Doctoral Thesis June 2020

The interaction between native insect herbivores, introduced plant species and climate change in Iceland

Brynja Hrafnkelsdóttir

Landbúnaðarháskóli Íslands
Agricultural University of Iceland
Faculty of Environmental and Forest Sciences

The interaction between native insect herbivores, introduced plant species and climate change in Iceland

Brynja Hrafnkelsdóttir

A 150 ECTS Academic Dissertation Presented in Candidacy for the Degree of Doctor of Philosophy in Forest Science

Main supervisor
Adjunct professor Guðmundur Halldórsson
Soil Conservation Service of Iceland & Agricultural University of Iceland

Co-supervisors
Dr. Edda S. Oddsdóttir, Icelandic Forest Research
Dr. Halldór Sverrisson, Icelandic Forest Research

Opponents
Professor emeritus Gísli Már Gíslason
University of Iceland
Assistant professor Hans Peter Ravn
University of Copenhagen

Faculty of Environmental and Forest Sciences
Agricultural University of Iceland
June 2020

ORCID 0000-0003-2222-0728

This thesis should be cited as:
Hrafnkeldóttir, B. (2020). The interaction between native insect herbivores, introduced plant species and climate change in Iceland. PhD thesis. Agricultural University of Iceland, Hvanneyri, Iceland. 70 p. ISBN 978-9979-881-99-5

Vitna skal til þessarar ritgerðar sem:
Brynja Hrafnkeldóttir (2020). Samspil á milli innlendra beitarskordýra, innfluttra plantna og loftslagsbreytinga á Íslandi [The interaction between native insect herbivores, introduced plant species and climate change in Iceland]. Doktorsritgerð. Landbúnaðarháskóli Íslands, Hvanneyri. 70 bls. (á ensku, með íslenskum útdrætti). ISBN 978-9979-881-99-5

Faculty of Environmental and Forest Sciences
Agricultural University of Iceland
Hvanneyri
IS-311 Borgarnes
Telephone: 433 5000

Clarification of contribution

I hereby declare that the writing of the following thesis and the four accompanying papers is my work, done with the supervision of dr Guðmundur Halldórsson, dr Edda S. Oddsdóttir and dr Halldór Sverrisson.

The contribution of Brynja Hrafnkelsdóttir to the papers included in the thesis was as follows:

Paper I: Hrafnkelsdottir collected part of the data presented in this paper. The paper was drafted by Halldorsson and Sigurdsson and further revised by all co-authors. Statistical analysis was done by Sigurdsson. Halldorsson was responsible for correspondence with the scientific journal.

Paper II: Hrafnkelsdottir, in collaboration with Halldorsson, Oddsdottir and Sverrisson, designed the experiment and was responsible for experimental work. All co-authors contributed to the interpretation of the results. Statistical analysis was done by Hrafnkelsdottir under the supervision of Sigurdsson. Hrafnkelsdottir made a draft of the paper, further revised by the co-authors. Hrafnkelsdottir was responsible for correspondence with the scientific journal.

Paper III: Hrafnkelsdottir, in collaboration with Halldorsson, Oddsdottir and Sverrisson, designed the experiment and was responsible for the experimental work. All co-authors contributed to the interpretation of the results. Statistical analysis was done by Hrafnkelsdottir under the supervision of Sigurdsson. Hrafnkelsdottir made a draft of the paper, further revised by the co-authors. Hrafnkelsdottir was responsible for correspondence with the scientific journal.

Paper IV: Hrafnkelsdottir, in collaboration with Halldorsson, Oddsdottir and Sverrisson, designed the experiment and was responsible for the experimental work. All co-authors contributed to the interpretation of the results. Statistical analysis was done by Hrafnkelsdottir. Hrafnkelsdottir made a draft of the paper, further revised by the co-authors.

____

Brynja Hrafnkelsdóttir

Abstract

Climate warming has had significant effects on insect herbivores in Iceland, including an increased rate of establishment of new species as well as changes in outbreak patterns and distribution of insect herbivores. Many of these herbivores live on trees and shrubs. Concurrent with the onset of a warmer climate around 1990, a distinct host shift occurred in a few native insect species which started to feed on the exotic Nootka lupin (*Lupinus nootkatensis*), which until then had been free from any significant insect herbivory. Later, as the climate has warmed, many outbreaks of native insect species, primarily the Broom Moth (*Ceramica pisi*) and Satyr Pug (*Eupithecia satyrata*), have occurred in lupin fields. Broom Moth distribution and damage on young tree seedlings have also increased recently.

The main objectives of this thesis were to study: (1) the effects of climate change on the population dynamics and distribution potential of native herbivores on Nootka lupin, using the Broom Moth as a case study and (2) the effects of insect herbivory on the fitness of the Nootka lupin and exotic trees, using seed production and annual growth as proxies for plant fitness.

The effects of climate change on the population dynamics of the Broom Moth were studied in two phases: (1) the effects of warmer winters on pupal survival were studied by freezing pupae in a lab study at different sub-zero treatments and (2) the effects of warmer summers on larval development and pupal size, were studied by: (i) sampling and weighing larvae from lupin fields at different times and local climate during the larval growing season and (ii) weighing larvae just before pupation and after pupation. Additionally, the effects of herbivory intensity on the Nootka lupin seed production (fitness) were studied in a 3-year field study at two sites at contrasting ages and successional stages, including different manipulated herbivory treatments.

Winter temperatures were not found to affect Broom Moth survival as different sub-zero treatments had no effect on the survival of Broom Moth pupae. The major factor affecting the winter survival of Broom Moth pupae was, however, their autumn weight. Broom Moth larvae growth measurements also showed a significant positive relationship between total growing degree days from the beginning of June and summer larvae just before weight pupation. A significant positive relationship was also found between larval weight just before pupation and pupal weight.

Seed production of the Nootka lupin was negatively related to herbivory defoliation, as increased herbivory had a negative effect on the number of flowering stems. These negative effects were also affected by the age (successional stage) of the Nootka lupin, as they were only significant in the older Nootka lupin field.

Defoliation by Broom Moth larvae was found to have a negative effect on height growth of Sitka spruce, but no effect on black cottonwood. The results of a feeding study indicated that Broom Moth larvae grow better on Nootka lupin than tree seedlings.

The main results from these studies are: (1) Warmer summers, but not warmer winters, have enhanced the winter survival of Broom Moth pupae and, thereby, both facilitated its recent distribution expansion and its increased population density, which have resulted in intensive outbreaks in Nootka lupin fields in Iceland. The recent increase in population density has, however, also been greatly enhanced by the host shift of the Broom Moth over to the Nootka lupin. (2) This enhanced native insect herbivory may affect the exotic Nootka lupin in Iceland by reducing its seed production, seen as a lower expansion rate from older lupin fields and its competitive success. The effect of this may be reduced invasiveness of the Nootka lupin in Iceland.

The causes of the observed host-shift of the native insect herbivores over to the Nootka lupin are discussed and may be related to the adaptation of the lupin to the previously low herbivory environment.

Keywords: Age-specific effects of herbivory, frost tolerance, geographical range shifts, global warming, Iceland, larval mass, pupal mass, summer day degrees.

Ágrip

Hlýnun loftlags hefur nú þegar haft töluverð áhrif á skordýr sem lifa á gróðri á Íslandi. Til dæmis hefur hraði landnáms nýrra tegunda aukist en auk þess hafa breytingar orðið á faraldsfræði og útbreiðslu sumra skordýrategunda sem lifa á gróðri. Samfara þeirri hlýnun sem átti sér stað á Íslandi í kringum 1990 fór í fyrsta skipti að bera á breytingu á hýsilvali nokkurra innlendra skordýrategunda sem fóru að éta alaskalúpínu (*Lupinus nootkatensis*), sem er erlend tegund sem fram að því hafði verið laus við merkjanlega skordýrabeit. Síðan þá hefur fjöldi skordýrafaraldra orðið á lúpínusvæðum, einkum af völdum ertulygla (*Ceramica pisi*) og mófeta (*Eupithecia satyrata*). Einnig hefur en útbreiðslusvæði ertuyglu á Íslandi stækkað og skaði á ungum trjáplöntum af hennar völdum aukist.

Meginmarkmið þessa doktorsverkefnis voru að rannsaka: (1) áhrif loftlagsbreytinga á stofnstærðarþróun og útbreiðslu innlendra beitarskordýra á erlendri plöntutegund, alaskalúpínu, með ertuyglu sem tilviksrannsókn og (2) áhrif skordýrabeitar á þrótt alaskalúpínu og erlendra trjátegunda, þar sem fræframleiðsla og ársvöxtur eru notuð sem mælikvarðar á þrótti plantna.

Áhrif loftslagsbreytinga á stofnstærðarþróun ertuyglu voru rannsökuð í tveimur skrefum: (1) áhrif hlýrri vetra á lifun púpna voru rannsökuð með því að frysta púpur í tilraunastofu með mismunandi frystimeðferðum og (2) áhrif hlýrri sumra á þroskun lirfa og stærð púpna voru rannsökuð með því að: (i) safna lirfum í lúpínubreiðum og vigta þær á mismunandi tímum og svæðum á vaxtartíma þeirra og (ii) vigta lirfur rétt fyrir púpun og eftir púpun. Auk þess voru áhrif skordýrabeitar á fræframleiðslu alaskalúpínu rannsökuð með þriggja ára rannsókn í tveimur lúpínubreiðum á mismunandi aldri og framvindustigi.

Vetrarhiti hafði ekki áhrif á lifun ertuyglu, þar sem mismunandi frystimeðferðir höfðu engin áhrif á lifun púpna. Aðaláhrifavaldur á vetrarlifun púpna var hinsvegar þyngd þeirra að hausti. Mælingar á vexti ertuyglulirfa sýndu að það var marktækt jákvætt samband á milli daggráðusummu frá byrjun júní og lirfuþyngdar rétt fyrir púpun að sumri. Marktækt jákvætt samband fannst á milli lirfuþyngdar rétt fyrir púpun og púpuþyngdar.

Skordýrabeit hafði neikvæð áhrif á fræframleiðslu alaskalúpínu þar sem aukin aflaufgun hafði marktæk neikvæð áhrif á fjölda blómberandi stöngla. Þessi áhrif voru aftur á móti bundin við aldur (framvindustig) alaskalúpínu, þar sem þau voru eingöngu marktæk í eldri lúpínubreiðunni.

Aflaufgun af völdum ertuyglulirfa reyndist hafa neikvæð áhrif á hæðarvöxt sitkagrenis, en engin áhrif á hæðarvöxt alaskaaspar. Niðurstöður fóðrunartilraunar bentu til þess að ertuyglulirfur yxu betur á lúpínu en á trjáplöntum.

Meginniðurstöður þessara rannsókna eru: (1) Hlýrri sumur, en ekki mildari vetur, hafa aukið vetrarlifun ertuyglupúpna og þannig stuðlað að aukinni útbreiðslu og stærri stofni hennar á undanförnum árum, sem leiddi til tíðari faraldra á alaskalúpínu á Íslandi og (2) innlendar skordýrategundir geta haft árhrif á alaskalúpínu á Íslandi, með því að minnka fræframleiðslu plantna sem gæti hægt á dreifingu hennar frá lúpínubreiðum á síðari framvindustigum. Minni fræframleiðsla gæti einnig bent til þess að dregið hafi úr þrótti lúpínunnar og þannig dregið úr samkeppnishæfni hennar gagnvart öðrum plöntutegundum til lengri tíma. Saman gætu þessi tveir þættir hugsanlega minnkað ágengni alaskalúpínu á Íslandi.

Hugsanlegar ástæður þess að innlendar skordýrategundir byrjuðu að éta alaskalúpínuna á Íslandi eru ræddar en það gæti tengst aðlögun lúpínunnar að fyrrum beitarlausu umhverfi.

Lykilorð: Aldurstengd áhrif skordýrabeitar, frostþol, hlýnun jarðar, Ísland, lirfuþyngd, púpuþyngd, sumar daggráður, útbreiðslubreytingar.

