Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*

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This thesis is based on four papers.


III) Falahati-Anbaran M, Lundemo S, Stenøien HK. Quantifying dispersal in time and space in northern European populations of *Arabidopsis thaliana* (manuscript).


Declaration of contribution

In paper I, HKS initiated the project and organized, HKS and SL did the field work, HKS, SL and MFA performed the analysis and all authors contributed to write the paper. The project in paper II was initiated by HKS, SL did the field work, HKS, SL and MFA did the data analysis, MFA and SL wrote the paper with contribution from the other authors. In paper III, HKS initiated the experiments. HKS, MFA and SL designed and conducted the field work; MFA analysed the data and wrote the paper with the contribution from the other authors. In paper IV, HKS, SL and MFA initiated the project, MFA and SL planned and conducted the field work, MFA, SL analysed the data, MFA wrote the paper with contribution from the other authors.
Summary
In most plant species, seeds after dispersing from the mother plant (primary dispersal) may undergo secondary dispersal, either in time by remaining dormant in the soil and forming a seed bank, or in space by movement to other locations. Seed bank and dispersal in space are bet-hedging strategies that minimize the extinction risk and aid to population stability and persistence in temporally variable environments. The ability to establish seed bank via depositing a fraction of seeds into the soil may also increase the potential of early stage adaptation into new habitats. A persistent seed bank preserves genetic diversity and buffers populations from the loss of genetic variants due to random drift. Although theoretical studies have highlighted the role of seed banks in elevating effective population size, little information exists regarding the evolutionary potential of seed banks in natural populations.

In this thesis I studied inter- and intraspecific variation in genetic composition of seed banks and its significance in natural populations of two closely related species in the genus *Arabidopsis*. *A. thaliana* is an annual self-compatible plant whereas *A. lyrata* is perennial and self-incompatible. The potential contribution of seed banks to effective population size (*N_e*), generation time, genetic variation, and population dynamics has been addressed. The pattern of dispersal over time and space was investigated by monitoring of natural populations over five consecutive years in *A. thaliana*. In addition, regional differences in seed bank, genetic composition and structure in *A. lyrata* were investigated between three contrasting regions in northern Europe.

The results showed that both species form persistent seed banks throughout their Norwegian distribution range. Seedling density was lower in *A. lyrata* than *A. thaliana*, as would be expected from a perennial. Moreover, the seed bank contributes to total effective population size in perennial *A. lyrata*, though not to the same extent as in *A. thaliana*. In *A. lyrata* both seed bank and above-ground individuals seemingly have a similar contribution to the total *N_e*.

Monitoring *A. thaliana* populations over multiple years revealed that in most populations two or more distinct multilocus genotypes were present, which often varied in frequency between years, leading to variation in within-population diversity. Although most of the distinct multilocus genotypes within each population were genetically similar, probably due to historical mutation and recombination events, in some cases multiple colonization events due
to migration from other populations were evident. Many geographically closely situated populations shared common multilocus genotypes and expressed low differentiation compared to distant ones. The results show evidence dispersal in time, i.e., persistence of dormant or ungerminated seeds in ten populations in which 29% of seeds descended two or three years before present, on average. Additionally there are signs of seed and pollen immigration from other populations in almost one fifth of the studied cohorts, reflecting an effective migration rate of 1.8% per generation. Migration through pollen and seeds in *A. thaliana* is therefore common, and the seed bank plays, at the same time a substantial role in overall population dynamics.

Comparing natural populations of *A. lyrata* in different regions revealed that soil seed banks are either absent or small in Icelandic populations and average density of seed bank is 2.5 fold smaller than what was observed among Norwegian populations, though the overall differences between regions was not statistically significant. The level of genetic variation in Icelandic was similar to Swedish and significantly higher than what found in Norwegian populations. In addition population differentiation on Icelandic was significantly lower than what found in Swedish and Norwegian populations. When comparing similar distribution areas in the regions, the effect of habitat structure was found to be less important to explain the differences in genetic structuring. Immigration rate over time was similar between regions that show variable population differentiations. The results suggest that relatively low differentiation among Icelandic populations is more likely due to large historical effective population sizes compared to Scandinavian populations, rather than immigration *per se*. 
Introduction

