DISSERTATIONS IN
FORESTRY AND
NATURAL SCIENCES

**Kaisa Heimonen**

# *Plant-insect interactions on silver birch under a warming climate*

## *A latitudinal translocation experiment*

Publications of the University of Eastern Finland
*Dissertations in Forestry and Natural Sciences No 181*

UNIVERSITY OF
EASTERN FINLAND

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No 181

Academic Dissertation
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Author’s address: University of Eastern Finland
Department of Biology
P.O. Box 111
80101 JOENSUU
FINLAND
email: kaisa.heimonen@uef.fi

Supervisors: Professor Heikki Roininen, Ph.D.
University of Eastern Finland
Department of Biology
P.O. Box 111
80101 JOENSUU
FINLAND
email: heikki.roininen@uef.fi

Researcher Anu Valtonen, Ph.D.
University of Eastern Finland
Department of Biology
P.O. Box 111
80101 JOENSUU
FINLAND
email: anu.valtonen@uef.fi

University Researcher Sari Kontunen-Soppela, Ph.D.
University of Eastern Finland
Department of Biology
P.O. Box 111
80101 JOENSUU
FINLAND
email: sari.kontunen-soppela@uef.fi

Reviewers: Docent Tero Klemola, Ph.D.
University of Turku
Department of Biology
Section of Ecology
20014 TURKU
FINLAND
email: tero.klemola@utu.fi

Docent Tarmo Virtanen, Ph.D.
University of Helsinki
Department of Environmental Sciences
P.O. Box 65
00014 HELSINKI
FINLAND
email: tarmo.virtanen@helsinki.fi

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|---|---|
| Opponent: | Professor Julia Koricheva, Ph.D.<br>Royal Holloway, University of London<br>School of Biological Sciences<br>Egham<br>Surrey<br>TW20 0EX<br>UNITED KINGDOM<br>email: julia.koricheva@rhul.ac.uk |

## ABSTRACT

Due to climate warming it is predicted that the abundance of insects will increase and many herbivore species will shift their ranges to higher latitudes. Boreal forests will thus face increasing herbivore pressure in the future. Silver birch (*Betula pendula* Roth) is a common deciduous tree species in boreal forests of high ecological and economical significance. It has been predicted that the proportion of birch in boreal forests will increase as a result of climate warming, but because herbivore pressure is also likely to increase, it is important to study the vulnerability of silver birch to polewards-spreading herbivores.

The research involved using a latitudinal translocation experiment consisting of 26 micropropagated silver birch genotypes originating from six latitudinal populations (60°N-67°N) in Finland. The genotypes were planted at three different sites (60°N, 62°N and 67°N) to test the susceptibility of birch genotypes from different latitudinal populations to local herbivorous insects. The effect of the latitudinal translocation of birch genotypes towards higher or lower latitudes on the susceptibility of genotypes to herbivorous insects was also studied. Furthermore, this thesis explored which plant traits related to plant growth and phenology were associated with susceptibility.

Local herbivores were able to colonize and feed on all the silver birch genotypes, indicating that herbivorous insect species, which are expected to shift their ranges to higher latitudes with climate warming, will be able to colonize and utilize novel birch genotypes. In addition, the community compositions of herbivores differed among the birch genotypes originating from different populations. These results imply that the community composition of herbivorous insects on silver birch will change in the future, and this may affect the herbivory.

Latitudinal translocation towards lower latitudes increased herbivore damage, whereas a shift towards higher latitudes decreased the damage. This supports the idea that high-latitude plants are preferred by herbivores, and as the insects spread towards higher latitudes they will be encountering host plants, which are more susceptible to herbivore damage than those in their present ranges. This, combined with the increasing abundance of insects, will increase herbivore damage to birch in the future.

The phenological syndrome of late bud burst and early growth cessation found in the high-latitude birch genotypes, which led to a short growing season and small size, made these genotypes susceptible to herbivore damage. Differences among the silver birch genotypes in their phenology and size also explained variation in the community composition of the herbivorous insects. These results highlight the importance of plant phenology and growth to herbivores, plant traits which will most likely be affected by rising temperatures in the future.

Together, these results imply that climate warming will increase herbivore damage to silver birch and cause changes in the community composition of herbivores on birch. The increase in herbivory should be taken into account when predicting the growth and productivity of birch as well as the future forest composition.

*Universal Decimal Classification: 504.7, 574.4*

*CAB Thesaurus: climate change; global warming; herbivores; insects; host plants; community ecology; insect communities; herbivory; Betula pendula; silver birch; phenology; populations; genotypes*

*Yleinen suomalainen asiasanasto: ilmastonmuutokset; kasvinsyöjät; hyönteiset; hyönteistuhot; eliöyhteisöt; isäntäkasvit; rauduskoivu; siirtoistutus; fenologia; populaatiot; genotyyppi*

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Joensuu *Kaisa Heimonen*

## LIST OF ABBREVIATIONS

| | |
|---|---|
| AIC | Akaike Information Criteria |
| DistLM | Distance-based linear model |
| DOY | Day of year |
| NMDS | Non-metric multidimensional scaling |
| PCO | Principal coordinate analysis |
| PERMANOVA | Permutational multivariate analysis of variance |
| SIMPER | Similarity percentage analysis |
| VOC | Volatile organic compound |

## LIST OF ORIGINAL PUBLICATIONS

This thesis is based on data presented in the following articles, referred to by the Roman numerals I-III.

**I** Heimonen K, Valtonen A, Kontunen-Soppela S, Keski-Saari S, Rousi M, Oksanen E and Roininen H. Colonization of a host tree by herbivorous insects under a changing climate. *Oikos, doi: 10.1111/oik.01986, 2014.*

**II** Heimonen K, Valtonen A, Kontunen-Soppela S, Keski-Saari S, Rousi M, Oksanen E and Roininen H. Insect herbivore damage on latitudinally translocated silver birch (*Betula pendula*) – predicting the effects of climate change. *Climatic Change 131: 245–257, 2015.*

**III** Heimonen K, Valtonen A, Kontunen-Soppela S, Keski-Saari S, Rousi M, Oksanen E and Roininen H. Susceptibility of silver birch (*Betula pendula*) to herbivorous insects is associated with the size and phenology of the host – implications for climate warming. Submitted manuscript.

The above publications have been included at the end of this thesis with their copyright holders' permission.

## AUTHOR'S CONTRIBUTION

Sari Kontunen-Soppela, Elina Oksanen and Matti Rousi designed and realized the common garden experiment. Heikki Roininen formulated the original research idea which was modified by the present author. The present author planned the studies together with her supervisors, was responsible for all the fieldwork concerning the herbivore data, conducted all data analyses and was the main author of the articles. The articles were produced together with the co-authors.