Acknowledgements

The studies covered in this thesis were performed at the Icelandic Forestry Research and the Agricultural University of Iceland. The work was funded by the Hjálmars R. Bardarsonar and Elsa S. Bardarson Memorial Fund (Minningarsjóður Hjálmars R. Bárðarsonar og Elsa S. Bárðarson) and The Science and Research fund of South Iceland (Vísinda og rannsóknasjóður Suðurlands). I am very grateful for their contributions.

I want to express my special thanks to my main supervisor and friend, Guðmundur Halldórsson. Thank you for being all the things perfect supervisors should be, patient, wise, helpful, motivational, and so much more. I would never have been able to do this without your support!

I am also very thankful to my two co-supervisors, Edda S. Oddsdóttir for always being there with support and guidance and Halldór Sverrisson for useful inputs to the project's planning and excellent knowledge. I would also like to thank Bjarni D. Sigurdsson for all his advice and help, especially with the statistical analyses in the papers. Thank you all for your friendship and patience.

Many thanks to my former and present co-workers at the Icelandic Forestry Research. Thank you for your assistance, advice, and stimulating discussions over the years. I especially want to thank Kjartan and Ólafur E. for fieldwork, Bjössi, and Bjarki for map-making, and Jóhanna for all the talks.

I also want to thank the staff of the Soil Conservation Service of Iceland for providing technical assistance and warm welcomes on my trips to Gunnarsholt.

Last but not least, I want to thank my family. My parents and Biddy, for all the support and taking care of my daughters when I was working. Gunni for his support and motivation. My two daughters, Laufey and Hugrún, for everything….. Elska ykkur endalaust.

Contents

List of Original Papers

The present thesis is based on the following publications, which will be referred to by their Roman numerals:

I. Halldórsson, G., Sigurdsson, B.D., Hrafnkelsdottir, B., Oddsdóttir, E., Eggertsson, Ó. & Ólafsson, E. 2013. New arthropod herbivores on trees and shrubs in Iceland and changes in pest dynamics: A review. *Icelandic Agricultural Sciences* 69-84.

II. Hrafnkelsdottir, B., Sigurdsson, B.D., Oddsdóttir, E., Sverrisson, H. & Halldórsson, G. 2019. Winter survival of *Ceramica pisi* (Lepidoptera: Noctuidae) in Iceland. *Agricultural and Forest Entomology,* **21,** 219-226.

III. Hrafnkelsdottir, B., Sigurdsson, B.D., Oddsdóttir, E., Sverrisson, H. & Halldórsson, G. 2019. The effect of insect herbivory on seed production of Lupinus nootkatensis, an introduced species in Iceland. *Agricultural and Forest Entomology,* **22,** 136-145.

IV. Hrafnkelsdottir, B., Oddsdottir, E.S., Sverrisson, H. & Halldorsson, G. 2020. The effect of summer temperatures on the development and population dynamics of *Ceramica pisi* (Lepidoptera: Noctuidae) in Iceland (unpublished manuscript).

List of tables

List of Figures

Introduction

Climate change

Even though changes in climate have always existed, recent climate changes are at an unprecedented rate (IPCC, 2014). It has been predicted that ongoing changes will even be faster in this century (IPCC, 2007). The changes are at a fast rate and 1983 – 2012 was the warmest period from 1400 in the Northern Hemisphere (IPCC, 2013).

The climate in Iceland is mostly characterized by mild winters and cool summers. The climate is milder than in many other areas at the same latitude, due to the warming effect of the North Atlantic current (Einarsson, 1984; Ólafsson *et al.*, 2007). Studies have shown that, similar to other areas in the Northern Hemisphere, the average long-term warming in Iceland has been higher than average due to global warming (Björnsson *et al.*, 2018). Regular temperature measurements started in 1850 in Iceland, and since then the mean annual temperature has risen 0.8°C per century. However, during the last few decades, this warming has been much faster, or 0.47°C per decade during the period 1980-2015 (Björnsson *et al.*, 2018).

The warming in Iceland has not been continuous, with some cold periods occurring between the warm ones. The last cold period was from the early 1960s to the late 1980s (Hanna *et al.*, 2004; Björnsson *et al.*, 2018). The warming has also not been spread equally in space within Iceland; the most pronounced changes have been in the south, west and north-west parts of the island (Björnsson *et al.*, 2018). The warming also has a seasonal aspect; two-thirds of the observed warming in Iceland during the past 30 years has occurred during the wintertime (Björnsson *et al.*, 2018). Björnsson *et al.* (2018) further predicted that in 2050 warming in Iceland will be between 1.3 – 1.6 °C and between 1.5 – 4.1 °C by the end of the 21st century, varying greatly between different scenarios of further greenhouse gas emissions. The lowest warming prediction numbers (1.5 – 2.4) are those scenarios where the release of atmospheric greenhouse gases will decrease strongly from what it is today.

Insects and climate change

Climate change is predicted to be a significant factor driving shifts in biodiversity and species composition, and recently, many studies have shown that animals and plants have already responded to the ongoing change (Parmesan & Yohe, 2003; Root *et al.*, 2003; IPCC, 2013).

Effects on organisms can be direct (Bale *et al.*, 2002; Karban & Strauss, 2004) or indirect through climate change effects on other organisms, such as host plants, competitors and natural enemies (Price *et al.*, 1980; Dukes *et al.*, 2009). Due to insect´s poikilothermic nature, their life cycles and metabolic rates are very dependent on environmental conditions, such as temperature, and will therefore respond rapidly to changes in their environment (Neven, 2000; Logan *et al.*, 2003; Régnière, 2009).

Direct effects (lifecycles, survival, and distribution)

Rising temperatures can affect an insect's geographical range, population dynamics, and phenology (Parmesan *et al.*, 1999; Bale *et al.*, 2002; Johnson & Jones, 2017), and insects in northern latitudes that are currently restricted by low temperatures will likely benefit greatly from climate changes (Bale *et al.*, 2002).

Winter temperature

Temperature is often the limiting factor in insect distribution to higher latitudes and altitudes (Ayres & Scriber, 1994; Ungerer *et al.*, 1999; Crozier, 2004). The highest proportion of the ongoing warming is during the wintertime (Nigam *et al.*, 2017; Björnsson *et al.*, 2018), and many species have already responded to that by expanding their ranges and increasing populations (Bale *et al.*, 2002; Pureswaran *et al.*, 2018).

Higher winter temperatures can increase an insect´s winter survival rates, especially of species that do not go into diapause and are active during the wintertime (Ungerer *et al.*, 1999; Sinclair *et al.*, 2003; Battisti *et al.*, 2005). The northern distribution limits of the Southern Pine Beetle (*Dendroctonus frontalis*) in the United States are, for example, constrained by winter temperature. It is predicted that with increased minimal annual (winter) temperature, this species could greatly expand its distribution range (Ungerer *et al.*, 1999; Trân *et al.*, 2007).

Mobile species that have a broad host range and no diapause, like the Sachem Skipper (*Atalopedes campestris*), are very likely to benefit from higher winter temperatures. Crozier (2003) found that, since 1950, this species has already expanded its distribution range along with rising winter temperatures in the southern USA and Mexico. Studies have also shown that several Lepidoptera species in Europe have shifted their ranges poleward in response to warming (Parmesan *et al.*, 1999).

Summer temperature

Species that spend their wintertime in a diapause stage do not benefit as much from higher winter temperatures as those that do not. Instead, it is much more likely that they will benefit from longer and warmer summer temperatures during their larval growth (Bale & Hayward, 2010).

In colder climates, most insects' growth period is during the warmest part of the year (i.e. summer), and a temperature rise during that period generally increases the speed of larval development (Bale *et al.*, 2002). Faster growth and increased development rates can help insects in many ways. Reynolds *et al.*, (2007), for example, found a positive correlation between summer temperature and the abundance of Lepidoptera larvae in the White Mountains in the USA in the following year.

Increased summer temperatures are often combined with warmer spring and autumn temperatures (Hanna *et al.*, 2004). In Iceland, for example, warming after 1985 has been most pronounced in the autumn (Björnsson *et al.*, 2018). Warmer autumns, however, may not necessarily increase the growing period of insects. At higher latitudes, the timing of the diapause is usually governed by the daylength in the autumn, when the days get shorter and northern populations may therefore not benefit from longer summers (Bradshaw *et al.*, 2004). Each such insect species has a special daylength, called the *critical daylength*, that activates diapause (Bradshaw *et al.*, 2004; Bale & Hayward, 2010). This *critical daylength* is different, not only between species but also between individuals of the same species at separate locations (Bradshaw & Holzapfel, 2010). For example, the *critical daylength* for the Pitcher Plant Mosquito (*Wyeomyia smithii*) larvae increases with altitude and latitude (Bradshaw & Lounibos, 1977).

All insects also have a specific *optimal temperature* where they achieve the fastest possible developing rate, and higher or lower temperatures may decrease or stop their development rate (Ikemoto, 2005). Furthermore, insets require a *minimal thermal budget* to finish larval growth and gain enough weight before they enter diapause, which is predetermined by the *critical daylength*. When the temperature rises, an increase in the available thermal budget for growth is expected, and higher summer temperatures in colder areas may result in a faster growth rate of insects (Bale *et al.,* 2002). As increasing weight in the overwintering stage can increase the likelihood of winter survival (Hokkanen, 1993; Liu *et al.*, 2007; Paper II), this can change the northward distribution and population growth of many insect species (Bale *et al.*, 2002). Bradshaw *et al.* (2004) found, for example, that the northern population of the Pitcher Plant Mosquito benefitted greatly from warmer and more southern temperatures, combined with their usual northern daylength.

Additionally, many insect species are most exposed to natural enemies during their larval stage (Bernays, 1997), and faster larval growth can, therefore, increase survival and population growth by reducing the number of days insects are exposed to natural enemies (Bale *et al.*, 2002).

Direct phenological changes

Higher temperatures can lead to changes in the timing of some insect's phenological events.

Along with the recent warming, many British butterflies have earlier first appearances and more extended flight periods (Roy & Sparks, 2000). Earlier appearances can have beneficial effects on many species, especially on those that have flexible voltinisms. Many insect species that are univoltine at higher latitudes are bi- or multivoltine at lower latitudes (Tauber *et al.*, 1986). Those species may benefit from longer favourable seasons and a faster development rate by increasing the number of generations per year at higher latitudes (Yamamura & Kiritani, 1998; Johnson & Jones, 2017). In Central Europe, many multivoltine butterfly species have already responded to the last 40 years of warming by increasing the number of generations per year (Altermatt, 2010).

Indirect effects of climate change

Insect herbivores are not the only group that is affected by climate change. The host plants and natural enemies of insect herbivores are also affected by climate change, which may have indirect effects on insect herbivores (Jamieson *et al.*, 2012). A herbivore's development rate often speeds up when the temperature rises (see earlier), but sometimes other factors, for example, reduced nutrient value of the host plant, are stronger drivers of change than the benefits of the rising temperature (Pincebourde *et al.*, 2017).

Host plants

Climate change can affect plant growth, health, and nutrient quality. Studies have shown that a rising CO_2 concentration alone does not have a strong direct effect on insect development (Kerr *et al.*, 2013; Pincebourde *et al.*, 2017). However, under increased CO_2 concentrations and a higher temperature regime, it can affect plant growth (Veteli *et al.*, 2002). It usually affects the plant carbon:nitrogen ratio, by lowering the nitrogen proportion, leading to lower food quality for the herbivore (Robinson *et al.*, 2012). Some insect herbivores can react to these changes by consuming more foliage of the host plant to get the necessary proteins, which also reduces the herbivore's growth rate (Coviella & Trumble, 1999). Lindroth *et al.* (1995) compared, for example, three silk moth (Saturniidae) species (*Hyalophora cecropia, Actias luna,* and *Antheraea polyphemus*) reared on paper birch (*Betula papyrifera*) that were grown under different CO_2 concentrations and found that elevated CO_2 decreased larval survival and growth rate and increased leaf consumption.

Other possible indirect effects of climate change are more pronounced temperature – and drought stress and their effects on hostplants. Stressed plants get weaker and have less energy to produce defensive chemicals against insects and diseases, e.g., when they experience a lack of water (Kolb *et al.*, 2016). Intense drought has, for instance, caused many bark beetle outbreaks in the USA (Kolb *et al.*, 2016). However, drought is not always beneficial for bark beetles as some studies have shown that moderately stressed trees are better defended against bark beetles (Lombardero *et al.*, 2000; Raffa *et al.*, 2008).