**Seeds and seed related traits**
Seed size, the establishment of seed banks and dispersal in space are important traits that may influence population persistence, the colonization and extinction time and interact with environmental variables (Cohen 1966; Silvertown 1981; Brown & Venable 1986; Venable & Brown 1988; Guo et al. 2000). In most flowering plants seeds after dispersing from the mother plant (primary dispersal), may experience dispersal events, either by remaining dormant in the soil (seed bank formation), or in space by movement to other locations (dispersal in space). Seed bank formation and seed dispersal are bet-hedging strategies which enable plants to escape unfavorable environmental conditions (Venable & Brown 1988). Seed size is highly variable and may vary over ten orders of magnitude among species, from dust-like seeds of orchids being as small as 0.3μg to the 20 kg seeds of the double coconut (Arditti 1967; Harper et al. 1970; Silvertown 1981; Moles et al. 2005; Linkies et al. 2010). Although large seed size has been attributed to higher survival rate, there is a tradeoff between seed size and seed number (Jakobsson & Eriksson 2000). A negative relationship has been observed between seed size and number for many species across different habitat types (Jakobsson & Eriksson 2000; Metz et al. 2010). Although large seeds generally have a higher chance to establish, they may experience higher mortality due to higher predation rate. In addition, a tradeoff exists between seed size and dispersal ability in which larger seeds may have limited possibilities for long distance dispersal (e.g., Parciak 2002). Generally speaking, small seeds are more easily dispersed and may thus facilitate colonization into new environments (e.g., Silvertown 1981).

**Ecology of seed banks**
A seed bank is a deposit of viable and ungerminated propagules, and can exist both as mature seeds on the plant (aerial seed bank) or in the soil (soil seed bank), whereas in animals this trait is evident through diapausing eggs (Cohen 1966; De Stasio 1990; Christoffoleti & Caetano 1998). Delayed germination of seeds is a bet-hedging strategy to minimize the risks of germinating at the wrong time of the growth season, and in face of unpredictable environmental disturbances (Cohen 1966; Childs et al. 2010). Bet-hedging has been widely investigated theoretically and empirically (e.g., Venable 2007 and references therein). While
fluctuations in environmental conditions may increase the rate of mortality and variance in reproductive success among years, seed banks may have substantial potential in buffering variation in reproductive success and minimize the extinction risk (Pake & Venable 1996).

Seeds can either persist in the soil for a short time until the next germination season (less than a year; transient seed bank) or remain in the soil as dormant beyond one year (persistent seed bank; Thompson & Grime 1979). The existence of seed banks in plants in terrestrial and aquatic ecosystems has been well documented (Thompson & Grime 1979; Leck et al. 1989; Thompson et al. 1997; Evans et al. 2007), and although seed dormancy has been strongly attributed to formation of seed bank, empirical studies have found no close relationship between dormancy and seed bank formation (Thompson et al. 2003; Honda 2008). Perennial and large seed species are less capable to establish seed banks than annual and small seed species (Silvertown 1981; Thompson 1987; Honda 2008), and large seeds usually less able to persist for longer periods of time in the soil (Thompson 1987). The number of seeds found in the seed bank of annual and biannual plants is often higher than in perennials, indicating the greater capacity of annual species to persist in the soil seed bank than perennials (Arroyo et al. 2006; Honda 2008; DeFalco et al. 2009). Seeds of plant species may remain in soil as dormant or ungerminated for a few years up to several decades, centuries, or even >1000 years (Kivilaan & Bandurski 1981; Shen-Miller et al. 1995; Thompson et al. 1997; Telewski & Zeevaart 2002). Although the ecological potential of seed traits has been extensively studied in numerous species (Howe & Smallwood 1982; Thompson 1987; Bakker 1996), little information exists about the evolutionary importance of secondary seed dispersal over time (seed bank) and space (migration) in plants that differ in several life history traits.

**Seed banks and effective population size**

Most annual species and some perennials maintain seed banks, and the seed bank will over time contain seeds of different genotypes as not all seeds germinate directly after reproductive events. This buffering effect can dampen the rate of loss of genetic variation due to stochastic variation in the environment and increase the effective population size (Templeton & Levin 1979; Hairston & De Stasio 1988). Genetic variation in plant populations harbouring seed banks is influenced by mutual gene flow between the seed-bank and the above-ground individuals. Theoretical expectations and experimental studies suggest that seed banks may moderate the effect of genetic drift through buffering against changes in census sizes in
above-ground cohorts (Epling et al. 1960; Templeton & Levin 1979; Nunney 2002; Vitalis et al. 2004; Honnay et al. 2008). Estimations of effective population size should therefore be based on both seeds from the seed-bank and above-ground individuals.

The effective size of a given population \( N_e \) can be defined as the size of an ideal population that loses genetic variation (through genetic drift) between generations at the same rate as the natural population under study (Wright 1931; Kimura & Crow 1963). Estimation of effective population size from genetic and ecological data is a challenging topic in evolutionary biology and many different methods have been proposed, though most of them are based on simplified assumptions that seldom apply to real populations (for review see: Leberg 2005; Wang 2005). These approaches, which can be used to estimate contemporary and historical \( N_e \), are based on both demographic and genetic models (Schwartz et al. 1999; Nunney 2002; Leberg 2005; Wang 2005). Genetic models based on heterozygosity excess (Pudovkin et al. 1996), temporal shifts in allele frequency (Krimbas & Tsakas 1971; Waples 1989; Wang 2001) and linkage disequilibrium, LD (Hill 1981; Waples 1991; Waples & Do 2008, 2010) have received considerable attention in the estimation of \( N_e \) (Luikart et al. 2010). The LD method offers an unbiased single sample estimator of contemporary \( N_e \) (Bartley et al. 1992; Waples & Do 2008), and has been shown to perform better than the temporal method (Waples & Do, 2010) as it needs only a single time point per population, whereas the latter require data from at least two time points for each population. Coalescent theory may also be used to infer the demographic history of populations through estimating historical \( N_e \) based on ancestral relationships among individuals (Fu & Li 1999). Historical \( N_e \) infers the amount of genetic diversity over evolutionary time since formation of a population, reflecting bottlenecks, range expansions, migration and admixture events in the past. Neutral genetic diversity within populations is positively related to the coalescence time and effective population size.