# Contents

# 1 Introduction

## 1.1 PLANT-INSECT INTERACTIONS UNDER A WARMING CLIMATE

The global climate has warmed by about 0.8°C over the last century and the predictions for the increase in temperature over the next century range from 0.3°C to 4.8°C (IPCC, 2013). In particular the high-latitude regions are expected to warm rapidly. Climate warming affects the ecology of nearly all living species and disturbs the interaction between species (Walther, 2010). One of the most important interactions is the one that takes place between plants and herbivorous insects. Together they represent over half of the described species on Earth and play a significant role in ecosystem functioning (Futuyma & Agrawal, 2009). Thus changes in the interactions between insects and their host plants can have cascading effects on the entire ecosystem.

Organisms can respond to changing environmental conditions by adapting through natural selection, via phenotypic plasticity (i.e., the ability of a genotype to show different phenotypes in different environments) and/or by moving to more favorable habitats (Hoffmann & Sgrò, 2011). The response of plants and insects to environmental changes and the speed of the response vary. Plants adapt to changes slowly because they are sessile, and many of the species have long generation spans (especially trees) (Jump & Peñuelas, 2005), whereas insects are mobile and have short generation spans and can therefore respond rapidly to changes (Bradshaw & Holzapfel, 2001).

Climate warming will affect the plants and insects both directly and indirectly (Figure 1). Direct effects include the accelerated growth of both plants and insects under elevated temperature (up to the limit of their temperature optima) (Topp

& Kirsten, 1991; Lindroth et al., 1997; Rustad et al., 2001; Way & Oren, 2010). Exposure to elevated temperature may have positive or negative effects on photosynthesis and the speed of development, depending on the plant species and the degree of warming (Morison & Lawlor, 1999; Stinziano & Way, 2014). Warming also influences the quality and quantity of primary production (Zvereva & Kozlov, 2006) and the levels of secondary metabolites in plants (Bidart-Bouzat & Imeh-Nathaniel, 2008). Warming accelerates insect metabolism (Gillooly et al., 2001) and increases their development rates, survival, reproductive potential and the number of generations produced per season (Bale et al., 2002; Pöyry et al., 2011; Savage et al., 2004). Additionally, as the climate warms, many plant and insect species will shift or expand their ranges towards higher latitudes or altitudes in order to obtain the optimum temperature for growth and reproduction (Chen et al., 2011; Harsch et al., 2009; Parmesan & Yohe, 2003; Virtanen & Neuvonen, 1999).

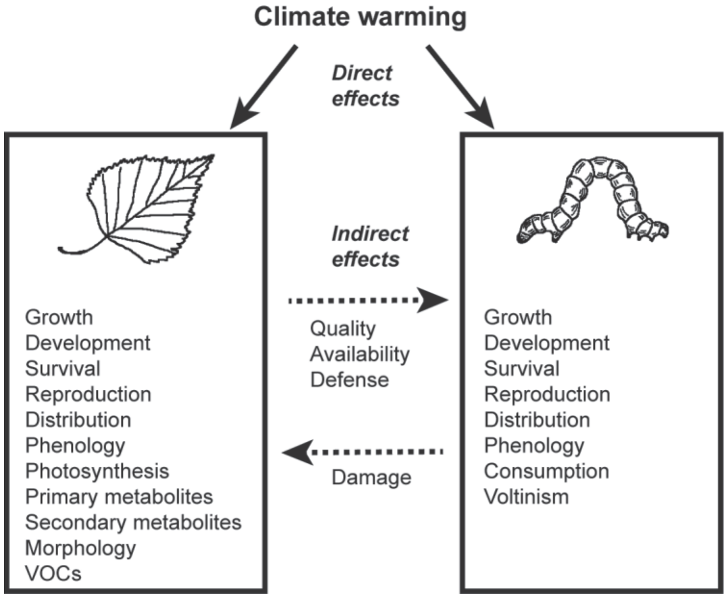

***Figure 1.*** *Direct and indirect effects of climate warming on plants and herbivorous insects.*

Climate warming will also impact the interacting species indirectly through the changes experienced by the reciprocal species. For example, the increased consumption by insects resulting from a faster metabolism leads to increased herbivory on plants (Lemoine et al., 2013). Warming also generally decreases concentrations of plant phenolics (Zvereva & Kozlov, 2006), which have been shown to act as deterrents against insects (Bennett & Wallsgrove, 1994). Decreased phenolic levels may lead to increased feeding by herbivores. Elevated temperature increases the production of volatile organic compounds (VOCs) in plants (Peñuelas & Staudt, 2010). VOCs are emitted, for example, when plants are under attack by herbivores and help the predators and parasitoids to locate their prey (Turlings et al., 1990). Changes in VOC emissions may therefore influence the top-down control of herbivores. Because vigorously growing plants have been found to attract insects (Price 1991; Carr et al., 1998; Cornelissen et al., 2008), and larger plants may be easily detected by the herbivores (Haysom & Coulson, 1998; Wise & Abrahamson, 2008), warming temperatures may lead to high herbivory on plants that can take advantage of the increase in temperature in their growth. Thus the interactions between plants and insects will most likely change in the future due to the warming climate.

Climate warming has already been found to alter the phenology of species. For example, in several tree species, bud burst occurs earlier than before (Chmielewski & Rötzer, 2001), and butterflies advance their spring flight (Forister & Shapiro, 2003) due to the warmer temperatures. These changes in the phenology of plants and herbivores may lead to phenological asynchrony of the interacting species (Schwartzberg et al., 2014; van Asch et al., 2007). Especially for early season herbivores, it is important that hatching is synchronical with the emerging of leaves, since too early hatching leads to starvation of the larvae in the absence of young leaves (Tikkanen & Julkunen-Tiitto, 2003; van Asch & Visser, 2007). Too late hatching, on the other hand, forces the larvae to feed on poor quality food, as older leaves are less nutritious, tougher and have lower water content than young leaves (Mattson, 1980; Haukioja et al., 2002; Riipi et al., 2002), which reduces the larvae's growth (Ayres & MacLean, 1987).

The range shift of many insect species towards higher latitudes due to global warming will increase the population sizes and species richness of herbivores at higher latitudes (Chen et al., 2011; Parmesan & Yohe, 2003). In addition, it is predicted that the abundance of insects will increase with the warming climate, because warming will enhance insect development, survival and growth (Roy et al., 2001; Savage et al., 2004). The increasing abundance of insects will lead to increased consumption of host plants.

Range shifts are taking place at a much slower pace in the case of plants than in insects (Parmesan & Yohe, 2003; Walther et al., 2002). The host plants will therefore be facing novel herbivore species in the future, and herbivore species will encounter new host plants or at least host plant genotypes in the new distribution area. Local adaptation has been recorded in both plants and insects (Garrido et al., 2012). If plant populations are adapted to defending themselves against local herbivores (Local host adaptation hypothesis; Sork et al., 1993), they might be less efficient in defending themselves against the new invading herbivore species. On the other hand, insects are expected to become locally adapted to their host plants (Adaptive deme formation hypothesis; Edmunds & Alstad, 1978). Insect species moving to higher latitudes encounter novel host plants or host plant genotypes that may have different combinations of defensive traits and nutritional quality, which in turn may hinder the ability of herbivores to utilize the novel plant material.