Indirect phenological effects

Both natural enemies and host plants can also undergo phenological changes in a changing climate (Root *et al.*, 2003; Jamieson *et al.*, 2012). However, the phenological changes of herbivores, host plants, and natural enemies, do not always match, which can either be beneficial or harmful for the herbivores (Visser & Holleman, 2001; Ekholm *et al.*, 2019). It can, for example, lead to asynchrony between herbivores and their host plants.

The Winter Moth (*Operophtera brumata*) larvae are, for instance, very dependent on young foliage of their host plants in the spring, which is often English oak (*Quercus robur*). In the Netherlands recent spring warming has both postponed the timing of Winter Moth egg hatching and oak budburst. However, the Winter Moth has responded more strongly than the oak to this warming, leading to asynchrony between Winter Moth larvae and oak budburst (Visser & Holleman, 2001). Even though this has affected the Winter Moth population negatively, there are indications that very high selection pressure will help the species in the future to adapt to these changes (van Asch *et al.*, 2013).

Indirect effects through natural enemies

Climate and phenological changes also affect insect herbivores indirectly by affecting their natural enemies. There is a risk of no or a shorter overlap between insect herbivores and their natural enemies when changes, such as phenological changes, are not parallel. Those effects may be different for these two groups, for example, due to variation in plasticity or different optimal temperatures (Jamieson *et al.*, 2012). It could, for example, lead to a mismatch if the natural enemies arrive earlier than their host (Grabenweger *et al.*, 2007) as was the case with spiders that feed on herbivore grasshoppers in Connecticut, USA (Barton, 2010). There, the herbivore grasshoppers were not affected by rising temperatures, but the spiders, however, moved lower in the canopy in response to the same temperature changes. This led to more herbivory by grasshoppers as there was less spatial overlap between them and their predators that, in normal conditions, would keep the population down (Barton, 2010). The same could occur if the natural enemies' responses to climate are weaker than the host's responses (Thomson *et al.*, 2010). Since natural enemies often hinder insect herbivores from causing outbreaks on plants, it is possible that climate change can cause more outbreaks, for example, in agriculture and forestry in the future by such indirect effects on insects' natural enemies (Jamieson *et al.*, 2012).

Effects on forest insect herbivores

Insects are crucial players in all terrestrial ecosystems, and insect herbivores have a significant impact on agricultural and forest production (Lehmann *et al.*, 2020). As described in the previous section, climate change is expected to affect insect herbivores in multiple ways, and some are likely to lead to more outbreaks in agriculture and forestry.

Disturbance by insect herbivores in forest ecosystems due to recent warming has already occurred (Logan *et al.*, 2003; Pureswaran *et al.*, 2018). Recently, insect outbreaks in forests have been getting more intense, and insect herbivores have been moving more rapidly into new areas, often to more northern latitudes (Ayres & Lombardero, 2000). Extreme examples are the Winter Moth that has been spreading northward with outbreaks in the subarctic birch (*Betula* spp.) forest (Jepsen *et al.*, 2008) and the Mountain Pine Beetle (*Dendroctonus ponderosae*) that has destroyed millions of hectares of pine forest in North America (Lehmann *et al.*, 2020).

Forest herbivores in Iceland

Studies in Iceland have shown that recent warming has also started to affect the Icelandic flora and fauna (Björnsson *et al.*, 2018; Paper I). During the past two decades, significant changes have been observed in Iceland in insect herbivory on tree species, primarily Sitka spruce and downy birch (*Betula pubescens*; Halldórsson & Kjartansson, 2005; Hallgrímsson *et al.*, 2006; Paper I). Outbreaks of the Green Spruce Aphid (*Elatobium abietinum*) have been occurring more rapidly and moving from autumn to spring (Paper I).

In isolated ecosystems like Iceland newly introduced insect herbivores can benefit significantly from two factors. Firstly, if the host plants are available in the new area and have not experienced heavy herbivory, the host plant could have lowered its energy usage on defence chemicals (Bossdorf *et al.*, 2005). Also, for polyphagous insects, some plant species have not yet evolved a defence against this particular insect species (see section 1.4). An example of this is the Emerald Ash Borer (*Agrilus planipennis*) which is native to Asia and does not do much harm there but is a very invasive pest outside its native range on ash (*Fraxinu*s spp.) in North America and European Russia (Herms & McCullough, 2014; Orlova-Bienkowskaja & Bieńkowski, 2016).

Secondly, if introduced insect herbivores have natural enemies that reduce their abundance in their native regions that are not present in the new area, they can benefit significantly from living in the new environment with less pressure from natural enemies (Menéndez *et al.*, 2008) (see section 1.4). Many insect herbivores species feed on birch in Iceland, but there are, however, rather few that cause extensive damage (Paper I). During recent outbreaks, the introduced moth Birch-aspen Leafroller (*Epinotia solandriana*) has caused extensive damage, while the native Rusty Birch Button (*Acleris notana)* and the introduced Winter Moth that has been much longer in Iceland also have caused some damage, but to a lesser extent (Hallgrímsson *et al.*, 2006).

Invasive plants and native herbivores

Exotic plants can often be very successful in a new habitat, and several hypotheses try to explain the success of invasive species (Hierro *et al.*, 2005). The *empty niche theory* proposes, for example, that invasiveness evolves because the exotic plant can exploit unused resources in their new environment (Holzmueller & Jose, 2011). Other hypotheses explain this success of exotic plants by the lack of natural enemies in the new habitat, and one of the most prominent is the *enemy release hypothesis* (ERH) (Elton, 1958; Keane & Crawley, 2002).

The larvae of the Brown Argus (*Aricia agestis*), for example, experienced less predation in newly introduced areas even though several of its natural enemies were present in the newly introduced location (Menéndez *et al.*, 2008). Blossey *et al.* (1995) also hypothesized that when the pressure of natural enemies decreases, such as when plants are introduced to a new region, plants may change their resource allocation towards less production of plant defence chemicals. This hypothesis is called the *evolution of increased competitive ability* (EICA).

Exotic plants, however, are not always successful in the new habitat despite favourable environmental conditions, and the *biotic resistance hypothesis* suggests that native herbivores can act as natural enemies of the exotic plants (Maron & Vilà, 2001; Parker *et al.*, 2006). In Parker *et al.* (2006), this herbivory was, however, mostly by vertebrate herbivores and the effects of native insect herbivores on the exotic plant invasion were small (Parker *et al.*, 2006).

There are several examples of native insect herbivores that shift from the primary native host to an exotic plant (Bezemer *et al.*, 2014). Graves *et al.* (2003) found, for instance, that in California many native butterfly species oviposit and feed on exotic plants. However, evidence of native insect herbivores providing enough biotic resistance to exotic plants to hinder their spread is conflicting (Maron & Vilà, 2001), but studies do show that native herbivores can slow the exotic plant species spread, for example, by affecting the plant growth rate and/or seed production (Maron & Vilà, 2001). For instance, in Nebraska, native herbivores that typically live on the native tall thistle (*Cirsium altissimum*) have been feeding on introduced bull thistle (*Cirsium* v*ulgare*) plants, destroying 71-88% of their potential seed production (Louda & Rand, 2003). It has been shown that those native insects in Nebraska are likely to be a biotic resistance to the invasion of the exotic bull thistle (Schultz *et al.*, 2017).

The Nootka lupin in Iceland

The Nootka lupin (*Lupinus nootkatensis*) is a perennial flowering plant in the Fabaceae family. It originates from North America and has been introduced twice into Iceland, the first time in 1885 when it was only used as an ornamental plant in gardens (Schierbeck, 1886). It was then re-introduced into the country in 1945 because of its usefulness in land reclamation (Bjarnason, 1957). In ca. 1975 the development of methods started for using lupin for vegetation reclamation on eroded lands and in agriculture (Arnalds & Runolfsson, 2004). After 1980, the Nootka lupin distribution area in Iceland increased significantly due to increased sowing of the species together with a decrease in free-range sheep grazing pressure (Icelandic Institute of Natural History *et al.*, 2010). In 1986, establishment of lupin seed harvesting fields by the Soil Conservation Service started, where seeds from Heiðmörk and a few other places were collected, and in 1990 sowing was started using seeds from these seed harvesting fields (Andrés Arnaldsson, personal communication). Most of the lupin sowing took place before 2000 and on ca. 800 ha per year, on average (Halldórsson *et al.*, 2011). The large sowing of Soil Conservation Service of Nootka lupin in Iceland continued until 2018 when it was declared that they would stop using the Nootka lupin for land reclamation activities (Runólfsson, 2018).

Icelandic studies show that Nootka lupin can readily spread into degraded areas by seed if these areas are protected from livestock grazing; the edge of established patches can advance by 1-4 m/

year (Magnusson *et al.*, 2004). A recent assessment has shown that the species had spread quite substantially in Iceland, and its total coverage at present is at least 299 km^2 (Guðjohnsen & Magnússon, 2019).

Like many other members of the Fabaceae family, Nootka lupin can enhance soil fertility by acquiring nitrogen from the atmosphere. This is due to their symbiosis with rhizobia, a nitrogen-fixing bacteria that forms nodules on the plant roots (Hiltbrunner *et al.*, 2014). Magnússon *et al.* (2018) have reported very dramatic increases in soil N and C stock following the establishment of Nootka lupin in their long-term monitoring of the succession trajectories of Nootka lupin in Iceland.

Nootka lupin has, for decades, been a matter of great controversy in Iceland (Benediktsson, 2015), where it is listed as an invasive plant (Magnússon, 2010). The main reason for concerns about the Nootka lupin is the effect it has on native plant biodiversity. In Iceland it has been shown to reduce the diversity of plants in heathlands and woodlands after 10-20 years in the field (Vetter *et al.*, 2018). Studies have shown that lupin plants can live up to 30 years (Sigurðsson, 1993). Björnsson (2011) found in remote-sensing studies that it retreated in Heiðmörk (SW Iceland) within 30 years from original colonization. Magnússon *et al.* (2018) also found that in lupin patches situated in different locations around Iceland the Nootka lupin can retreat within 25-45 years. It is, however, very dependent on the ground vegetation (moss) layer under the lupin and how that affects lupin regeneration by seed. For example, in many places in South Iceland where the lupin has retreated, a thick moss layer had formed over the lupin litter which hinders the emergence of lupin seedlings, and then dense grass vegetation has replaced the lupin as it has retreated (Magnússon *et al.*, 2018). However, in the drier climate in North Iceland, the thick moss and grass layers did not form, leading to more regeneration by seeds and no clear signs of the Nootka lupin retreating after 30-45 years (Magnússon *et al.*, 2018).

Insect herbivores on Nootka lupin in Iceland

There are not many records of insect herbivory on the Nootka lupin worldwide. *Liriomyza bryonia* is a polyphagous leaf miner that feeds on many plants, including Nootka lupin in its native habitat (Pitkin *et al.*, 2012). Even though there are not many records of insect herbivory on Nootka lupin, other lupins are suitable for many insect species (Fagan & Bishop, 2000; Bishop, 2002; Adamski *et al.*, 2009). There are also few records of bird (Preble, 1923; Emison & White, 1988) or mammal (Harting *et al.*, 1987) herbivory on Nootka lupin. However, Icelandic studies have shown that the lupin is very much preferred by domestic sheep (*Ovis aries*). This is surprising because Nootka lupin is not suitable for livestock as a feed due to its high alkaloid content (Guðmundsson, 1986).

Until recently, the Nootka lupin in Iceland seems to have been free from any significant insect herbivory and during an extensive survey of lupin fields in Iceland, conducted during 1988–1993, no major arthropod herbivory was noted, except in Þjórsárdalur in S Iceland in 1993 where few larvae were found on the lupin (Magnússon *et al.*, 2001; Bjarni D. Sigurðsson, perscomm.).

In 1991, the first insect outbreak in lupin in Iceland was recorded, caused by the larvae of the native Broom Moth (*Ceramica pisi*) (Sigurðsson *et al.*, 2003). Many extensive Lepidoptera larvae outbreaks have occurred since then, in most lupin fields in South-East and South Iceland and a few local outbreaks in West Iceland (Hrafnkelsdottir *et al.*, 2016).