**Gene flow through seed and pollen dispersal**

In flowering plants, dispersal is the movement of genes through seeds or pollen from one site to another (Endler 1977; Levin 1981). If a given dispersal event results in establishment or reproduction within the local gene pool, gene flow has occurred (Endler 1977). Gene flow among populations may increase within-population genetic diversity and reduces genetic differentiation between local populations (Ehrlich & Raven 1969). Type of mating system
play an important role in determining the level of gene flow through pollen dispersal, in which in an outcrossing plant exhibiting a self-incompatibility (SI) system, a higher level of gene flow is often expected between populations in a given space compared with predominantly self-pollinating species because the former is highly dependent on pollen flow from other individuals of the same species (e.g., Govindaraju 1988a,b; Mable & Adam 2007). The SI system in plants prevents fertilization by self-pollen and accepts only pollen from genetically unrelated individuals, thus facilitating outcrossing. Seed dispersal in plants is often expected to be a distance dependent process, i.e. with higher seed movement over short distances compared to long distances (Howe and Smallwood 1982 and references therein). However, long distance seed dispersal is very important because it can affect on colonization processes and metapopulation dynamics (Cain et al. 2000).

Molecular techniques have been used extensively to study the pattern of pollen and seed dispersal (Ouborg et al. 1999). Dispersal can be quantified using direct (parentage analysis and assignment test) and indirect approaches using population structure (e.g., genetic differentiation measures like $F_{ST}$; Slatkin 1987; Cain et al. 2000). Historical gene flow patterns has traditionally been studied using a simple population structure model introduced by Wright (1931), in which the relationship between the number of immigrants a population receive and population differentiation ($F_{ST}$) can be shown as $F_{ST} = [1/(1+4Nm)]$, where $N_e$ and $m$ is the effective population size and migration rate per generation, respectively. However, this model is based on a large number of simplifying assumptions that are unlikely to hold true for natural populations (Whitlock & McCauley 1999). In addition, this method is not appropriate to study the spatial patterns of genetic structure and gene flow among subpopulations (Hutchison & Templeton 1999; Sork et al. 1999).

The pattern of gene flow among populations in a given geographical area is often quantified through isolation by distance, IBD. Under a stepping-stone model of population structure, the relative influence of gene flow and genetic drift on regional population structure can be inferred from the relationship between genetic and geographic distance among pairs of populations (Kimura & Weiss 1964). The pattern of IBD can thus be compared between regions to determine how gene flow and drift have contributed in shaping the genetic composition within a given region compared with others. In this model, gene flow is expected to decline with increasing geographic distance between populations. In species with restricted seed and pollen dispersal between populations, a significant relationship is expected between
genetic and geographic distance, leading to isolation by distance (Slatkin 1993). Several factors may affect the pattern of IBD, such as the scale and regional topography in which populations are being sampled, number of populations, and time since colonization of a locality (Crispo & Hendry 2005). The absence of IBD has been attributed to several factors such as recent colonization of regions followed by rapid range expansion or fragmentation (Slatkin 1993; Hutchison & Templeton 1999; Crispo & Hendry 2005).

**Aims of the study**

In this thesis I have used two closely related species, both of which are widely used as models in research, to study the ecological and evolutionary importance of seed banks and dispersal. In particular, I have tried to discern how annual and perennial species differ in their strategies for dealing with environmental stochasticity, and more specifically, whether the importance of seed banks differ in annual and perennial plants.

The main objectives addressed in this thesis are:

1) To investigate the existence of seed banks in *A. thaliana* and *A. lyrata* and to determine the relative contribution of the seed bank to total effective population size and generation time (Papers I and II)

2) To study the pattern of secondary seed dispersal in time and space by quantifying the effective seed and pollen migration rate and dispersal in time in *A. thaliana* (Paper III)

3) To study the pattern of genetic diversity and structuring in *A. lyrata* inhabiting contrasting habitats (Paper IV)
Materials and methods