Increasing herbivore abundance and the movement of herbivore species towards higher latitudes represent a potential threat to the plant populations. Studies on the latitudinal gradients in plant palatability have shown that herbivores actually prefer plant material from high latitudes (Moles et al., 2011a; Morrison & Hay, 2012; Pennings et al., 2001), and the reason for this might lie in the level of defense, which is expected to be lower at high latitudes (Coley & Aide, 1991; but see Moles et al., 2011a; 2011b), but could also lie in the nutritional quality of the plants (Ho & Pennings, 2013). If high-latitude plants are more susceptible to herbivores than low-latitude ones, we can expect an even higher risk of increased herbivory in the future.

## 1.2 TRANSLOCATION STUDIES

Translocation studies along latitudinal gradients have been used to simulate the effect of climate warming on plants (Carter, 1996; De Frenne et al., 2011; Matyas, 1994) and also on insect herbivory and herbivore colonization (Andrew & Hughes, 2007; Nooten et al., 2014; Nooten & Hughes, 2014). In these experiments, plants are translocated towards lower or higher latitudes from their original growth site. The translocation site may be within the current distribution area of the plant species or outside it (the possible future distribution area). Translocation to lower latitudes mimics future environmental conditions. i.e., increasing temperature and herbivore pressure. In the Northern Hemisphere the temperature falls 1°C for every 150 km polewards (De Frenne et al., 2013). The latitudinal gradient in insect species richness shows a decrease towards higher latitudes (e.g., Kocher & Williams, 2000; Salazar & Marquis, 2012; Virtanen & Neuvonen, 1999), and the abundance of insects seems to follow the same gradient (Garibaldi et al., 2010; Kozlov et al., 2015, 2013; Salazar & Marquis, 2012).

The effect of translocation on plants is species-dependent. While some plant species show local adaptation, i.e., they show the best performance at temperatures close to those of their original growth site (De Frenne et al., 2011), in other species translocation towards lower latitudes increases their height and survival (Matyas, 1994). On the other hand, some species show decreasing performance when grown at lower latitudes (Carter, 1996). In addition, populations of species with wide latitudinal distribution can respond differently to translocation, depending on where they originate (Reich & Oleksyn, 2008).

There are few latitudinal translocation studies addressing herbivory and herbivore communities (Andrew & Hughes, 2007; Nooten et al., 2014; Nooten & Hughes, 2014). The host plant's translocation to warmer latitudes has not been found to affect the rate of herbivory on Australian shrub species (Andrew & Hughes, 2007; Nooten & Hughes, 2014), but the community composition of herbivores on the host plants showed considerable turnover between the control (current distribution area) and warmer sites (future distribution area) even though the guild structure remained similar (Andrew & Hughes, 2007; Nooten et al., 2014).

### 1.3 SILVER BIRCH AS A STUDY SPECIES

Silver birch (*Betula pendula* Roth) is a widely distributed deciduous tree species in the Northern Hemisphere (Atkinson, 1992). Silver birch is a light-demanding pioneer species that prefers fertile and moist soils. It is a sexually reproducing species with light seeds and relies on wind pollination, which secures high gene flow between populations (Rusanen et al., 2003). However, the genetic diversity of silver birch is high, within populations (Laitinen et al., 2000; Possen et al., 2014; Silfver et al., 2009) as well as between populations (Mutikainen et al., 2000; Pääkkönen et al., 1997). Because of the wide distribution area, local birch populations have adapted to the local light and temperature conditions and formed so-called ecotypes (Li et al., 2003; Myking & Heide, 1995). For example the birch ecotypes from high latitudes cease to grow earlier than those from lower latitudes when grown in similar conditions due to differences in how the photoperiod, temperature and other environmental factors cue their phenology (Myking & Heide, 1995; Viherä-Aarnio et al., 2005).

In Finland, silver birch is the most important deciduous tree both ecologically and economically (Niemistö, 2008). It is a host plant for many insect and mammalian species and it is used, for example, in the manufacture of plywood, furniture and high quality paper (Novriyanti et al., 2010). The proportion of birch in Finnish forests is expected to increase in the future due to global warming from 10% to 20% by the year 2100 (Kellomäki et al., 2008). However, the damage to birch caused by herbivorous insects is also predicted to increase as temperatures rise (Kozlov, 2008), which could cause a decrease in the growth and survival of birch (Wolf et al., 2008). Earlier studies have found that insect removal increases the height and diameter growth of *Betula pendula* saplings (Silfver et al., 2009) while artificial defoliation reduces the relative growth rate and biomass of *Betula pendula* saplings (Mutikainen et al., 2000) and the vertical growth, leaf size and leaf area of *Betula pubescens* saplings (Zvereva et al., 2012). Insect herbivory also increases seedling mortality in *Betula pendula* (Prittinen et al., 2003). Therefore, in the future, models predicting boreal forest composition need to take into account the effects of warming climate on both birch and its associated insect herbivores.

## 1.4 OBJECTIVES OF THE THESIS

Climate change will alter the complex interactions between plants and their herbivorous insects. As many herbivore species shift their ranges towards high latitudes and their abundance increases as a result of warming climate, we can expect herbivore damage to plants to increase in the future. However, it is still unknown whether the insect species that are spreading polewards due to warming climate can colonize and feed on the novel host plant genotypes they will be encountering in the future.

The aim of this thesis is to study the vulnerability of silver birch populations to polewards-spreading herbivorous insects and to explore which plant traits, especially those sensitive to changes in temperature, might expose silver birch to herbivore damage in the future. This was done by exploring the susceptibility of silver birch genotypes originating from a wide latitudinal gradient, grown in the same environmental conditions, to the local herbivorous insects. The more specific aims were to

1. study the colonization by the local herbivores of silver birch genotypes from different latitudinal populations (I).
2. study whether the latitudinal translocation of the silver birch genotypes towards higher or lower latitudes affects their susceptibility to herbivorous insects (I, II).
3. explore the plant traits associated with the herbivore damage, herbivore density and the herbivore communities (III).

# 2 Materials and methods

## 2.1 PLANT MATERIAL AND STUDY SITES

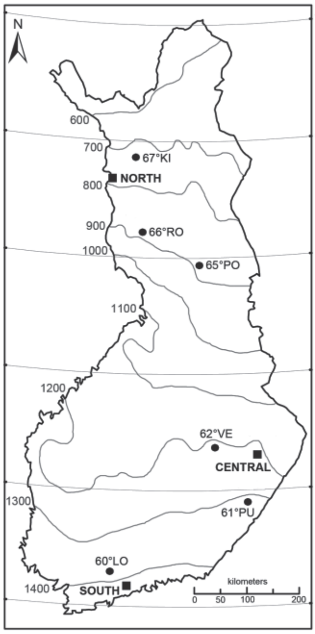

***Figure 2.*** *Map showing the six silver birch source populations (filled circles), the three study sites of the translocation experiment (filled squares), and mean annual temperature sum isoclines.*

A latitudinal translocation experiment using 26 micropropagated genotypes of silver birch was established at three sites in Finland: southern (Tuusula; 60°21.5'N, 25°00.2'E), central (Joensuu; 62°36.1'N, 29°43.4'E) and northern (Kolari; 67°21.2'N, 23°49.7'E) sites (Figure 2). The genotypes originated from six natural birch stands in Finland representing a south-north cline from 60°N to 67°N (Figure 2, Table 1). To my knowledge, this research is the first to use clonally reproduced genotypes of silver birch from several latitudinal populations to study the possible effects of climate warming on birch-insect interactions.

