmarker, 'våtar', på en i övrigt torr gräsmark på mycket tunn jord. Majvivan växer vanligen i fuktiga ängar och betesmarker och på alvaret hittar man dem följkaktligen i anslutning till våtarna. Men på grund av det tunna jordlagret torkar även våtarna ut under varma somrar och miljön blir då olämplig för majvivorna. Risken för uttorkningsskador är beroende av vädret och jordens förmåga att hålla vatten och varierar därför kraftigt i tid och rum.

Lokal anpassning

Vi kan förvänta oss att växterna är lokalt anpassade till sin miljö med avseende på hur snabbt de utvecklas till blommande individer och hur mycket resurser de fördelar till vegetativ tillväxt jämfört med reproduktion. Detta beroende på att den optimala strategin, dvs. hur man bäst fördelar sina resurser, bör variera med förväntad livslängd.

En strategi där mycket resurser fördelas till reproduktion istället för vegetativ tillväxt bör gynnas i miljöer där risken att dö av torka varje år är överhängande. En snabb livscykel innebär då att frön produceras fort. Dessa kan sen gro när torkan är över. En mer långsiktig strategi där resurser fördelas till vegetativ tillväxt och förbättrad vitalitet bör istället gynnas där risken att dö av torkskador är mindre. Stora plantor klarar nämligen av sjukdomar och konkurrens från andra plantor bättre än små plantor.

Dessutom kan vi förvänta oss att plantor börjar blomma tidigare på tunnare än på djupare jord om risken för uttorkning ökar snabbare under säsongen

i dessa miljöer. På tunn jord gäller det för majvivorna att hinna blomma och sätta frön innan torkan dödar plantorna. På djupare jord kan det däremot löna sig att vänta med blomningen och istället satsa på blad och rötter.

Reproduktiv framgång påverkas av lokala miljöfaktorer...

Under flera år följde jag enskilda majviveplantor, från små groddplantor till vuxna, blommande individer, både i naturliga populationer och i odling. I fält fördelade plantor sina resurser enligt förväntan; populationer på tunn jord satsade större resurser på reproduktion än populationer på djup jord. Att låta plantor från dessa populationer växa i en gemensam miljö i trädgården skulle ge en fingervisning om huruvida lokal anpassning hade gett upphov till genetiska skillnader mellan olika populationer.

Mina resultat från trädgården tyder på att plantor från olika populationer skiljer sig åt vad gäller hur mycket resurser de avsätter för blomproduktion och i blomningstid. Däremot fann jag inga bevis för att detta är kopplat till risken för uttorkning. Detta tyder på att det var plastiska effekter som låg bakom populationsskillnaderna i fält. Dessutom verkar de två varianterna av majviva fördela sina resurser något olika. Om detta är resultatet av naturligt urval behöver utvärderas ytterligare experimentellt.

... och av vädret

I de naturliga populationerna dog alla plantor i samband med den mycket torra sommaren 2002 då det bara kom 2 mm regn under juni och juli vid den ekologiska forskningsstationen intill undersökningslokalerna. Detta gav en unik möjlighet att studera återkolonisation och populationsdynamik i området. Baserat på dessa data kunde jag med hjälp av matematiska modeller simulera hur frekvensen av liknande torrsomrar påverkar populationernas dynamik och möjligheten för majvivorna att överleva i olika miljöer.

De förväntade klimatförändringarna kommer att medföra en högre andel torra och varma somrar i södra Sverige. Enligt mina simuleringar kommer strategier som medger en snabb livscykel och en hög produktion av frön att i framtiden premieras före strategier som fördelar mer resurser till vegetativ tillväxt och överlevnad.

Slutsatser

Min avhandling visar hur samspelet mellan individuella egenskaper, populations genetiska sammansättning, pollinatörer, fröpredatorer, den lokala miljön och klimatet kan påverka livsbetingelserna för enskilda individer. På senare år har många evolutionsbiologer insett att det naturliga urvalet formar blommornas egenskaper som ett resultat av ett komplicerat samspel mellan många olika aktörer. Få studier har dock undersökt hur flera faktorer samtidigt kan påverka evolutionen i naturliga populationer. Mina resultat exemplifierar hur en populations genetiska sammansättning påverkar utgången av interaktioner med både pollinatörer och predatorer samt hur den lokala mil-

jön påverkar evolutionen av reproduktiva egenskaper. Resultaten visar hur viktigt det är att notera både populationssammansättning, egenskaper hos den lokala miljön och samspelet med flera aktörer när man ska studera naturligt urval och förutspå evolutionära tendenser.

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