Study species

*Arabidopsis thaliana* (L.) Heynh. (Figure 1), known as mouse-ear cress or wild thale cress, is a weedy annual, self-pollinating plant in the mustard family (Brassicaceae). The plant has small, white flowers, and can produce large amounts of small seeds (~0.1-0.5 mm long, Figure 2). In Scandinavia it predominantly germinates in the autumn, overwinters as a rosette and does flower and sets seed in early spring. It is diploid (2n = 10) with a relatively small genome, 125Mb, and has been extensively used as a model for molecular biology and ecological and evolutionary studies (Mitchell-Olds & Schmitt 2006; Koornneef & Meinke 2010). The plant is native to Eurasia and North Africa (O’Kane & Al-Shehbaz 1997; Al-Shehbaz & O’Kane 2002). Additionally, the species has been introduced and successfully established in central and Northern Europe, North America, southwest Asia, Australia and New Zealand (Sharbel *et al.* 2000; Al-Shehbaz & O’Kane 2002; Hoffmann 2002).

![Figure 1: Floral display in *Arabidopsis thaliana* (right) and *A. lyrata* (left). Photo: M. Falahati-Anbaran.](image)

In Norway *A. thaliana* occurs in wide range of habitats from sea level and up to 1150 m asl and distributed from 58°N to 69°N. The plant occupies mainly disturbed areas such as road verges, railway tracks, and rocky slopes with thin soil layer and low vegetation cover (Figure 3).
Arabidopsis lyrata subsp. petreae (L.) O’Kane & Al-Shehbaz (1997), northern rock cress, is a perennial and self-incompatible herb that is distributed over disjunctive regions in Central and Northern Europe (Jonsell et al. 1995). A. lyrata is closely related to A. thaliana, and it is believed they diverged from a common ancestor about 5-10 million years ago (Koch et al. 2000; Hu et al. 2011). In contrast to A. thaliana, A. lyrata has larger flowers (Figure 1) and seeds (1-1.5 mm long, Figure 2). It is diploid (2n = 16) with a larger genome (207 Mb, Hu et al. 2011) than A. thaliana, and has been extensively used as a model in ecological and evolutionary studies (Mitchell-Olds 2001). In northern Europe, the plant is restricted to mountainous areas of south-western Norway, a small part of the eastern coast of Sweden, United Kingdom, Faeroe Islands and across most of Iceland (Jonsell et al. 1995; Schmickl et al. 2010). In Norway, the plant grows in habitats located from the sea level up to ~ 1700 m asl and deep valleys and mountain peaks my thus create physical barriers limiting connectivity between populations (Figure 3). In contrast, A. lyrata in Sweden occur mostly in open habitats.
along the coast, with no major physical barriers between sites. In Iceland the plant is found on lava plain and disturbed and open habitats from see level to highlands.

Figure 3: Typical habitat of *Arabidopsis thaliana* locality at Byneset, Trondheim (top), and *A. lyrata* locality in Sæbo, Eidfjord (bottom). Photo: M. Falahati-Anbaran.
**Seed and soil samples**

Seeds from above-ground plants were sampled from natural populations of *A. thaliana* across its Norwegian distribution range between 2005 and 2009 (Papers I and III). Soil samples (ten samples in each population; ~10 × 10 cm, 1-5 cm deep) were randomly collected throughout each population before seed dispersal in late May and early June 2005, 2008 and 2009 (Papers I and III).

In *A. lyrata*, soil samples were collected from 14 populations in southwestern Norway, in which the above-ground individuals were previously analysed by Gaudeul *et al.* (2007), (Paper II) in July 2006, before that year’s seed rain. Soil and rosette leaves from ten Icelandic populations of *A. lyrata* were sampled in 2009 (Paper IV).

*A. thaliana* seeds were sown in the greenhouse and leaf tissue was collected from one individual per maternal plant (Papers I and III). Soil samples were stored at 4 °C before germination trials to break dormancy of seeds. Thereafter, the soil was spread out in a thin layer on top of commercial potting soil in 12.8 × 14.5 cm pots to stimulate germination of seeds (Papers I, II, III and IV). Pots were placed in the greenhouse under 16 h day length for about 10 months until no more seedlings emerged. The temperature and humidity during the germination experiment were 20 °C and 65%, respectively. Leaf tissue from each emerged seedling was collected separately. The leaves obtained from above-ground individuals and seedlings emerging from the soil samples were dried at 45 °C for 24 h (Papers I, II, III and IV).