***Table 1.*** *Silver birch populations, their coordinates, abbreviations referring to the populations used in this thesis, number of genotypes originating from each population included in the experiment and the mean annual temperature sum (GDD5 = the sum of daily mean temperatures above 5 °C) for each birch stand (1959-2012; Haylock et al., 2008).*

| **Population** | **Coordinates** | **Abbrev.** | **Number of genotypes** | **Temperature sum (GDD5)** |
|---|---|---|---|---|
| Loppi | 60°36'N, 24°25'E | 60°LO | 4 | 1287 |
| Punkaharju | 61°48'N, 29°19'E | 61°PU | 2 | 1308 |
| Vehmersalmi | 62°45'N, 28°10'E | 62°VE | 5 | 1258 |
| Posio | 65°53'N, 27°39'E | 65°PO | 5 | 876 |
| Rovaniemi | 66°27'N, 25°14'E | 66°RO | 5 | 957 |
| Kittilä | 67°44'N, 24°50'E | 67°KI | 5 | 800 |

Branches from the six birch stands were collected in February and March 2009, and dormant vegetative buds were used for the micropropagation of the 26 genotypes. Ten plantlets per genotype were planted at each study site in July 2010, and thus the total number of plantlets per site was 260.

The study sites differ in thermal conditions and photoperiodic rhythm due to their latitudinal location (Figure 3). The mean annual temperature sum (the sum of daily mean temperatures above 5 °C) varies at the southern site between 1300–1500, at the central site between 1100–1300 and at the northern site between 700–800 (Finnish Meteorological Institute, 2015).

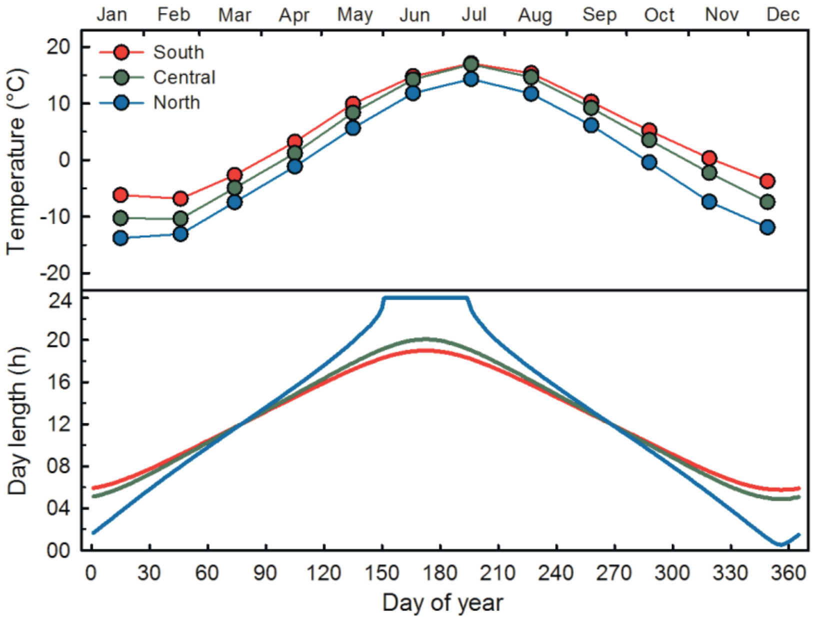

***Figure 3.*** *Monthly mean temperatures (1959-2012; Haylock et al., 2008) and the length of day at the three study sites.*

## 2.2 FIELD MEASUREMENTS

### 2.2.1 Herbivore density, species richness, community composition and herbivore damage

In the first full growing season in 2011, all the chewing, mining and galling insects and the herbivore damage caused were examined visually three times (censuses) on all the plantlets at each study site (Figure 4). In 2012 the insect communities and damage were examined twice. The number of insects from the whole plantlet was calculated and the individuals were assigned to morphospecies instantly or later, on the basis of photographs taken in the field (I). The damage caused by the leaf chewing and leaf mining insect herbivores was estimated visually as the percentage of leaf area lost from 10–30 leaves per plantlet (II).

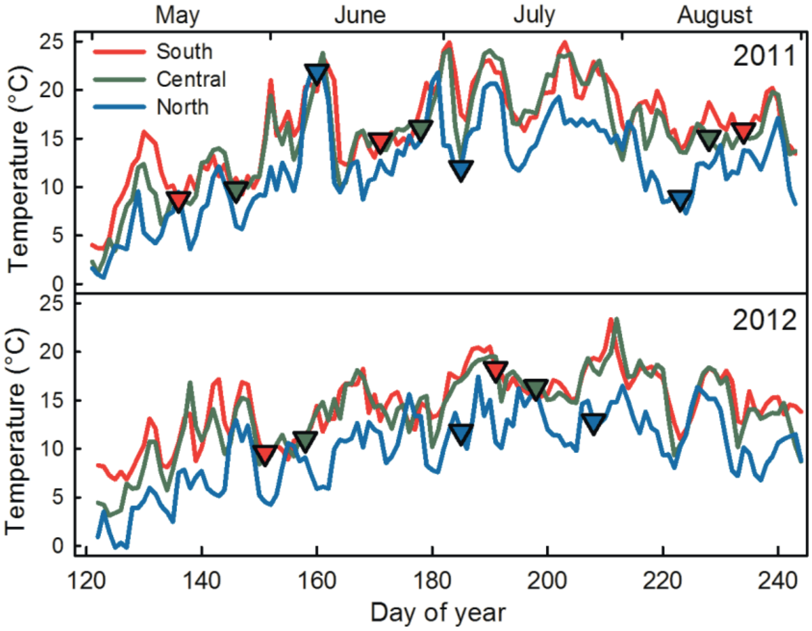

***Figure 4.*** *Daily mean temperatures during the summers 2011 and 2012 at the study sites (Haylock et al., 2008). The triangles indicate the starting day of herbivore damage scoring and community examination, which was done three times (censuses) at each site in 2011 and twice in 2012.*

Herbivore density (individuals/m$^2$ leaf area) was calculated for each plantlet within each census. The total herbivore density per plantlet was calculated by pooling the abundance of herbivores across the censuses within a study year. The mean herbivore damage per plantlet for each census was calculated by averaging all the examined leaves. The mean total herbivore damage per plantlet was calculated by averaging the means of the censuses for both years separately. The mean herbivore damage and density for each genotype at each site was calculated (census-wise and total), for both years separately. Species richness was estimated for each birch population at each study site for both study years separately, using individual-based rarefaction (Gotelli & Colwell, 2001). Herbivore abundance was too low (<20) on some genotypes to allow rarefaction at genotype level. The density of each morphospecies on each plantlet for each census was calculated for the herbivore community composition analysis. The herbivore data of different censuses was pooled within a year to calculate the herbivore density of each morphospecies for the whole growing season. These calculations were made for each study site and each year separately.