Within the Broom Moth current distributional range, which is mostly restricted to S and SE Iceland, it is the primary herbivore on Nootka lupin in Iceland (Paper II). Other native Lepidoptera species, mainly the Satyr Pug (*Eupithecia satyrata*), have, however, contributed to these recent outbreaks. Also, two other insect species have had sporadic outbreaks on Nootka lupin and have been getting more common in recent years. The larvae of the Red-backed Cutworm (*Euxoa ochrogaster*) are known to feed on the roots of Nootka lupin in Iceland and cause the death of young plants (Jónsson & Halldórsson, 2009). The Rusty Tussock Moth (*Orgyia antiqua*) has also caused local defoliation of lupin in southern Iceland in recent years (Oddsdóttir *et al.*, 2014). All four of these species are native to Iceland and can also cause damage to tree seedlings (Wolff, 1971; Ottósson, 1983; Paper I). They are described in more detail below.

Broom Moth (Ceramica pisi)

The Broom Moth is found all over Europe, from the north to the Mediterranean Sea. It is also found east through middle Asia to Japan (Olafsson & Bjornsson, 1997). It is native to Iceland but not found in all parts of the country (Wolff, 1971; Olafsson & Bjornsson, 1997; Hrafnkelsdottir & Oddsdóttir, 2010). Around 2000 its distribution range in Iceland started to change (Hrafnkelsdottir *et al.*, 2016), but before that time it ranged from Hornafjordur in South-East Iceland to Hvalfjordur in South-West Iceland (Olafsson & Bjornsson, 1997). A survey in 2009 showed that at that time a considerable expansion in the distribution range had happened, primarily in western Iceland (see chapter 4.4.). The reasons for thee distribution changes are unknown. Around the same time, outbreaks of the Broom Moth in Iceland became more frequent.

The Broom Moth flies from June until late June and early July when it lays eggs on food plants. Larvae emerge in July and start to feed on host plants until pupation in late August to early September. The Broom Moth overwinters as pupae in the soil, often under a thick moss layer near its hostplant (Hrafnkelsdottir & Oddsdóttir, 2010). The larvae of the Broom Moth are highly polyphagous feeding on leaves of a variety of plant species.

In Iceland the Broom Moth is most common on the introduced Nootka lupin (*Lupinus nootkatensis*) but is also often found on various other native and introduced plant species (Wolff, 1971; Olafsson & Bjornsson, 1997).

As stated earlier, the first recorded Broom Moth outbreak on lupin in Iceland was in Morsárdalur, South-East Iceland, in 1991, but Nootka lupin was present in the area, even though the outbreak extended to native vegetation (Sigurðsson *et al.*, 2003). Another more extensive Broom Moth outbreak was in Skaftafellssýsla, South-Iceland, in 1995 (Sigurðsson *et al.*, 2003). Since then, many intense outbreaks have occurred in lupin fields in SE, S and W Iceland.

The Broom Moth has also been causing more damage in forestry in recent years (Sigurðsson *et al.*, 2003; Hrafnkelsdottir *et al.*, 2016) but the first recorded outbreak of its larvae in forest plantations in Iceland was in 1998 in Fellsmörk, South Iceland (Sigurðsson *et al.*, 2003). There have been many Broom Moth outbreaks since then on various tree species. However, the effects of Broom Moth herbivory differ with tree age, species and even clones of the same tree species (Sigurðsson *et al.,* 2003; Gudmundsdottir, 2008). Sigurðsson *et al.* (2003) found that herbivory seems to affect spruce (conifer) more negatively than birch and poplar (*Populus* spp) (deciduous).

There are not many references of predation on the Broom Moth. In Constantineanu *et al.* (2009), the Broom Moth was listed as a host of the parasitic wasp, *Netelia (Bessobates) cristata*. Bayes *et al.* (1964) described that a chick of the Great skua (*Stercorarius skua*) regurgitated 40 larvae of Broom Moth in Southeast Iceland in 1952 (but that was within the historical native range of the Broom Moth before Nootka lupin was introduced), and Helgason (2008) also found that Broom Moth pupae were on average almost 10% of the stomach contents of 15 arctic foxes collected in South Iceland. The Wood mouse (*Apodemus sylvaticus*) also eats Broom Moth pupae in Iceland (personal observation).

Satyr Pug

The Satyr Pug is found from Northern Europe to the Mediterranean Sea. It is also found in Asia, North America and North Africa. It is native to Iceland and is found in the lowlands (<400 m a.s.l.) all over the country (Wolff, 1971).

The Satyr Pug flies from late May until early June when eggs are laid on food plants. Larvae emerge in late June and feed on host plants. They start to feed on plant leaves until late summer when they pupate in the soil. The pupae survive the winter (Olafsson & Bjornsson, 1997).

Satyr Pug is a polyphagous species that feed on many plant species in Iceland, for instance, yarrow (*Achillea millefolium*) and members of the *Galium* genius (Olafsson & Bjornsson, 1997). In addition to outbreaks on Nootka lupin, it has caused damage in young tree plantations (Oddsdóttir *et al.*, 2017). Like the native Broom Moth larvae, the native Satyr Pug larvae only recently started to cause damage in Nootka lupin fields in Iceland. The first instance of Satyr Pug larvae feeding on lupin pods was observed in the 1990s (Jon Gudmundsson, personal communication).

Red-backed Cutworm s (Euxoa ochrogaster)

The Red-backed Cutworm is found from central Russia east to Kamchatka and in North America. Also, a few individuals have been found in Scandinavia (Olafsson & Bjornsson, 1997). It is native to Iceland, present in all parts of the country, but it is most common in the south-east region and prefers habitat in dry sandy areas and feeds on a variety of plants and plant parts (Olafsson & Bjornsson, 1997).

Adults of the Red-backed Cutworm fly from early July until September. Eggs are laid in July and hatch in May of the following year (Olafsson & Bjornsson, 1997; Jónsson & Halldórsson, 2009). The larvae feed at the soil surface, the younger larvae on the leaves but the older larvae on the plant stems near the surface (Capinera, 2001). At the end of June, the larvae pupate in the soil (Jónsson & Halldorsson, 2009). It is a polyphagous pest on various plant species and has caused considerable local damage for growers, for example on potatoes, turnip and Nootka lupin seed fields in Iceland (Ottósson, 1983; Ólafsson, 1988; Jónsson & Halldórsson, 2009).

It feeds on roots, root collar, and the lower leaves of Nootka lupin and is the only insect species that feeds belowground on lupin in Iceland. The first outbreak with extensive damage of the Red-backed Cutworm in Nootka lupin fields in Iceland was probably in 1993 at Hólasandur, North Iceland (Bjarni D. Sigurdsson, personal communication) but the first confirmed damage of Red-backed Cutworm on Nootka lupin in Iceland was in 2004 in Þorlákshafnarsandur, South Iceland (Jónsson & Halldórsson, 2009). However, damage by this species on lupin seems to be in smaller areas than damage by the Broom Moth and Satyr Pug.

Rusty Tussock Moth (Orgyia antiqua)

The Rusty Tussock Moth is found throughout most of the Holarctic region in Asia, Europe and North America (Ciesla, 2011). It is native to Iceland, but only present in the southern part of the country (Wolff, 1971; Olafsson, 2020).

The Rusty Tussock Moth lays eggs in September and overwinters in the egg stage. The larvae emerge in the early summer and feed on host plants in June – July and start feeding after that (Olafsson, 2020).

In other countries, it is a forest pest, feeding on many broadleaves and conifer species (Ciesla, 2011). Even though it is most commonly a forest pest, the Rusty Tussock Moth, can also feed on various other plant species (Harrison *et al*., 2005). For instance, it feeds mainly on two lupin species in the coastal areas of California, USA (Harrison *et al*., 2005). In recent years, local outbreaks of the Rusty Tussock Moth on Nootka lupin have also been getting more common in Iceland (Oddsdottir *et al.*, 2014).

The effects of insect herbivory on Nootka lupin

The effects of insect herbivory on the development of Nootka lupin in Iceland have not been studied previously, but studies from other countries show that insect herbivory can affect the survival, fitness and growth of other lupin species (Maron & Jefferies, 1999; Maron & Gardner, 2000; Fagan *et al.*, 2005).

Belowground herbivory can cause massive death in other lupin species, for example, like the bush lupin (*Lupinus arboreus*) (Maron & Jefferies, 1999). The only belowground herbivore recorded on Nootka lupin in Iceland is caused by the Red-backed Cutworm, which has been observed killing young lupin (Jónsson & Halldórsson, 2009), but there are no records of it killing older lupin plants.

It is very variable how herbivory affects perennial plant species with long-living seedbanks like the Nootka lupin (Maron & Gardner, 2000; Sigurdsson & Magnusson, 2004). Often herbivory does not affect those plants because seed-safe sites rather than seed numbers are the limiting factor for their spread (Maron & Gardner, 2000). Studies on the bush lupin in California showed that it can survive heavy defoliation by Western Tussock Moth larvae (*Orgyia vetusta*) and the defoliation had no measurable effects on growth and seed production in the following year (Harrison, 1995; Harrison & Maron, 1995). However, other studies showed that herbivory could indeed have a significant effect on plant abundance and seed bank longevity of other lupin species (Maron & Gardner, 2000). Studies on prairie lupin (*Lupinus lepidus*) on Mount St. Helens, USA, showed that insect herbivory had a negative effect on its growth and regeneration (Fagan *et al.*, 2005). It also had negative effects on the seed production and establishment of new plants in the border region, although not in the core region of each patch (Fagan & Bishop, 2000).

Studies on Nootka lupin in Iceland

Several studies have been conducted on Nootka lupin in Iceland, for example on the alkaloid and other contents of Nootka lupin (Magnusson & Sigurdsson, 1995; Þórsson & Hlíðberg, 1997), nitrogen fixation (Pálmason *et al.*, 2004), seed ecology (Sigurðsson, 1993; Riege, 2004; Sigurdsson & Magnusson, 2004), distribution dynamics (Svavarsdóttir *et al.*, 2004; Björnsson, 2011; Guðjohnsen & Magnússon, 2019), the effects of fertilization on growth of tree seedlings inside lupin fields, and the use of lupin in revegetation and afforestation (Óskarsson & Sigurgeirsson, 2004; Riege, 2004; Riege & Sigurgeirsson, 2009). Furthermore, there are several studies on other biota within the lupin stands, such as studies on plant succession and soil development (Magnússon *et al.*, 2001; Aradottir, 2004; Magnusson *et al.*, 2004; Magnússon *et al.*, 2018), invertebrates and birds (Davíðsdóttir, 2013; Erhardt, 2013), and soil biota (Sigurdardottir, 2004; Oddsdóttir *et al.*, 2008).

More related to the present study are studies on the seed production of lupin and the effect of cutting on the survival and fitness of the lupin. Sigurdsson & Magnusson (2004) found that the seed production of the Nootka lupin in Iceland is strongly dependent on the plant's age, as the young lupin plants produced more seeds annually than the older lupin. This age-dependent seed production was partly connected to the number of flowering stems (Sigurdsson & Magnusson, 2004), but probably also to the number of seeds per stem, as Baldursson (1995) found that fewer flowers developed into seed pods in older plants than in younger Nootka lupin plants located at the patch edge.

The fitness of the Nootka lupin is dependent on the timing of its defoliation, as Sigurdsson *et al.* (1995) showed that the lupin was most sensitive to cutting in late June to early July at the same time as its root biomass is lowest, resulting with higher plant mortality within this period. There was, however, little mortality in Nootka lupin when it was cut later in the summer and autumn (Sigurdsson *et al.*, 1995) when most of the herbivory on Nootka lupin in Iceland occurs (Paper III). Nevertheless, the late summer cutting reduced the lupin fitness in the following year, as shown by lower seed production of the cut lupin patches compared to the uncut control (Sigurdsson *et al.*, 1995; Björnsson & Dalmannsdóttir, 2004).