**Molecular and data analyses**

Genomic DNA was extracted from individual plants of above-ground and seed-bank cohorts using the E.Z.N.A.™ SP Plant DNA Kit (Omega Bio-Tek, Inc). *A. thaliana* samples were screened using 107 (Paper I) and 103 (Paper III) SNP markers described in Törjék *et al.* (2003). Eleven (Paper I) and twenty one (Paper III) SNPs were excluded with no call or low efficiency after genotyping. *A. lyrata* samples were screened with 15 (Paper II) and 21 (Paper IV) microsatellite markers. The primer sequences of flanking regions for microsatellite loci used in *A. lyrata* are described in Bell and Ecker (1994), Clauss *et al.* (2002), Loudet *et al.* (2002), and Kuittinen *et al.* (2004).
Seed bank density between species was compared using a Mann-Whitney $U$ test (Paper II). The within-species variation between contrasting habitats was investigated by comparing density of seed bank in Icelandic $A. \text{lyrata}$ to that in Norwegian populations (Paper IV). Population genetic parameters and pairwise $F_{ST}$ (Weir & Cockerham 1984) were estimated using Arlequin 3.5 (Excoffier et al. 2005), FSTAT (Goudet 1995) and Genepop (Rousset 2008; Papers I, II, III and IV). Analysis of molecular variance, AMOVA, was conducted using Arlequin (Paper I). Genetic structure was also inferred by model based Bayesian methods as implemented in Structure (Pritchard et al. 2000; Falush et al. 2003; Papers I, II and IV), BAPS (Corander & Marttinen 2006; Corander et al. 2008; Papers I and II) and Instruct (Gao et al. 2007; Paper III). The results of Bayesian analyses were summarized across multiple runs using CLUMPP (Jakobsson & Rosenberg 2007). Spatial structure was investigated using isolation by distance (IBD). IBD was performed by regressing genetic distance against geographical distance and the significant was tested by permutation test using GeneAlex (Peakall & Smouse 2006; Papers I and IV). Contemporary $N_e$ was estimated with a linkage disequilibrium approach implemented in NeEstimator 1.3 (Peel et al. 2004; Paper II). Historical effective population size ($N_e$) was estimated based on a coalescent-based maximum likelihood method implemented in Migrate (Beerli & Felsenstein 1999, 2001; Papers I, II and IV). Dispersal in space was quantified by a conservative estimate based on distance criterion using an assignment test (Cornuet et al. 1999). Migration through pollen dispersal was also computed by identifying individuals carrying two or more private alleles at heterozygous SNP loci in each cohort. The effective migration rate, i.e. dispersal and establishment, was calculated combining both seed and pollen flow events for each population. Dispersal in time was estimated by assigning above-ground individuals sampled in 2009 to the previous above-ground cohorts using a distance based criterion (Nei et al. 1983) implemented in GeneClass2 (Piry et al. 2004). Analysis of variance, ANOVA, was conducted to test for differences between regions for various parameters (Iceland, Norway and Sweden) and the difference between regions was examined using a post hoc Bonferroni test (Paper IV). A Welch F test was used to examine differences in population differentiation (pairwise $F_{ST}$) among regions and multiple comparisons was conducted using Tamhane’s test (Paper IV). Analysis of covariance, ANCOVA, was used to test the regression slope of isolation by distance between regions (Paper IV). All statistical analyses were performed using SPSS version 16.
Results and discussion

Seed banks in A. thaliana and A. lyrata (Papers I and II)
The results revealed that both species maintained persistent seed banks in their northern European distribution range. The seed bank density as determined by the germination method varied considerably within A. thaliana and A. lyrata populations. Overall, the seedling density in A. thaliana was an order of magnitude higher than in A. lyrata. Because soil samples were collected before seed rain, any evidence of germination from soil samples indicates the presence of a persistent seed bank. Seed banks were detected in all A. thaliana populations in 2005. In contrast, in 2 out of 14 A. lyrata Norwegian populations, no seedlings were detected. The results may indicate that the existence of a persistent seed bank is more important for annual plants than for perennials. The discrepancy in seedling density between the study species can mainly be attributed to differences in life history traits, which is in agreement with theoretical predictions and empirical studies, showing that annual plants in general have higher reproductive output than perennials (Harper & Ogden 1970; Hirshfield & Tinkle 1975; Primack 1979). Moreover seed size in A. thaliana a priori is considerably smaller than A. lyrata and it has been shown that large seed species may capable less to persist in the soil for long time relative to small seed ones (Silvertown 1981; Thompson 1987). The results are in agreement with previous studies showing a higher seed bank density in annual than perennial species (e.g., Arroyo et al. 2006). Although the seed bank density in Icelandic populations of A. lyrata was 2.5 fold smaller than that in Norwegian populations, the difference was not statistically significant (P = 0.088). Most Icelandic A. lyrata populations either lacked completely a seed bank (30%) or had low seedling densities (60%; < 50 viable seeds pr m$^{-2}$) and in only one population the density of seed bank was high (10%; > 100 viable seeds pr m$^{-2}$). The results also showed no differences between population densities (rosettes per m$^{-2}$) between regions. Variation in seed production between regions may be attributed the differences in seed production rather than population density (Vergeer & Kunin 2011). Other ecological and biological factors such as soil particle size, soil nutrient levels, and microbial activities may also influence the density of seeds in the seed bank (Wagner & Mitschunas 2008; DeFalco et al. 2009)
Genetic diversity and structure (Papers I and II)
The level of genetic diversity did not vary between seed bank and above-ground cohorts in either *A. thaliana* or *A. lyrata*, suggesting that most genetic variability in the seed bank is present in above-ground cohorts. This has also been reported in other studies, both for annual and perennial species (Mahy *et al.* 1999; Mandák *et al.* 2006). The average between-cohort differentiation, i.e. between seed bank and above-ground plants, was considerably lower than that among populations for both *A. thaliana* and *A. lyrata*. Similarly, model based Bayesian clustering revealed a high level of structure in Norwegian populations of *A. lyrata* and *A. thaliana*. In *A. thaliana*, populations were assigned to 15 ancestral clusters based on seed-bank (2005 samples) and above-ground (2005 and 2006) data. In most populations the seed-bank and above-ground cohorts were genetically similar. A significant correlation was detected between genetic and geographical distance in Norwegian populations of *A. thaliana*, indicating isolation by distance pattern for all cohorts. This suggests a high level of gene flow relative to drift over short geographical distance, and relatively lower gene flow relative to genetic drift at longer distance (Hutchison & Templeton 1999). In *A. lyrata*, Bayesian clustering based on seed bank and above-ground data revealed a high level of structure among populations and most of seed bank and above-ground cohorts for each population were grouped to similar ancestral clusters.