### 2.2.2 Plant traits

In order to study which plant traits are associated with herbivore damage and insect communities on silver birch, nine plant traits were measured from the plantlets: height (cm), height in the previous growing season (cm), relative growth rate during the growing season (cm/day), number of leaves, total leaf area ($m^2$), date of bud burst (day of the year), duration of bud burst (days), date of growth cessation (day of the year) and length of the growing season (days). The specific measurement techniques are described in manuscript III.

## 2.3 DATA ANALYSIS

In order to compare the relative differences in herbivore density, damage and species richness across the study sites, the genotypic mean values (in the case of species richness, the population mean values) within each study site and year were standardized to a mean of zero and a standard deviation of one. To be able to estimate the effect of latitudinal translocation, the latitudinal shift (in degrees) for each genotype at each site was calculated as the difference between the study site latitude and the latitude of the population from which the genotype originated.

Linear mixed models were used to test the fixed effects of latitudinal shift and the square of the latitudinal shift (non-linear response) on the standardized herbivore density (I), species richness (I) and herbivore damage (II), and in the case of herbivore density and damage, the random effect of genotype was included in the model. Linear mixed models were also used to test the effect of population, study site and their interaction on relative herbivore density and species richness (I). The Akaike Information Criterion (AIC) was used in model selection.

Linear regressions were used to test the effect of relative herbivore density on relative herbivore damage (II) and the effect of different plant traits on herbivore damage and density (III). In order to analyze whether the herbivore community explains variation in herbivore damage, principal coordinate analysis (PCO) was used to compress the herbivore community data into three axes explaining most of the variation in the original community data. These three axes were then used to explain variation in the herbivore damage in linear regression (II).

Permutational multivariate analysis of variance (PERMANOVA) was used to analyze whether herbivore community compositions at each site and in each year differed among the birch populations originating from different latitudes (I). The effect of latitudinal shift on herbivore community composition was analyzed by a distance-based linear model (DistLM) (I). DistLM was also used to test the effect of different plant traits on herbivore community composition (III). Non-metric multidimensional scaling (NMDS) was used to illustrate the community patterns. Genotype centroids and the Bray-Curtis similarity measure were used in all the community analyses.

Similarity percentage analysis (SIMPER) was used to identify the herbivore species that were causing the dissimilarities in community compositions among the birch populations (I).

A more detailed description of the methodology is provided in the original papers I–III.

# 3 Results and discussion

## 3.1 LOCAL HERBIVORES ARE ABLE TO COLONIZE AND FEED ON NOVEL HOST PLANT GENOTYPES

Herbivorous insect species, which are expected to shift their ranges to higher latitudes due to climate warming, will be able to colonize and utilize novel silver birch genotypes (I, II). Local herbivores were colonizing and feeding on all the birch genotypes (Figure 5) but the preference of different species for certain genotypes led to differences in community compositions on the different birch populations at the southern study site in both years and at the central study site in 2012 (I). The differences in herbivore community composition among the populations at the southern site in 2011 were best explained by differences in the density of *Heliozela hammoniella* (Figure 6A), *Parornix* sp. 1, *Operophtera brumata*, *Strophosoma capitatum* and Tenthredinidae sp. 3, and in 2012, by the density of *Deporaus betulae* (Figure 6B), *Incurvaria pectinea* (Figure 6C), *Eriocrania* spp. (Figure 6D) and *Parornix* sp. 1. At the central site in 2012 the differences in community composition among the populations was mostly driven by *Phyllobius pyri* (Figure 6F), *Caloptilia* sp. 1, *Stigmella lapponica* (Figure 6G) and *Coleophora* sp. 1.

Silver birch populations from different latitudes do not differ clearly in their susceptibility to herbivores where herbivore density and species richness are concerned (I). Relative herbivore density differed among the silver birch populations only in 2012, and the difference was caused by the lower relative herbivore density in the population originating from Rovaniemi (66°RO) compared to the populations from Vehmersalmi (62°VE) and Posio (65°PO). Species richness did not differ among the populations. High-latitude birch populations were not colonized by more herbivores than the low-latitude populations as would

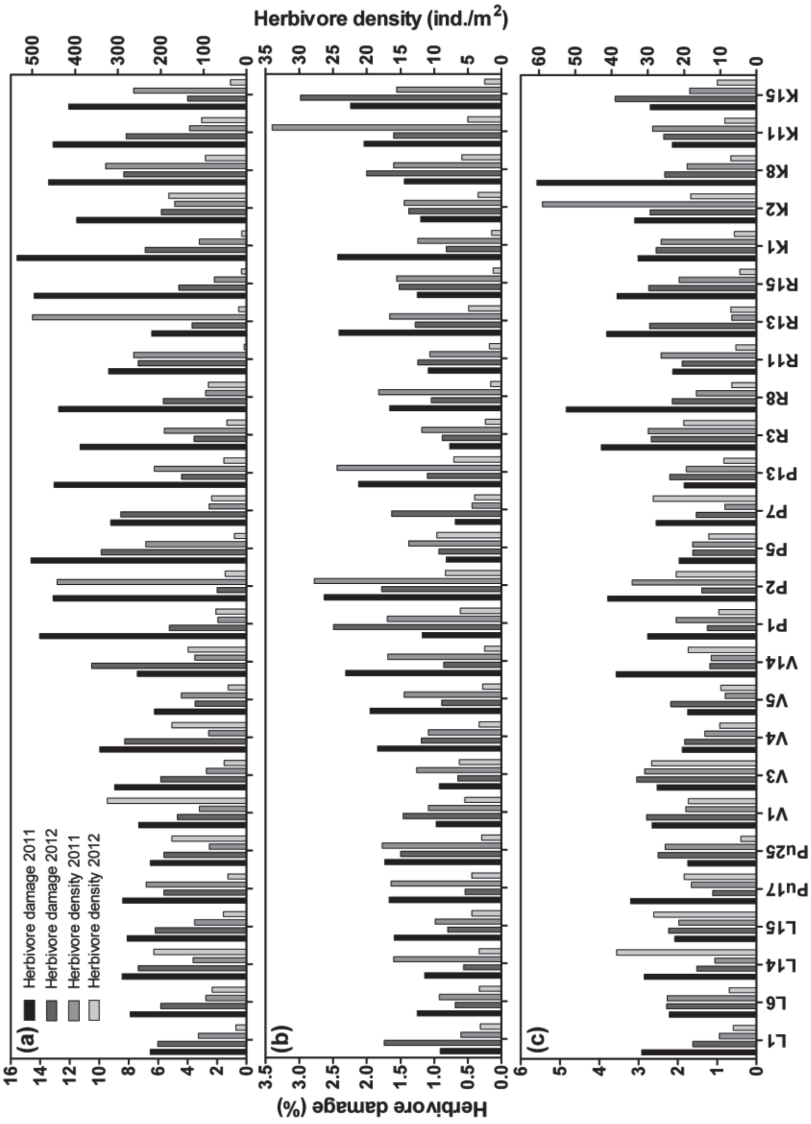

***Figure 5**. Herbivore damage and density in 2011 and in 2012 in silver birch genotypes (a) at the southern, (b) at the central and (c) at the northern study sites. The letters in genotype names indicate the population of origin.*