The onset of large scale, intensive and prolonged insect outbreaks in Nootka lupin gave rise to speculations on their possible effects on the dynamics of lupin dominated ecosystems, primarily if this would facilitate the development of Nootka lupin fields into different ecosystems and reduce the invasiveness of this species in Iceland. The causes of these outbreaks have also been discussed, as Nookta lupin, which had been free from insect herbivory for many decades, suddenly became subjected to massive insect outbreaks in the 1990s and 2000s. Before the present study, no other studies had addressed the effect of herbivory on the fitness and the successional dynamics of Nootka lupin in Iceland, or the impacts of the ongoing climate change on the population and distribution dynamics of native herbivores on Nootka lupin in Iceland.

Aims

The overall aims of this thesis were to assess: (a) the effect of climate change on the population dynamics and distribution potential of native herbivores on Nootka lupin, using the Broom Moth as a case study, and (b) study the effect of insect herbivory on the fitness of the Nootka lupin, using seed production as a proxy for its fitness.

The more specific aims were:

- Assess the effects of climate change on the population dynamics of forest insect herbivores in Iceland and the introduction of new species (Paper I).
- Study the effects of winter and summer temperatures on the population dynamics of the Broom Moth (native forest insect herbivore) (Papers II and IV).
- Describe and map changes in the distribution range of the Broom Moth in recent years (unpublished data presented in the thesis).
- Study the growth rate of Broom Moth larvae on different plant species (unpublished data presented in the thesis).
- Study the effects of insect herbivory (native species) on the seed production of the Nootka lupin (introduced species) (Paper III) and the growth of Sitka spruce and black cottonwood (introduced species) (unpublished data presented in the thesis).

Summary of investigation

Review of new forest insect herbivores (Paper I)

Introduction of new herbivore species into Iceland

Data on the establishment of new herbivore insect species from 1900-2012 were obtained from the literature and my own studies and analysed for the potential effect of temperature on the rate of establishment of new species. The study period was divided into four interchanging warm and cold climatic periods and two distinct periods of low vs. high activity of planting of exotic tree species (Table 1).

Table 1. Planting of exotic species and the Mean Annual Temperature in Iceland, 1900-2012

Period	Planting of exotic tree species	Mean Annual Temperature
Ia: 1900-1920	Very limited	Low
Ib: 1921-1945	Very limited	High
II: 1946-1963	Intensive	High
III: 1964-1994	Intensive	Low
IV: 1995-2012	Intensive	High

Outbreaks of insect pests in birch woodlands in East Iceland

The annual reports of the forest district officer in East Iceland and other sources were used to construct the history of insect outbreaks in the region during the period 1913-2012. The data were used to construct a score of outbreak intensity with the following grades: 0 = no herbivory observed, 1 = some herbivory, no outbreaks, 2 = small local outbreaks, 3 = intense local outbreaks, and 4 = widespread, intense outbreaks, tree mortality observed.

The data were compared with the mean annual temperature (MAT) at the weather station at Stykkisholmur, West Iceland. This station was chosen as it has the longest unbroken record in Iceland. Insect outbreak patterns were analysed by comparing 5-year MAT averages to outbreak intensity and outbreak frequency.

Changes in the outbreak patterns of the Green Spruce Aphid

Data on the outbreak history and the timing of outbreaks (spring or autumn) of the Green Spruce Aphid in Reykjavík from the introduction of the species in 1959 until 2012 were obtained from the literature and the studies of the authors. The outbreak pattern was then compared to the mean November – April temperature over the same period.

Field sites (papers II, III, IV, unpublished data)

Field sampling of larvae (Paper IV, unpublished data)

In order to monitor larval growth during the larval growing season, Broom Moth larvae were sampled from three different Nootka lupin fields in 2014, 2016, 2017, and 2018 (Paper IV). The sampling locations were in Ölfus, Þjórsárdalur and Geitasandur (Figure 1; Table 2). Larvae sampling dates were variable between locations (see Table 2 in Paper IV). Four sampling sites were selected within each sampling location, and five sampling plots (0.5 x 0.5 m) were randomly selected within each sampling site at each sampling time. All lupin stems within each plot were cut near the base and carefully placed into a large plastic box. Each batch of stems was then shaken thoroughly into the box until all larvae had detached from the leaves and fallen into the box. All Broom Moth larvae in the plastic box were then collected and put into small marked plastic containers, with holes for ventilation. The larvae were brought to the laboratory and weighed after having been deprived of food for 20 h.

Broom Moth larvae collected from the lupin field in Ölfus in early August 2014 were used to study larval growth on different food plants (unpublished data). A total of 75 larvae were collected for the feeding experiment by shaking Nootka lupin plants thoroughly into a box until all larvae had detached from the leaves and fallen into the box.

To study the relationship between final larval weight and pupal weight (Paper IV), larvae were collected in Ölfus on August 31, 2016. They were deprived of food for 20h before weighing and then put into plastic cups (1 larva per cup) and left for pupation at outdoor temperature. On October 11, 2016, all pupae were weighed, and the larvae that did not pupate counted.

Field sampling of pupae (Paper II)

Pupal sampling for a freezing experiment took place in 2012. Pupae were collected from five different Nootka lupin fields: Markarfljótsaurar; Geitasandur; Þjórsárdalur; Ölfus and Hafnarmelar (Figure 1; Table 2). The climatic characteristics of the sampling locations are shown in Table 1 in Paper II. At each sampling location, a total of 50 pupae were collected from four different randomly selected sampling sites (Paper II). The pupae were collected from moss or the layer between the topsoil and moss since a previous study had shown that most of the Broom Moth pupae in lupin fields in Iceland are located in this layer (Brynja Hrafnkelsdottir, unpubl. data). The pupae were transported to the laboratory, and all damaged pupae removed. A total of 600 pupae (120 from each sampling location) were randomly selected, weighed on a scale (AA-160, Denver Instrument Company, U.S.A.) to the nearest 0.0001g and put into plastic cups (1 pupae/cup). The containers were kept at 4° C over a three-month period to ensure normal cold hardening of the pupae, before being transferred to the freezing experiment.

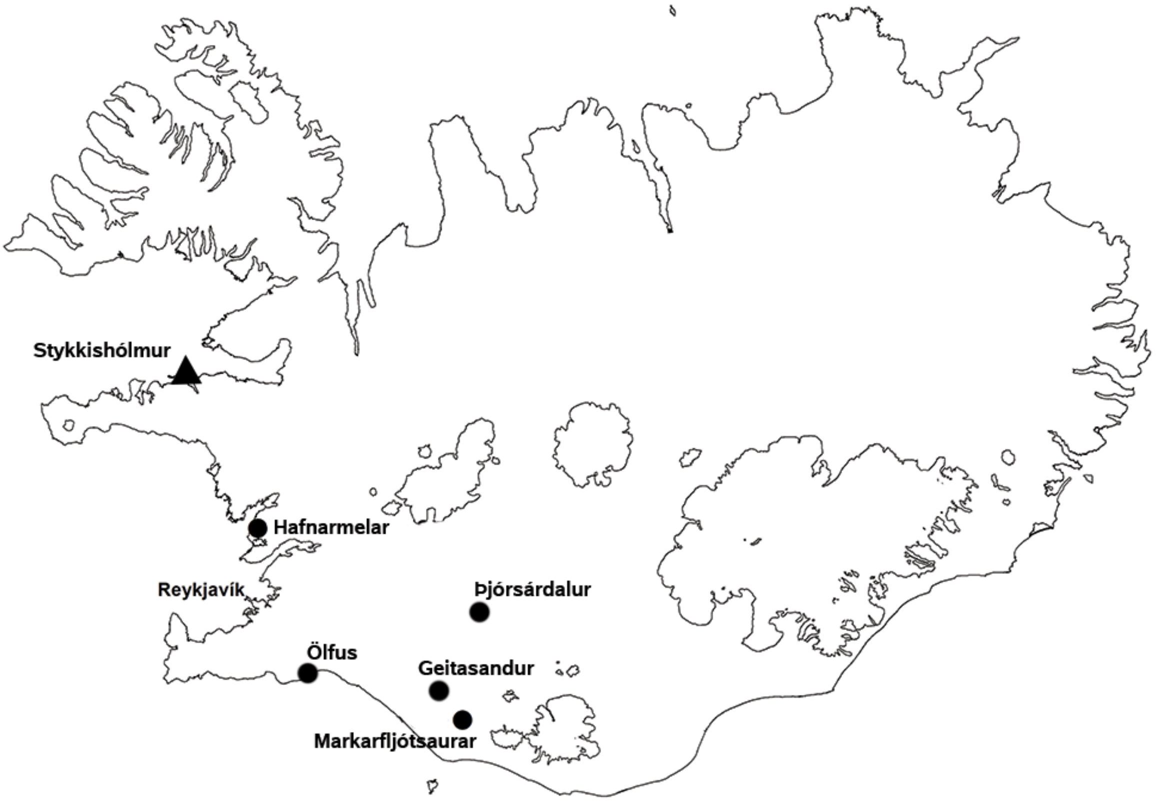

Figure 1. Map of Iceland showing all sampling and study locations (●) and the location of the climate station in Stykkishólmur (▲). For information on studies conducted at different locations see text in section 3 (Map: Björn Traustason)

Table 2. Geographical coordinates and altitude of the field sites.

	Geographical coordinates		**Altitude**
Location	**Latitude**	**Longitude**	**(m.a.s.l)**
Geitasandur	N 63.809258	W-20.209994	36
Hafnarmelar	N 64.441070	W-21.953815	20
Markarfljótsaurar	N 63.663890	W-20.029391	42
Þjórsárdalur	N 64.098077	W-19.955172	159
Ölfus	N 63.892431	W-21.305491	4

Lupin field herbivory experiment (Paper III, unpublished data)

The herbivory study sites were located within two Nootka lupin fields at different ages and successional stages, at Markarfljótsaurar (The Old Lupin Site) and Hafnarmelar (The Young Lupin Site) (Figure 1; Table 2). The Nootka lupin fields were established by direct seeding in 1999 at the Young Lupin site and in 1990-1993 at the Old Lupin site. Both sites were fenced and have been mostly protected from mammal grazing since lupin establishment. At the beginning of the study, the lupin at the Young Lupin site did not show any signs of retreat, but the lupin at the Old Lupin site showed marked signs of retreat and other vegetation had overtaken the vacant space (Figure 2).

Figure 2. Overview over the Young Lupin site (left) and the Old Lupin Site (right) taken on September 5 and 4, 2013, respectively. The Nootka lupin at both locations is still green, but the grass in between the lupin at the Old Lupin site has already wilted.

Tree measurements (unpublished data)

The tree measurements took place at Markarfljótsaurar (Figure 1) in 2012-2014 in 20-year-old stands of Sitka spruce (*Picea sitchensis*) and black cottonwood (*Populus trichocarpa*).

Experimental designs and setup (Paper II, III, unpublished data)

Nootka lupin herbivory study (Paper III)

The herbivory study was carried out over a three-year period, from 2011 to 2013. The same treatments were applied in all years. The experimental plots were established at the beginning of August 2011, and different treatments initiated. There were four blocks at each location, each 6x6 m in an area with four fully randomized 2x2 m treatment plots located in each corner of the blocks (Figure 3). Each plot was subjected to the same treatment in each year, except the simulated increased herbivory. The treatments were:

(1) Unmanipulated herbivory (control).

(2) Reduced herbivory. The reduced herbivory plots were treated with a 0.03% solution of Permasect C.

(3) Increased herbivory. Broom Moth larvae were collected and added to plots; 40 larvae/m^2 in 2011, and 20 larvae/m^2 in 2012 and 2013.

(4) Simulated increased herbivory. About 1/3 of the lupin foliage in each plot was cut manually and distributed over the ground floor of the same plot. This treatment was only done during the first project year (2011) when plants at both study sites were cut two times, whereas no treatment was applied in the consequent two years (to study potential legacy effects of grazing).