Evolutionary consequences of seed banks (Papers I and II)
The contribution of the seed bank to total effective population size (*N*<sub>e</sub>) was quantified by estimating the scaled mutation parameter (*θ*) for individual seed-bank (*θ*<sub>S</sub>) and above-ground 2005 (*θ*<sub>A-5</sub>) and combined (*θ*<sub>T</sub>) cohorts using SNP data in *A. thaliana*. The results showed that the total *N*<sub>e</sub>, i.e. when combining seed-bank and above-ground individuals, was greater than when considering the above-ground cohort alone. A similar result was observed based on estimates of historical and contemporary effective population size in *A. lyrata*. Interestingly, the relative ratio measured by *θ*<sub>S</sub>/*θ*<sub>T</sub> was higher in *A. thaliana* than *A. lyrata*, suggesting a weaker contribution of the seed bank to *N*<sub>e</sub> in the later species. In *A. lyrata*, *θ*<sub>A-5</sub>/*θ*<sub>T</sub> was slightly lower than *θ*<sub>S</sub>/*θ*<sub>T</sub>, but not statistically significant, suggesting a similar contribution of both seed-bank and above-ground cohorts to total *N*<sub>e</sub>. Although the historical effective *N*<sub>e</sub> based on the coalescence method was significantly higher than contemporary *N*<sub>e</sub> estimates, a similar relative ratio was obtained based on both methods for *A. lyrata*. Generation time in *A. thaliana* was estimated based on the model introduced by Vitalis *et al.* (2004). This was
conducted by estimating the total effective population size from a subset of populations using microsatellite data obtained from Stenøien et al. (2005). Thus, generation time in Norwegian populations of *A. thaliana* was found to be on average 4 years (range 1-8), and only two out of six (33%) populations showed a generation time of one year. This is a rough estimate of generation time in natural populations of plant species based on molecular data. This indicates that presence of seed bank elevate generation time by differential recruitment of seeds of different genotypes preserved in the soil. Taken together these results support theoretical expectations, that seed banks can substantially increase the total $N_e$ in both annual and perennial species (Hairston & De Stasio 1988; Kaj et al. 2001; Nunney 2002; Vitalis et al. 2004; Waples 2006).

**Pattern of dispersal in time and space in *A. thaliana* (Paper III)**

*A. thaliana* can spread rapidly into new areas (Jørgensen & Mauricio 2004) and it has been suggested that local populations experience extensive metapopulation dynamics with occasional extinctions and subsequent recolonization by immigrations from other populations (Bergelson et al. 1998; Lavigne et al. 2001; Le Corre 2005). Both dispersal in space (immigration from other populations) and dispersal in time (regeneration from the seed bank) could contribute to recolonization (Husband & Barrett 1996). However, no studies have so far described the relative contribution of dispersal in space and time in plant populations. Through sampling the seed-bank and above-ground cohort in natural populations of *A. thaliana* over several years, it was possible to measure the level of migration within (dispersal in time) and between (immigration) populations. Evidence of immigration of seeds and/or pollen from other populations was observed in 49 out of 222 study cohorts, yielding an average migration rate of 1.8% per generation. Dispersal through seeds was considerably higher than pollen dispersal, with an average seed to pollen ratio being 7.06 across 10 populations. The estimated migration rate is considerably higher than what we may expected from the high $F_{ST}$ values found across populations. The inconsistency between high population differentiation and high migration rate could be due to large effect of random genetic drift in purging rare migrants. However, one may expect a high migration rate for a weedy species that inhabits disturbed areas with a large anthropogenic impact. Moreover, some closely situated populations (< 1 km) were highly differentiated, suggesting the possible role of other factors such as long distance seed dispersal due to anthropogenic activities. Long distance dispersal has also been reported in other studies on *A. thaliana* that found common
multilocus genotypes were shared between populations (Bomblies et al. 2010; Lewandowska-Sabat et al. 2010).