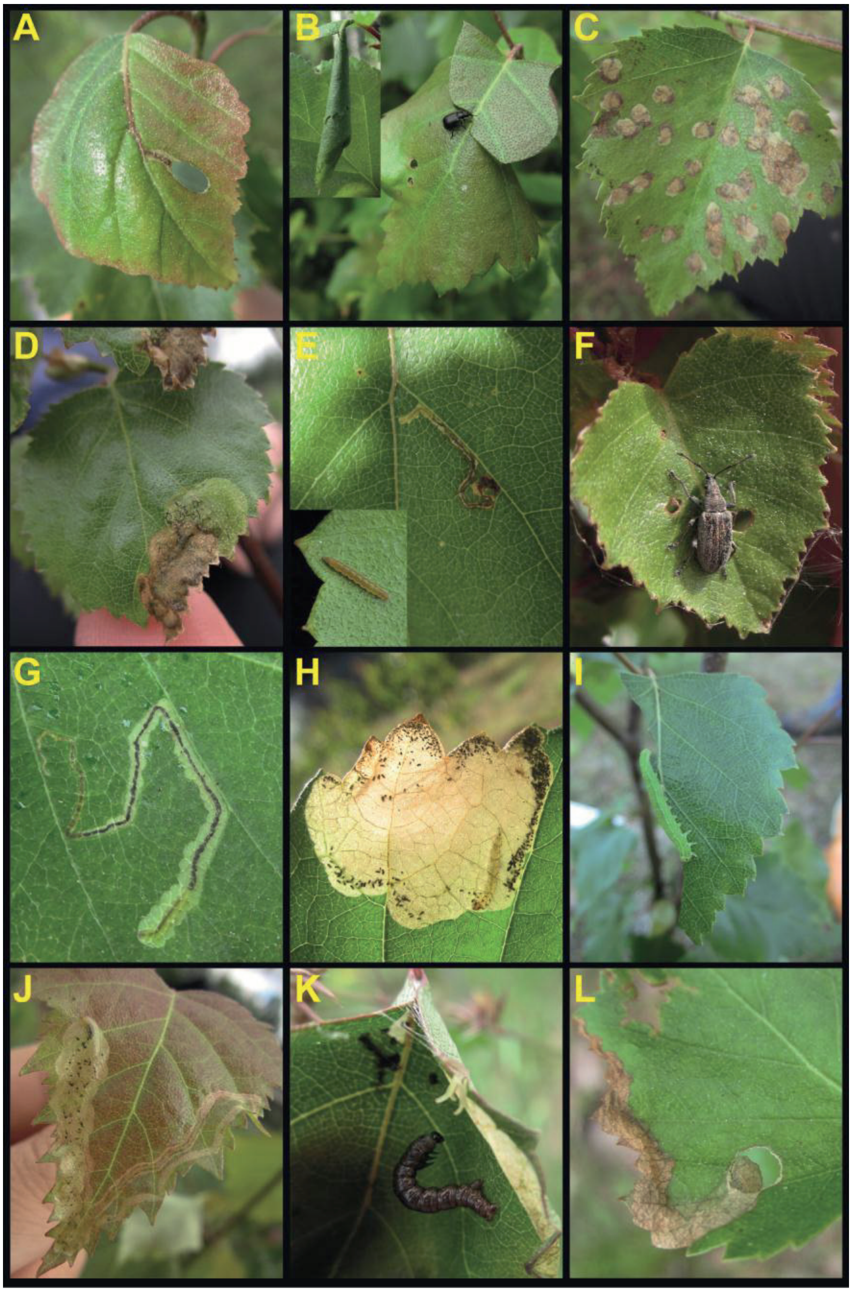

***Figure 6.*** *Some of the most common herbivore species found on the studied Betula pendula genotypes. A) Heliozela hammoniella,, B) Deporaus betulae, C) Incurvaria pectinea, D) Eriocrania sp., E) Bucculatrix demaryella, F) Phyllobius pyri, G) Stigmella lapponica, H) Scolioneura betuleti, I) Amauronematus sp., J) Agromyza alnibetulae, K) Rheumaptera hastata and L) Orchestes rusci. Photos by K. Heimonen.*

have been expected if the herbivorous insect were to prefer high-latitude host plants (Moles et al., 2011a; Morrison & Hay, 2012; Pennings et al., 2001). However, the community composition of herbivores on silver birch is likely to change in the future since insect species moving polewards may shift to novel host plant genotypes. The ability of herbivores to utilize novel birch genotypes was perhaps not a surprising result, since the genetic variability of silver birch within (Laitinen et al., 2000; Possen et al., 2014; Silfver et al., 2009) and between populations is high (Mutikainen et al., 2000; Pääkkönen et al., 1997), which requires herbivore resilience to varying food quality. In addition, many of the insect herbivores feeding on birch are generalists (Seppänen 1970) and are therefore adapted to variation in the quality of nutrition. For example, Ammunét et al. (2011) found that winter moth (*Operophtera brumata*) and scarce umber moth (*Agriopis aurantiaria*), which have been found to invade new areas in northern Fennoscandia with warming climate, were not greatly affected by variation in host plant quality.

## 3.2 LATITUDINAL TRANSLOCATION CAUSES CHANGES IN HERBIVORE DAMAGE AND COMMUNITY COMPOSITION

Latitudinal translocation towards lower latitudes, i.e., future environmental conditions, increased herbivore damage, whereas the shift towards higher latitudes reduced the amount of damage (II). This result from the first study year supports the earlier studies, which have shown that herbivores prefer to feed on high-latitude plants (Moles et al., 2011b; Morrison & Hay, 2012; Pennings et al., 2001). Consequently, as many herbivore species shift their ranges towards higher latitudes, they will encounter host plants, which are more susceptible to herbivore damage than at present ranges. This could increase herbivore damage to birch in the future. Other studies have also predicted an increase in herbivory on trees due to climate warming (Garibaldi et al., 2010; Kozlov, 2008). Fossil records have shown that insect damage to plants increased radically when the global temperature suddenly rose by about 5°C in 10 000 years (Currano et al., 2008).