Pupal freezing experiment (Paper II)

The pupal freezing experiment took place at a low-temperature laboratory at Mödruvellir in North Iceland in December 2012, following the same procedure as Edvardsen *et al.* (2000). All pupae were stored in a cooler at 4 °C and transported to Mödruvellir where they were kept in a cooler at 4 °C. Twelve hours later, the pupae were placed in a freezer (Freezer-1) at 4 °C, in which temperature was subsequently lowered at the rate of -1 °C per hour until it reached -18 °C. When the freezer temperature reached -6 °C, -9 °C, -12 °C, -15 °C and -18 °C, 20 pupae from each sampling site were moved to another freezer that was constantly running at -1 °C (Freezer-2). The pupae were kept at -1°C for one hour and then transported back to the cooler at 4 °C. A control of 20 pupae from each sampling site were kept at 4 °C throughout the experiment (Figure 3). After the low-temperature treatment, the pupae were stored for one month at 4 °C to ensure normal diapause development, and then placed at room temperature (18-22 °C). Every day, new successful emergence of adults was recorded until all viable pupae had hatched.

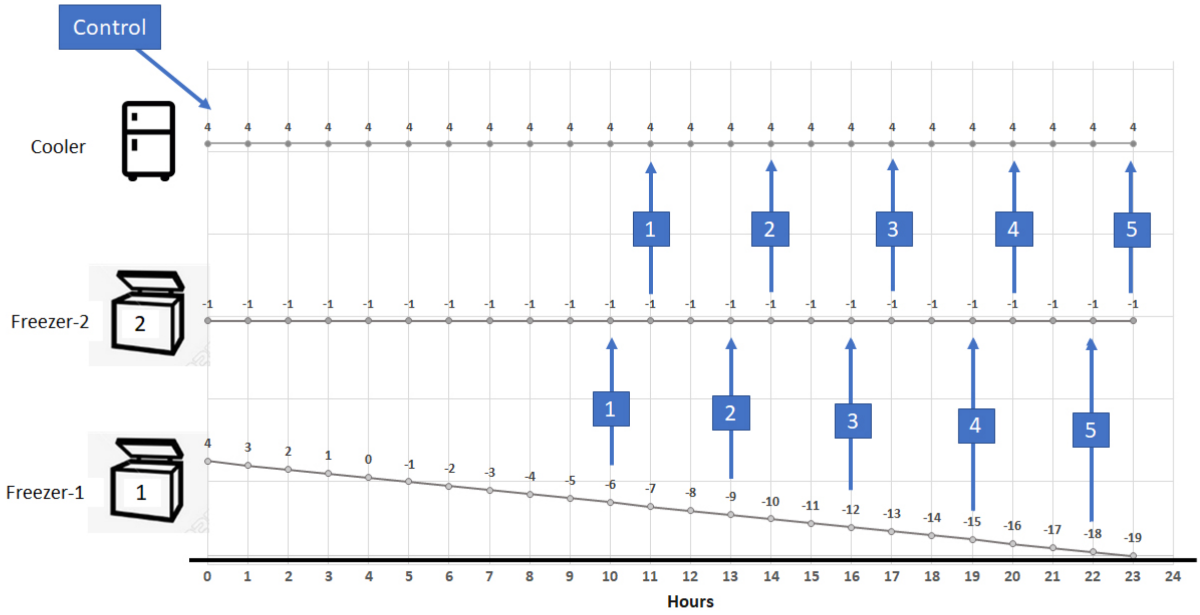

Figure 3. The experimental setup and timing of Broom Moth (Ceramica pisi) pupae freezing experiment. The five freezing treatments were: 1 = -6 °C, 2 = -9 °C, 3 = -12 °C, 4 = -15 °C and 5 = -18 °C. The transfer of pupae from the freezing experiment is indicated by blue boxes with white numbers. Arrows show the timing of transfer between freezers and cooler. Temperature development in freezers and cooler and hours from the start of the experiment are also shown.

Feeding study (unpublished data)

The feeding study was set up as five blocks with three fully randomized treatments/plant species: Nootka lupin, black cottonwood, and Sitka spruce. The Nootka lupin plants were dug up at Hafnarmelar (Figure 1) in 2013, transplanted into pots and kept outside for one year. Two-year-old black cottonwood and Sitka spruce tree seedlings in pots were obtained from a plant nursery and arranged in 5 blocks. Each block consisted of five plants of each of the three species, 15 pot plants in total within each block and 25 plants of each species in the whole experiment. The Broom Moth larvae were transported to the laboratory at room temperature and deprived of food for 20h, to ensure all gut content had emptied and subsequently weighed on a scale (AA-160; Denver Instrument Company, Arvada, Colorado) to the nearest 0.0001g. Then the larvae were individually placed into a specific cage (Figure 4.) which was then attached to a selected plant, one larva/cage/each plant (Figure 4). The assignment of cages with larvae to plants was fully randomized.

Figure 4. The Broom Moth (Ceramica pisi) larval cages used in the feeding study.

All larvae were weighed again after one and two weeks to establish their weight gain on each plant species.

Field measurements (Paper III, unpublished data)

Monitoring of larval density in the herbivory study (Paper III)

In order to identify species feeding on the Nootka lupin and assess interannual natural herbivory pressure, larvae were sampled adjacent to each block in 2011-2013 at both herbivory experimental sites: the Old Lupin Site at Markarfljótsaurar and the Young Lupin Site at Hafnarmelar. In 2011 two 1x1 m randomly selected plots per block were sampled, but the number of sampling plots was increased in 2012 and 2013 to four 0.5 x 0.5 plots/block. Sampling was done by cutting all vegetation from each plot and shaking it over a plastic box until all larvae had fallen into the box. All larvae were then identified as to species and counted.

Lupin defoliation and coverage in the herbivory study (Paper III, unpublished data)

The effect of different treatments in Nootka lupin herbivory study on the lupin coverage at each experimental herbivory site was measured in 2012-2013 by taking aerial photographs from a ladder of all plots with 1 x 1 m grid, subdivided into 0.1 x 0.1 m cells (unpublished data; Figure 5 top panel). No coverage measurements were done in 2011, as defoliation, which had already started at the time of the establishment of the experiment, would have confounded the measurements. Nootka lupin cover was measured from the photographs by manually colouring the lupin on photos with Adobe Photoshop CC 2018 (Adobe Inc., San José, CA) and measuring the proportion of coloured areas in the same computer program (Figure 5 lower panel).

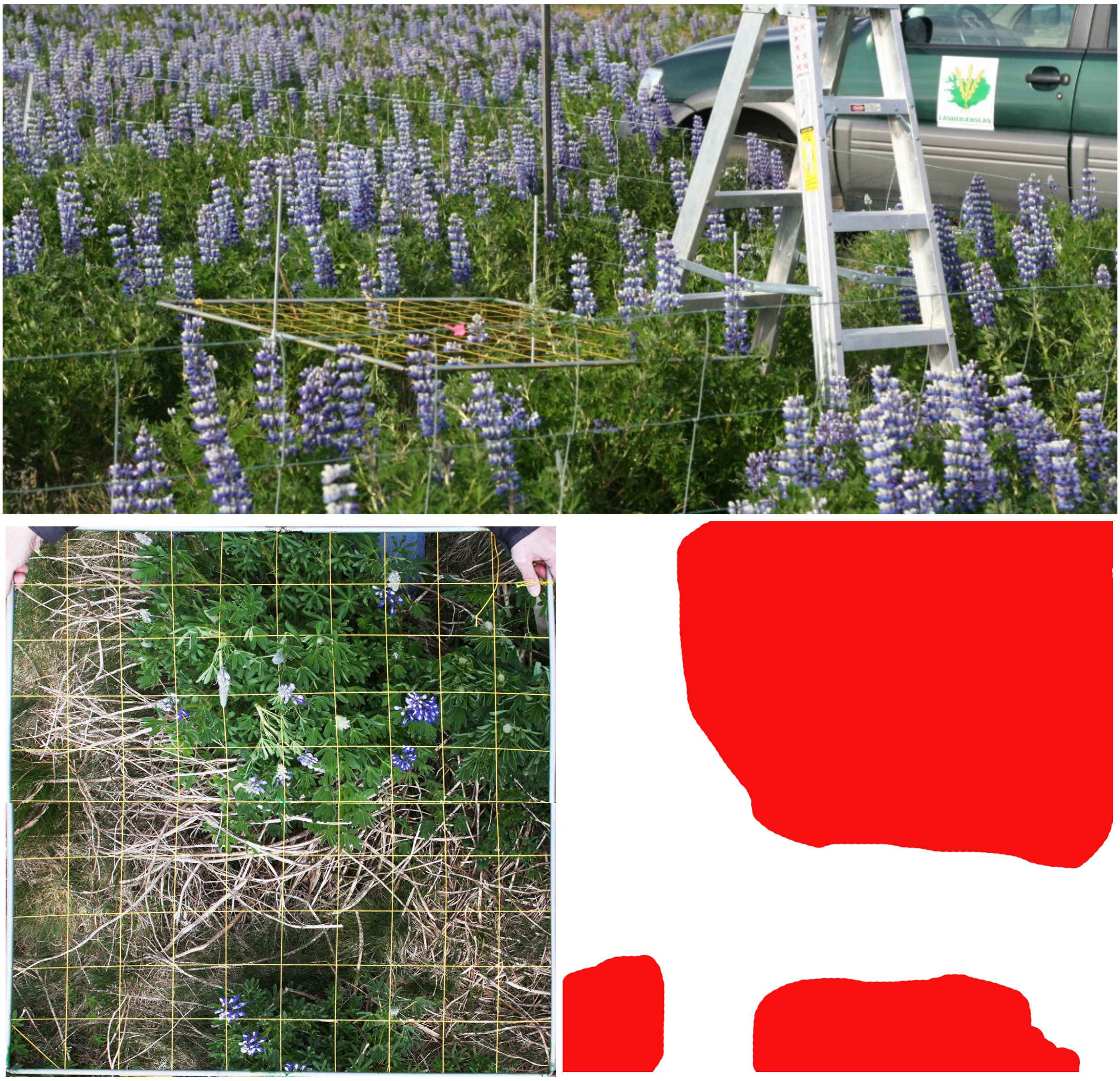

Figure 5. Lupin cover was measured by taking photographs over plots from a ladder over a 1 x 1 m grid, subdivided into 0.1 x 0.1 m cells (top panel) and then the lupin was manually coloured on photos and the proportion of coloured areas measured with a computer program (lower panel) .

The Nootka lupin defoliation was also visually assessed in all plots in the autumn each year after herbivory had ended but before lupin leaf fall, and then including 2011 (Paper III). Lupin defoliation was assessed using the following defoliation classes: 0 = no signs of herbivory, 1 = 1-10% defoliation, 2 = 10-25% defoliation, 3 = 25-50% defoliation 4 = 50-75% defoliation, 5 = 75-99% defoliation and 6 = plot totally defoliated. For analysis, median values for each defoliation class were used.

Seed sampling (Paper III)

Flowering Nootka lupin plants were counted in July 2013 at the Old Lupin Site at Markarfljótsaurar and the Young Lupin Site at Hafnarmelar. Seedbearing stems were also counted at both locations in early August the same year. Up to 12 seedbearing stems from each plot were subsequently randomly selected, and all their seedpods collected and moved into the laboratory for further analysis. In the laboratory, the number of seeds, seedpods, and seedbeds inside pods were counted. All seeds and seedpods were dried and then weighed on a scale to the nearest 0.0001 g.

Tree growth measurements (Unpublished data)

On August 2, 2012, Broom Moth damage was assessed on 20 year old Sitka spruce and black cottonwood trees at the Old Lupin Site at Markarfljótsaurar. The trees' height in this plot varied from 50-200 cm. Two tree lines of each species were randomly selected, the defoliation of all living trees was assessed, and tree height measured to the nearest cm. A total of 93 Sitka spruce and 114 black cottonwood plants were measured. The damage on the trees was assessed using the following defoliation classes: 0 = no signs of defoliation, 1 = 0-25% defoliation, 2 = 25-50% defoliation, 3 = 50-75% defoliation and 4 = 75-100% defoliation. In 2014, tree height growth from 2012-2013 was also measured with the help of bud scars (black cottonwood) or whorls (Sitka spruce). No Sitka spruce trees were found in defoliation group 0-1, and no black cottonwood trees were found in defoliation group 4. As there were no Sitka spruce trees found in class 0 within the research area, similar aged nearby trees with no damage were measured (height).