Additionally dispersal in time was observed in one third of populations (10 out of 29) in which 29 % of seeds on average descended from two or three years before present. The average generation time for these populations exhibiting dispersal in time was 1.5 years. This is lower than the estimates based on historical effective population size (average 4 years). The discrepancy between two estimates is probably due to the fact that historical $N_e$ reflects allelic variation over a long period relative to estimates based on short-term temporal sampling. In populations where no plants in the above ground were observed during field work in a given year, recolonization happened the subsequent year, likely due to regeneration from seed bank. This indicates a significant contribution of seed bank to population dynamic in Norwegian population of A. thaliana. In many cases a high fluctuation in genetic diversity between years observed in genetically diverse populations is mostly attributed to the variation in regeneration of distinct multilocus genotypes, MLGs, from the seed bank. The average between-year population differentiation was low ($F_{ST} = 0.095$). This was lower than that recently reported for A. thaliana surveyed over four years in southern Europe ($F_{ST} = 0.16$, Gomaa et al. 2011). In some populations the two most frequent MLGs were differentiated at only one SNP site, indicating a mutation as the source of variation. In addition, signature of historical recombination events was observed through the presence of all four possible allele combinations at two-locus haplotype in several populations (sensu Stumpf & McVean 2003). The results indicate that the current pattern of genetic variation in natural populations of A. thaliana in Norway is shaped by historical events such as mutation, colonization and recombination. Despite of frequent migrations events through seed and pollen dispersal in the natural populations of A. thaliana, seed bank play a substantial role in overall population dynamic.

**Patterns of genetic diversity and structure of A. lyrata in contrasting regions (Paper IV)**

Patterns of genetic diversity and differentiation in natural populations of A. lyrata were compared between three regions in northern Europe. The level of genetic differentiation among Icelandic populations ($F_{ST} = 0.1$; mean geographical distance 93 km, range 8.6-182 km) was smaller than observed for Swedish ($F_{ST} = 0.19$; mean geographical distance 40 km,
range 2-85 km) and Norwegian ($F_{ST} = 0.30$; mean geographical distance 165 km, range 2-385 km) populations. Additionally genetic differentiation among populations distributed over similar area in Icelandic was still considerably lower compared to Swedish and Norwegian populations. Genetic diversity in Icelandic populations ($H_E = 0.35$) was similar to that observed in Sweden ($H_E = 0.33$), and both were substantially higher than what found in Norwegian populations ($H_E = 0.25$). The discrepancy in the level of genetic diversity between regions is probably due to a high allelic richness in the Icelandic and Swedish populations compared with Norwegian ones. A significant relationship between genetic and geographical distance was observed in Icelandic populations ($r = 0.55$, $P = 0.01$) indicating a pattern of isolation by distance (IBD) and IBD was also evident in Norway and Sweden. However, the slope of the regression line ($b$) was steeper in Norwegian ($b = 0.44$) and Icelandic ($b = 0.45$) populations compared to Swedish ($b = 0.15$) populations. The observed pattern of IBD in Icelandic populations of *A. lyrata* is inconsistent to what Schierup *et al.* (2008) found when examining the self-incompatibility gene, S-locus. The observed IBD pattern at neutral markers is as expected because it has been shown that gene flow by both seed and pollen dispersal is restricted in *A. lyrata* (Schierup *et al.* 2006). IBD in natural populations of *A. lyrata* has also been documented in other studies, at both a local (Clauss & Mitchell-Olds 2006; Gaudeul *et al.* 2007) and continental scale (Muller *et al.* 2008; Ansell *et al.* 2010; Lloyd *et al.* 2011).

Interestingly, there was no significant differences in historical migration rate, $M$ ($M = m/u$, where $m$ and $u$ are immigration and mutation rate per generation respectively) between regions. However, historical effective size measured based on theta ($\theta$) was significantly larger in Icelandic than Swedish and Norwegian populations. The discrepancy between similar levels of genetic diversity, but considerably different historical sizes is probably due to higher private allelic richness found in Icelandic compared with Swedish populations. Icelandic populations, with low levels of population differentiation, exhibit larger effective population sizes compared to Scandinavian populations. It is therefore likely that the low level of population structure ($F_{ST}$) in Icelandic populations can be explained by a high historical effective population size, rather than high levels of gene flow.
Conclusions and further remarks

The results of this study show that both *A. thaliana* and *A. lyrata* maintain seed banks, preserve genetic variation and increase the effective population size in their distribution range in Norway. However, the investment in the seed bank is considerably higher in *A. thaliana* than in *A. Lyrata*, and is consistent with other studies showing high seed bank density in annuals relative to perennials. Rapid germination of *A. lyrata* seeds probably leads to low seed bank densities, while the large seed size limits the dispersal ability. In *A. thaliana*, the results indicate that populations experience a relatively high degree of immigration from other populations (dispersal in space), a pattern which is expected from a weedy species inhabiting disturbed habitats impacted by human activities. Moreover, one third of the populations exhibit dispersal in time. Further studies should be aimed at understanding the molecular mechanisms of this. This is the first study that attempts to estimate real-time migration rate and dispersal in time in plant populations. More studies are therefore needed to test whether the observed pattern is valid for other plants, and to develop better models to understand the process.