Latitudinal translocation also caused changes in herbivore community composition (I). The more latitudinally distant the genotypes were, the more dissimilar were their herbivore communities. This result supports the hypothesis that plant populations originating from geographically close proximity support similar herbivore communities and this could result from the genetic similarity of the plants (Bangert et al., 2006a; Barbour et al., 2009; Hochwender & Fritz, 2004; Rusanen et al., 2003).

High intensity of herbivore damage to high-latitude birch genotypes was not explained by the higher herbivore density, species richness or community composition of the herbivores (II). Neither herbivore density nor species richness were affected by the latitudinal translocation of the birch genotypes (I). These results imply that the intensity of herbivore damage is not always dependent on the total abundance of the herbivores. The higher nutritional quality and/or lower defense level of high-latitude plants could lead to heavy consumption by the herbivores. On the other hand, poor quality food can also lead to compensatory feeding by herbivores (Lavoie & Oberhauser, 2004). We also need to bear in mind that the estimates of herbivore density, species richness and community composition are based on a few visual day-time examinations during the growing season, and therefore it was not possible to observe all the herbivores that were causing damage (e.g., ephemeral and nocturnal herbivores).

No herbivore species that could potentially become pests affecting high-latitude birch populations were found in this study (I). Only one of the herbivore species (*Swammerdamia caesiella*) that was found to explain differences among the birch populations in their herbivore community compositions had slightly higher density on the high-latitude genotypes compared to the low-latitude ones. However, this pattern was observed only at one study site in one year. Some of the species showed no latitudinal gradient, while others appeared to prefer low-latitude genotypes.

### 3.3 NO SIGNS OF LOCAL ADAPTATION

No indication of either birch adaptation to local herbivores or adaptation of herbivores to local birch genotypes was detected. The local adaptation hypothesis was rejected because the silver birch genotypes that had been translocated further away from their original growth site did not have higher herbivore damage or density than the genotypes translocated only short distances (I, II). The adaptive deme formation hypothesis was also rejected, since the birch genotypes that were translocated short distances did not have higher herbivore damage or density than the genotypes translocated further.

The lack of local adaptation of birches and herbivores could result from the efficient gene flow between populations of silver birch, since it is a sexually reproducing species with wind pollination and light seeds (Rusanen et al., 2003). The adaptation of herbivores to local host plants depends on the feeding and breeding mode of the insects (Van Zandt & Mopper, 1998). Moreover, many of the herbivorous insect species feeding on silver birch are generalists (e.g., Seppänen, 1970) and should therefore be flexible in their feeding preferences. In addition, this experimental set-up does not allow for the testing of fine-scale local adaptation as none of the translocated genotypes originated from the study sites. Thus, the silver birch genotypes did not encounter their local herbivore communities, and the local herbivores did not encounter their local host plant genotypes.

## 3.4 PHENOLOGICAL SYNDROME LEADS TO INCREASED HERBIVORE DAMAGE

The phenological syndrome (a set of characteristics that co-occur) of late bud burst and early growth cessation, which resulted in a short growing season and small size, made the birch genotypes susceptible to herbivore damage (III). Since these genotypes ceased to produce new leaves early, the existing leaf material was heavily consumed by the herbivores. Photoperiod and temperature are the main factors regulating the phenology of trees. Photoperiod has been thought to be the main regulator of growth cessation in trees (Chen et al., 2012; Li et al., 2003; Takahashi & Koike, 2014), whereas their spring phenology has been found to be controlled more by the temperature (Takahashi & Koike, 2014; Vitasse et al., 2009a; 2009b). In the future, photoperiod may limit the growing season of trees even though increasing temperatures may prolong the active season of some herbivorous insects. Thus, if the trees do not produce new leaves at the end of the growing season, herbivory will concentrate on the late-season leaves, which are also poor nutrition for herbivores and can add to the need for compensatory feeding. Herbivore damage may therefore increase in trees due to climate warming. However, rising temperatures may also enhance the growth of trees (Mäenpää et al., 2011; Rustad et al., 2001; Way & Oren, 2010), and this may, at least partly, compensate for the increasing herbivory.

Birch genotypes with late bud burst may be especially vulnerable to herbivore damage. In both study years, late bud burst led to high herbivore damage (III), probably because insects prefer newly produced leaves which are more nutritious and have a high water content (Haukioja et al., 2002; Mattson, 1980; Riipi et al., 2002). In addition, the abundance and number of herbivore species increases as spring advances and consequently the late emerging young leaves are subject to high herbivore pressure.

### 3.5 VARIATION IN PLANT TRAITS SHAPES THE COMMUNITY COMPOSITION OF THE HERBIVORES

Differences in plant traits among the silver birch genotypes explain variation in the community composition of the herbivorous insects (III). Especially the size of the genotypes and the timing of growth cessation were good predictors of herbivore community composition. It seems that some herbivore species are attracted by or specialize in slow-growing host plants with less above-ground resources, whereas other species prefer vigorous growth and large size. The size of the plant was found to structure the community composition of herbivores also on aspen (Robinson et al., 2012) and coastal willow (Barbour et al., 2015). Different herbivore species also prefer different phenological stages of their host plants, which can lead to differences in the community compositions of herbivores on trees with different phenologies (Crawley & Akhteruzzaman, 1988). Since climate warming is expected to change plant growth and phenology, traits which affect the host-plant selection of herbivores, we can also expect changes in herbivore community composition on plants in the future, which again may have an effect on herbivory.

The genetic similarity rule formulated by Bangert et al. (2006a) suggests that genetically similar plants support similar arthropod communities. The rule has been found to apply at least on many hybridizing tree species (Bangert et al., 2006b; Hochwender & Fritz, 2004; Wimp et al., 2005). Also in study I of this thesis the genotypes originating from geographically close populations, which can be expected to be more genetically similar, had more similar herbivore community composition than did genotypes from distant populations. Bangert et al. (2006a) and Wimp et al. (2007) found that cottonwood trees that were genetically similar also had similar chemical composition in addition to similar arthropod communities. These studies imply that heritable plant traits shape the associated herbivore community and that these traits can be used to predict the community composition of herbivores.

### 3.6 VARIATION IN BIRCH PHENOLOGY AND SIZE EXPLAIN LATITUDINAL PATTERNS IN HERBIVORE DAMAGE AND COMMUNITY COMPOSITION

The higher herbivore damage observed in the high-latitude birch genotypes and the increasing differences in the community composition along the latitudinal translocation gradient could be explained by the differences in phenology leading to differences in size among the birch populations (III). The high-latitude genotypes had late bud burst and early growth cessation, which led to small size and heavy consumption by herbivores (III). We can expect other unmeasured plant traits also to influence the high susceptibility to herbivory of high-latitude genotypes. The preference of herbivores for high-latitude plants, also found in other studies (Moles et al., 2011a; Pennings et al., 2001), could be caused by the lower defense capability of high-latitude plants (Coley & Aide, 1991). This has been a common belief for a long period of time (Moles, 2013), although recent studies have contradicted these results (Moles et al., 2011b). The better nutritional quality of the high-latitude plants has also been suggested as an explanation for the herbivore preference for these plants (Ho & Pennings, 2013). The selection of a host plant by herbivores is a complicated process, and herbivorous insects do not form a uniform group of herbivores that all respond similarly to variation in host plant quality. The ranking of host plant individuals by different herbivore species differs, and even individual insects within species may have different preferences, depending on their degree of development, sex and the population of origin (Bernays & Chapman, 1994). The variation among herbivores in their preferences for different plant traits makes it hard to draw general conclusions about the reasons for the latitudinal susceptibility gradient, but it seems that in silver birch the phenology and size of the host plant play a role in this pattern.