Calculation of Growing Degree Days (Paper IV)

Daily maximum and minimum temperature data from the weather stations nearest to the larvae sampling sites were obtained from the Icelandic Meteorological Office (personal communication). Growing degree days (GDD) were calculated with the formula given below (Herms, 2004; Murray, 2008):

$$\mathrm{GDD} = \left[\frac{(T_{MAX} + T_{MIN})}{2}\right] - T_{BASE}$$

where T_{MAX} is the daily maximum temperature, T_{MIN} is the daily minimum temperature, and T_{BASE} is the lower development threshold of the Broom Moth larvae. The base temperature for the development of

Broom Moth larvae is not known, but here it was set at 5°C because this base temperature reflects the principal threshold for butterfly larvae growth (Hill *et al.*, 2003) and is often used for the minimum threshold for insect development in northern Europe (Luoto *et al.*, 2006; Ekholm *et al.*, 2019).

Distribution changes of Broom Moth (unpublished data)

The historical distribution range of Broom Moth in Iceland, as published by Wolff (1971) and Ólafsson and Björnsson (1997), was compared to the distribution as monitored during my own surveys from 2009 to 2020. During 2009, 2011, 2013, 2016, and 2019 this was done by visiting Nootka lupin fields spread over the whole of Iceland. In between the country-wide surveys, or at least every second year, lupin fields close to the borderline of the species distribution range were inspected for Broom Moth larvae. In addition to this, contacts were established all over Iceland by an open electronic survey, and respondents were asked to survey lupin fields for Broom Moth larvae.

Statistical analyses (Papers I, II, III, IV, unpublished data)

Data were analysed with the SAS enterprise guide (Davis, 2007) and Sigmaplot (Systat Software 2008).

Papers I-IV

The statistical analyses used in different papers are shown in Table 3.

Table 3. Overview of statistical analyses used in papers I, II, III and IV.

Statistical methods	Paper I	Paper II	Paper III	Paper IV
Data transformation (log)			x	
One-Way ANOVA followed by LSD		x		
Two-Way ANOVA followed by LSD		x	x	
Mixed-effects model followed by LSD			x	
Lineal regression analyses	x	x		x
Non-lineal regression analyses		x		x
Non-parametric Spearman correlation	x		x	

Unpublished data

Feeding study

Logarithmic transformation was carried out because the data failed to meet the requirements of normal distribution. One-way analysis of variance (ANOVA) was used to test the differences between larval weight gain on different plant species. The student’s t-test (LSD) was used to test the difference between larval weight gain on lupin and trees.

Tree measurements

One-way analysis of variance (ANOVA) was used to test for differences in tree height growth between different larval defoliation classes. When the difference was significant, Tukey’s range test was used to compare the difference.

Main findings

New herbivores and changes in outbreaks in Iceland (Paper I)

Introduction of new herbivore species Iceland

The average rate of introduction of new insect herbivores on trees and shrubs to Iceland was found to be significantly linked to mean annual temperature, although the total area of exotic tree species (habitat availability) also seemed to have some moderating effect in the early 20th century. The rate of introduction of new insect herbivores was found to be significantly highest during the warm periods: Period II and Period IV, 0.45 species/year for both periods (Figure 1 in Paper I). The average rate of introduction during Period III was 0.20 species/year. This period was cold, but the planting rate of exotic tree species was also high as well as for the periods before and after (Periods II and IV). The average rate of introduction was lowest during Period I, when it was only 0.08 species/year, which was significantly lower than that of all other periods. This period was also characterized by a limited area of exotic tree species in Iceland (habitat availability), but split into a cold period in the beginning, followed by a warm period in its latter half.

Outbreaks on birch in East Iceland

During the study period, 1920-2011, herbivory on downy birch in East Iceland was continuous but frequently at a sub-outbreak level, i.e., Grade 1 (Figure 2a in Paper I). The most intense outbreak years were during the periods 1930-1940 and 1990-2011. The results match with the fluctuations in mean annual temperature in the same period (Figure 2b in Paper I). Intense and widespread outbreaks, followed by considerable tree mortality, i.e., Grade 4, were found to be limited to the warmer periods. A highly significant correlation ($P<0.001$) was found between the 5-year running average of insect outbreak intensity and the mean annual temperature (MAT) in Stykkishólmur during the same period (Figure 3 in Paper I).

Green Spruce Aphid outbreaks

Green Spruce Aphid outbreaks were found to be clearly linked to mild winters. No outbreaks occurred in the Reykjavík area after cold winters during the study period (1959-2012), but outbreaks did not always occur after mild winters. Until 1996, all outbreaks were in the autumn, but all outbreaks from 2003 have been during the spring (Figure 4 in Paper I). This shift in outbreak pattern may be linked to warmer winters, which are likely to facilitate population buildup during the spring, and possibly the introduction of natural enemies of the aphid, which are likely to suppress population buildup during the autumn.

Effect of temperature on survival and growth of Broom Moth (Papers II, VI)

Winter temperature and survival of Broom Moth (Paper II)

The survival of pupae was found to be strongly linked to pupal weight, but not to temperature treatments. The mean survival rate of Broom Moth pupae was 44% across all locations and cooling/freezing treatments. Freezing intensity did not affect Broom Moth pupal survival as there was no significant difference in pupal survival found across all locations and cooling/freezing treatments (P = 0.774; Figure 3 in Paper II). However, a highly significant regression was found between pupal weight and pupal survival across all locations and cooling/freezing treatments (P < 0.001; Figure 4 in Paper II). Furthermore, a Sigmoid curve showed that the 50% likelihood of weight-related winter survival (LT50) occurred at 398 mg final larval weight (274 mg pupal weight) and that the autumn weight-related survival was as high as 95% at 570 mg larval weight (393 mg pupal weight), but only 5% at 228 mg larval weight (157 mg pupal weight) (Figure 6 Paper IV; Figure 5 Paper II).

Summer temperature and larval growth (Paper IV)

The larval growth rate and the weight just before pupation were both found to be significantly linked to temperature. The average larval weight, during its growing period, ranged from 49-533 mg, across all sampling locations and dates (Figure 3 in Paper IV). A highly significant regression was found between summer growing degree days (GDD) from June 1. and the average Broom Moth larval weight, across all sampling dates and locations (df=27; P<0.001; Figure 4 in Paper IV). The r^2 of the relationship was 0.863, indicating that up to 86% of the variability of weight observed across the whole dataset could be explained by June GDD.

A significant relationship was also found between the larval weight on August 28, just before pupation, and GDD from June 1st across all three larval sampling locations and years (P = 0.012; Figure 5 in Paper IV). The r^2 of the relationship was 0.824, indicating that up to 83% of the variability of weight observed across this dataset could be explained by June GDD. A highly significant regression was found between larval weight, just before pupation, and pupal weight (P<0.001; Figure 6 in Paper IV). The r^2 of the relationship was 0.682, indicating that up to 68% of the variability of pupal weight observed across the whole dataset could be explained by larval weight. No larvae under 300 mg pupated, indicating that the minimal larval weight for pupation is near 300 mg. A sigmoid curve fitted to the pupation rate of different larval weight groups showed a 50% likelihood (LT50) of pupation at 383 mg larval weight. The sigmoid curve also showed that weight-related pupation was as high as 95% at 650 mg but 5% at 191 mg (Paper IV).

Feeding study (unpublished data)

Over the two week study period, the larval weight gain ranged from 29 – 585 mg across all groups. The results showed that Broom Moth larvae grew relatively faster on lupin than on the two tree species as there was a significant difference between the growth of larvae feeding on lupin and larvae feeding on both tree species combined (P = 0.013; Figure 6). However, no significant difference was detected between the growth of larvae across all the groups of Nootka lupin, Sitka spruce, and black cottonwood (P = 0.0786), even though the larvae gained most weight proportionally on lupin plants and least weight feeding on black cottonwood plants, or 228% and 142% on average, respectively.

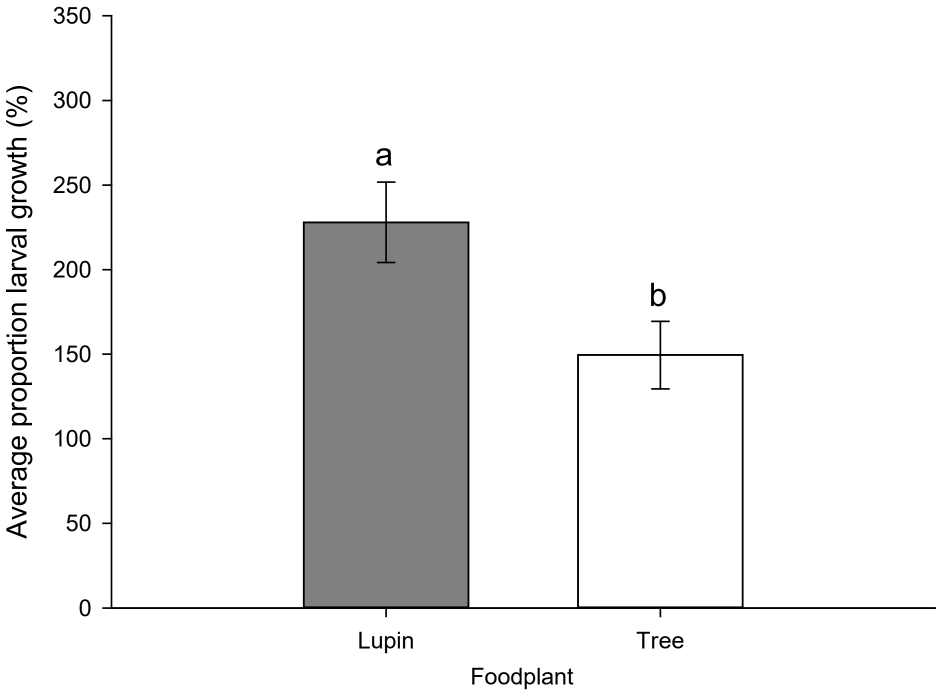

Figure 6. The average proportion of Broom Moth (Ceramica pisi) larval growth of Broom Moth larvae on Nootka lupin (Lupinus nootkatensis) and tree seedlings (Sitka spruce - Picea sitchensis and black cottonwood - Populus trichocarpa) over a two week period in August 2014. Different lower case letters indicate significant differences in weight gain between host plants (Student's t-test).

The distribution range of Broom Moth (Unpublished data)

The historical distribution range of the Broom Moth was found to be the lowlands of southern Iceland (Wolff, 1971; Ólafssson & Björnsson, 1997). It had also been recorded in two locations in western Iceland, and one in northern Iceland (Wolff, 1971). One of the locations in west Iceland cannot be confirmed, as the name of the location given cannot be found in the area (Erling Ólafsson, personal communication). Surveys conducted during 2009-2019 showed a large northward expansion of the distribution area of the Broom Moth in the lowlands of western Iceland and a slight expansion in the lowlands of south-eastern Iceland. In total, nine new locations of Broom Moth larvae were recorded during surveys from 2009 to 2018 (Table 4). During the study in 2019, Broom Moth larvae were not recorded in any new locations. Locations where the Broom Moth has been recorded are shown in Figure 7, giving the historical distribution according to Wolff (1971) and records of new locations where the Broom Moth has been found during my own surveys during 2009-2019 (Figure 7.)

Table 4. The locations and the years of new records of Broom Moth larvae in Iceland.