Comparing patterns of genetic diversity and structure in *A. lyrata* populations from different regions revealed extremely low population differentiation among Icelandic populations compared to in Scandinavia. This pattern is more likely due to large effective population size rather than immigration *per se*, and this suggests that comparing patterns of genetic structure between habitats could be a powerful approach to understand the evolutionary mechanisms behind the current distribution of plant species.
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Lloyd MW, Roche B, Roberts RP (2011) Genetic variation and population structure of Arabidopsis lyrata ssp. lyrata (Brassicaceae) along the eastern seaboard of North America. Castanea 76, 28-42.


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# Doctoral theses in Biology

**Norwegian University of Science and Technology**  
**Department of Biology**

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<td>Åsa Maria O. Espmark Wibe</td>
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<td>Marit Stranden</td>
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<td>Coastal heath vegetation on central Norway; recent past, present state and future possibilities</td>
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<td>Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (Heliothis virescens, Helicoverpa armigera and Helicoverpa assulta)</td>
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Biology  
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Levels and effects of persistent organic pollutants (POPs) in seabirds  
Retinoids and \( \alpha \)-tocopherol – potential biomarkers of POPs in birds?

2006 Ivar Herfindal  
Biology  
Dr.scient  
Life history consequences of environmental variation along ecological gradients in northern ungulates

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Biology  
ph.d  
Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*

2006 Jan Ove Gjershaug  
Biology  
Dr.philos  
Taxonomy and conservation status of some booted eagles in south-east Asia

2006 Jon Kristian Skei  
Biology  
Dr.scient  
Conservation biology and acidification problems in the breeding habitat of amphilians in Norway

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Biology  
ph.d  
Aceta Oophaga and Aceta Excavata – a study of hidden biodiversity

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Biology  
ph.d  
Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway

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Biology  
ph.d  
Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates

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Biology  
ph.d  
Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania

2006 Anna Maria Billing  
Biology  
ph.d  
Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction

2006 Henrik Pärn  
Biology  
ph.d  
Female ornaments and reproductive biology in the bluethroat

2006 Anders J. Fjellheim  
Biology  
ph.d  
Selection and administration of probiotic bacteria to marine fish larvae

2006 P. Andreas Svensson  
Biology  
ph.d  
Female coloration, egg carotenoids and reproductive success: gobies as a model system

2006 Sindre A. Pedersen  
Biology  
ph.d  
Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine

2006 Kasper Hancke  
Biology  
ph.d  
Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae

2006 Tomas Holmern  
Biology  
ph.d  
Bushmeat hunting in the western Serengeti: Implications for community-based conservation

2006 Kari Jørgensen  
Biology  
ph.d  
Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Helothis virens*

2006 Stig Ulland  
Biology  
ph.d  
Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry

2007 Snorre Henriksen  
Biology  
ph.d  
Spatial and temporal variation in herbivore resources at northern latitudes

2007 Roelof Frans May  
Biology  
ph.d  
Spatial Ecology of Wolverines in Scandinavia

2007 Vedasto Gabriel Ndiblema  
Biology  
ph.d  
Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
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<td>Anne Skjetne Mortensen</td>
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<td>&quot;The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (<em>Gadus morhua</em>): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations&quot;</td>
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Biology  
Neurons forming the network involved in gustatory coding and learning in the moth Heliothis virescens; Physiological and morphological characterisation, and integration into a standard brain atlas

2009 Trygve Devold Kjellsen  
Biology  
Extreme Frost Tolerance in Boreal Conifers

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Biology  
Coevolutionary interactions between common cuckoos Cuculus canorus and Fringilla finches

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Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter

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Functional responses of perennial grasses to simulated grazing and resource availability

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Egg characteristics and development of larval digestive function of cobia (Rachycentron canadum) in response to dietary treatments -Focus on formulated diets

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Intraspecific competition in stream salmonids: the impact of environment and phenotype

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Biology  
Molecular studies of genetic structuring and demography in Arabidopsis from Northern Europe

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Biology  
Wildlife Conservation and People’s livelihoods: Lessons Learnt and Considerations for Improvements. Tha Case of Serengeti Ecosystem, Tanzania

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Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis

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Population Ecology of Eriophorum latifolium, a Clonal Species in Rich Fen Vegetation

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The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits

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Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy

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Arabidopsis thaliana L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS— The science of space experiment integration and adaptation to simulated microgravity

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