Since birch pollen and seeds are light and are spread easily by wind, birch populations are a mixture of genotypes adapted to different environmental conditions. Within these mixed stands, the genotypes from low-latitude populations will have a competitive advantage in a warming climate, since they have a longer growing season and can therefore produce leaves over a longer period and also grow larger, which again helps them to compensate for increasing herbivore damage (III). This advantage may also help the low-latitude genotypes to spread to higher latitudes in the future. However, it has been debated whether low-latitude birches are capable of surviving at higher latitudes resulting from spring frost damage caused by the too early bud burst of low-latitude trees (Augspurger, 2013; Vitasse et al., 2014).

### 3.7 TEMPORAL VARIATION IN BIRCH-INSECT INTERACTIONS

The susceptibility of silver birch genotypes to herbivorous insects changes between years. A latitudinal gradient in herbivore damage was found only in the first study year (II), and there was an interaction between population and study year and between genotype and year in herbivore density (II). Moreover, most of the plant traits were associated with herbivore damage only in the first study year (III). Changes in the growth environment, such as temperature and precipitation, between years may also change the susceptibility of the genotypes to herbivores (Cronin et al., 2001). Also, the ontogenetic phase of plants has been found to change the defense capability and the nutritional quality of plants, which in turn affects their palatability (Barton & Koricheva, 2010). The size of herbivore populations fluctuates from year to year, and therefore the community compositions of herbivores also vary between years (I, Figure 7). Different insect species have been found to prefer different host plant genotypes (Maddox & Root, 1990). In addition, different herbivore species prefer different ontogenetic phases of their host plants (Boege & Marquis, 2005). However, if even in some years high-latitude genotypes are particularly susceptible to herbivore damage, more intense herbivory can be expected in the future.

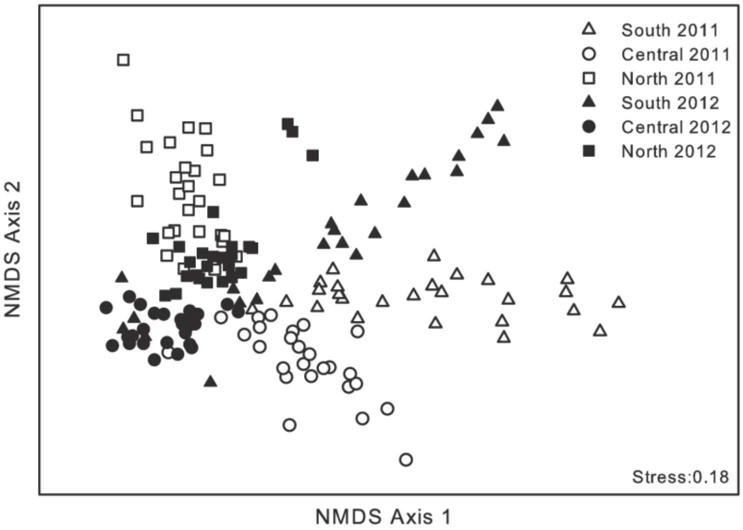

***Figure 7.*** *Non-metric multidimensional scaling ordination of the community composition of herbivorous insects on Betula pendula genotypes at the three study sites in two study years, based on Bray-Curtis similarity. Each symbol represents the centroid of a genotype. Genotypes (symbols) close to each other in the figure have similar community compositions, while increasing distance indicates growing dissimilarity.*

# 4 Conclusions

The aim of this thesis was to study the vulnerability of silver birch populations to herbivorous insects under conditions of warming climate. Climate warming is expected to increase herbivory on forest trees, and the results of this thesis support this view. Herbivorous insect species which are increasing in abundance and shifting their ranges polewards are able to colonize and feed on novel silver birch genotypes. It also seems that the birch genotypes that herbivores will encounter in the future at higher latitudes are more susceptible to herbivore damage than those utilized at present. Predictions made about the increasing proportion of birch in boreal forests should take into consideration the effects of increasing herbivore damage on the growth and survival of birch.

Climate warming can be expected to alter the phenology and growth of trees, and this will in turn cause changes in the community composition of herbivores and herbivory on trees. Especially the late bud burst and early growth cessation of birches from high-latitude populations, which causes reduction of their size, leads to heavy consumption by the herbivores. This means that if photoperiod restricts the length of the growing season of trees, but at the same time the warming climate enables some herbivorous insects to prolong their active season, the concentration of herbivory on the existing leaves during the late season may have a profound effect on the trees. The longer growing season and larger size of low-latitude birches may give them a competitive advantage in a warmer world if they can compensate for the increase in herbivory by increasing growth.

The areas at higher northern latitudes will warm most rapidly due to climate change. Thus, boreal forests are facing rapid, both abiotic and biotic, changes in their growth environment, which will in turn affect the productivity and composition of the forests. To predict the future of boreal forests, studies on plant-insect interactions under conditions of changing climate are needed, since herbivorous insects can greatly influence the survival and growth of trees. The latitudinal translocation experiments used in this thesis offer one tool for these studies.

Plant-insect interactions are a complicated subject of research. It is nevertheless an extremely relevant topic, due to the rapid changes taking place in the global environment, changes which affect single species, interactions among species, communities and entire ecosystems. Experiments in field conditions are challenging, but the most natural way to study plants and their herbivores. Different abiotic conditions at different locations, temporal changes in these environmental conditions, temporal fluctuations in herbivore populations and ontogenetic changes in plants all shape the relationship between plants and herbivorous insects. In addition, plants and insects interact with other members of the same or higher trophic levels. Climate warming will undoubtedly lead to changes in plant-insect interactions in the future. Furthermore, the increase in $CO_2$ and other greenhouse gases, ozone, UV radiation and extreme weather events will also affect both plants and insects. It is therefore hard to make predictions for the future on the intensity of herbivory and its effects on different host plants, and further research is needed.

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**Kaisa Heimonen**

# *Plant-insect interactions on silver birch under a warming climate*

## *A latitudinal translocation experiment*

Climate warming will increase the abundance of herbivorous insects and shift their ranges towards higher latitudes, thus posing a threat to boreal forests. This thesis provides information about the vulnerability of silver birch (Betula pendula) populations from different latitudes to polewards-spreading herbivores and about the plant traits associated with the vulnerability. This information can be used when predicting the growth and productivity of birch as well as future forest composition.

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