Location	Region	First year of recording
Búðardalur	Western Iceland	2009
Ólafsvík	Western Iceland	2009
Stykkishólmur	Western Iceland	2009
Bíldhóll, Skógarströnd	Western Iceland	2009
Grundarfjörður	Western Iceland	2009
Hafnarmelar	Western Iceland	2009
Laugar í Sælingsdal	Western Iceland	2010
Lónið	South-eastern Iceland	2011
Urðateigur, Berufirði	South-eastern Iceland	2018

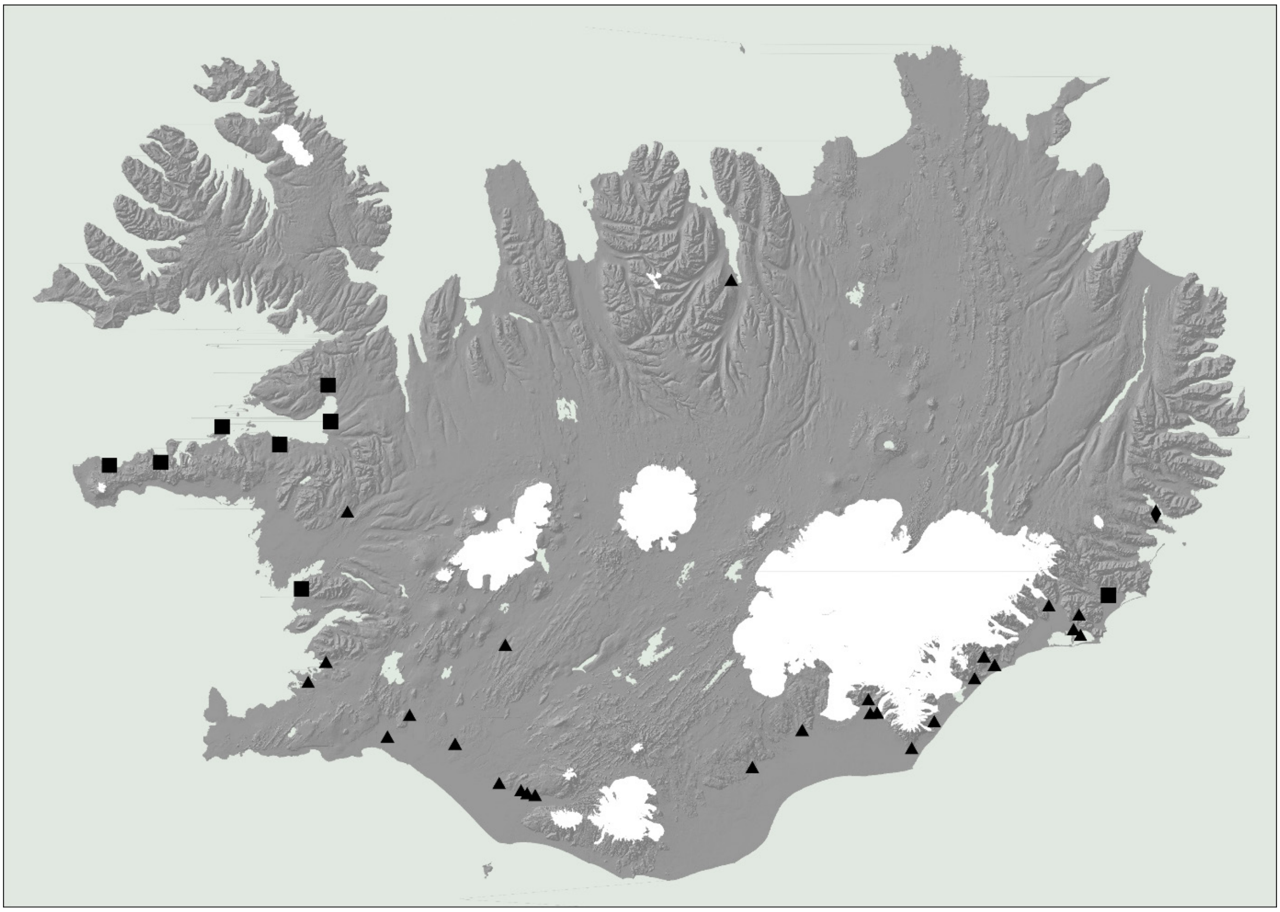

Figure 7. The distribution changes of the Broom Moth in Iceland. Different symbols show new records of the distribution of the Broom Moth in Iceland: (a) distribution as recorded by Wolff (1971) (▲), (b) new records observed during 2009-2011 surveys (■) and during the 2018 survey (♦) (Map: Bjarki Þ. Kjartansson).

Effects of insect herbivory on lupin seed production (Paper III)

Effects of lupin defoliation on seed production (Paper III)

Seed production across all treatments was found to be negatively related to defoliation and depended on age and/or the successional stage, as they were only significant at the Old Lupin Site. The lupin defoliation varied between years and treatments but not between the Young Lupin Site and the Old Lupin Site (Table 4 in Paper III). The defoliation was highest in 2012, but lowest in 2013. When treatments were compered within years, lupin defoliation was lowest in the reduced herbivory treatment ($P<0.0001$; Figure 3 in Paper III).

At the Old Lupin Site, the average number of flowering stems per m^2 in 2013 was significantly higher in the reduced herbivory treatment compared to the control ($P=0.005$), increased herbivory ($P=0.0129$) and simulated herbivory ($P <0.0001$). However, there was no difference in the average number of flowering stems per m^2 found between treatments at the Young Lupin Site ($P = 0.665$). There was also no significant difference found between treatments on the average number of pods per stem and seeds per pod at the Young and Old Lupin Sites (Table 5 in Paper III).

The average number of seeds per m^2 in 2013 was significantly higher in the reduced herbivory treatment, compared to all other treatments, the control ($P = 0.0145$), increased herbivory ($P = 0.0365$) and simulated herbivory ($P = 0.0011$), at the Old Lupin Site. However, there was no significant difference in seed density between any of the treatments at the Young Lupin Site (Figure 5 in Paper III). As the lupin did not have full cover at the Old Lupin site and there was variation in lupin coverage between treatments, seed production was also calculated per m^2 lupin, instead of m^2 total plot area. This was shown not to change the results of the study (Paper III Supplement).

Effects of insect herbivory on tree height (unpublished data)

No significant effect of insect herbivory was found on the height increment of black cottonwood, but it was shown to significantly reduce the height of Sitka spruce. The height growth of Sitka spruce trees that experienced no herbivory in 2012 was significantly better the year after the defoliation than of trees that experienced 50-75% defoliation ($P = 0.047$) and 75-100% defoliation ($P = 0.015$; Figure 8). However, there was no significant difference in height growth of trees that had no defoliation or 25-50% defoliation in 2012 ($P = 0.137$; Figure 8).

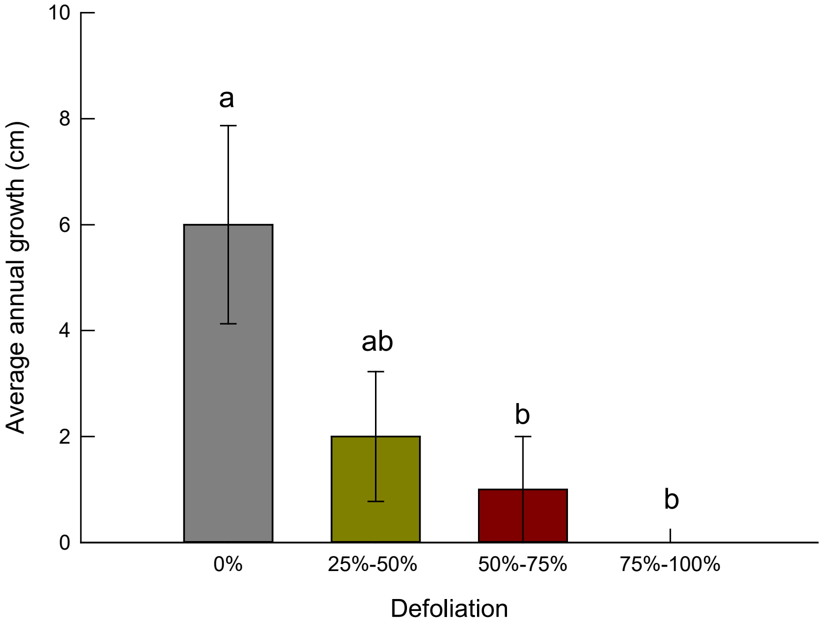

Figure 8. The average height growth of Sitka spruce (*Picea sitchensis*) trees in 2013 that experienced different Broom Moth (*Ceramica pisi*) larval defoliation in 2012. Different lower case letters indicate a significant difference in growth between different defoliation classes. Trees with 0% defoliation were not within the same stand as the defoliated trees, but within a comparable stand close by, which had not been defoliated in 2012.

No significant differences were found in height growth measured in 2013 of black cottonwood trees that experienced different herbivory of Broom Moth larvae in 2012 (P=0.2584), but there was a tendency for better height growth of defoliated trees up to 50% defoliation (Figure 9).

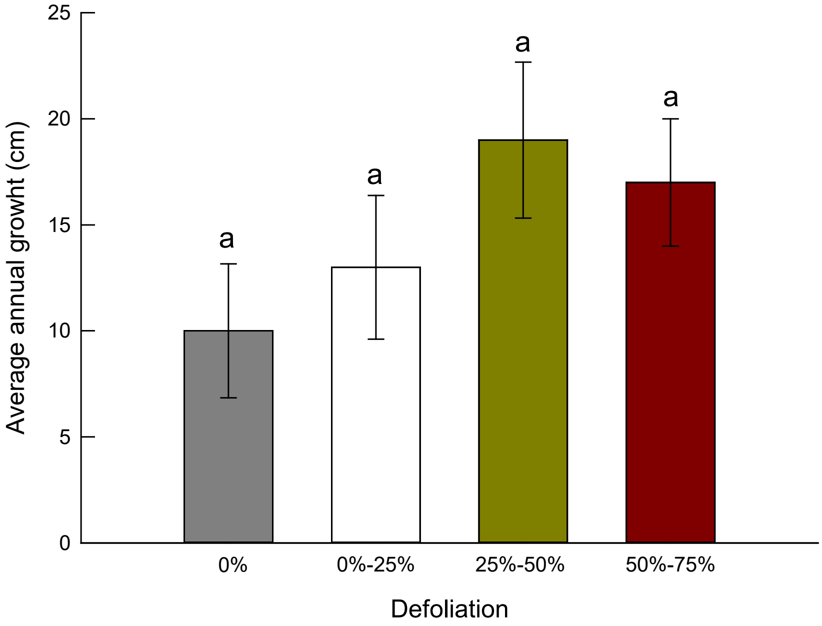

Figure 9. The average height growth of black cottonwood (*Populus trichocarpa*) plants in 2013 that experienced different Broom Moth (*Ceramica pisi*) larval defoliation in 2012. Lower case letters indicate a significant difference in growth between different defoliation classes.

Discussion

Insect herbivores and climate change in Iceland

Climate change has been shown to have a marked effect on insect herbivores in Iceland. This involves changes in the introduction rate of new forest insects, in outbreak patterns, and in outbreak intensity (Paper I). The introduction rate of new forest insect herbivores since the beginning of the 20th century was shown to be significantly lower during cold periods than warmer ones (Figure 1 in Paper I). Those results are in line with many other studies that show that temperature is often a critical factor for insect introduction into new areas (Logan *et al.*, 2003; Pureswaran *et al.*, 2018).

Since the beginning of the 20th century, considerable changes have also been observed in outbreak patterns and outbreak intensity of insect herbivores in Iceland, primarily in the Green Spruce Aphid outbreaks on Sitka spruce, species feeding on Nootka lupin, and species feeding on the native downy birch. Outbreak patterns in birch forests in East Iceland were shown to be positively related to temperature, and intense outbreaks occurred primarily during warmer periods (Figure 2 in Paper I; Figure 3 in Paper I). Extensive insect outbreaks in birch forests in northern Scandinavia have also been found to be linked to a warmer climate (Jepsen *et al.*, 2008; Jepsen *et al.*, 2011). Other studies abroad have shown that more intense insect outbreaks on trees have been getting more frequent as the climate has got warmer (Ayres & Lombardero, 2000; Reynolds *et al.*, 2007).

The observed shift in outbreaks of the introduced Green Spruce Aphid from the autumn to the spring which occurred between 1996 and 2003 (Figure 4 in Paper I) was most likely due to warmer winters, as population buildups during the spring have been shown to be linked to winter temperatures (Bejer-Petersen, 1962). The introduction of new natural enemies of the aphid, observed during the 1990s (Paper I), is likely to suppress population buildup during the autumn, as shown by Leather & Kidd (1998). Native insect herbivores like the Broom Moth have also been causing more damage in forestry in Iceland (Sigurdsson *et al.*, 2003; Hrafnkelsdottir *et al.,* 2010)

Insect herbivores on Nootka lupin and climate change

Since 1990 the outbreak patterns and outbreak intensity of native herbivores species on the Nootka lupin in Iceland have been changing, especially for the native Broom Moth and the Satyr Pug (Paper I).

At the same time, there has been a considerable northward expansion in the distribution area of the Broom Moth, primarily in the lowlands of western Iceland, and some expansion has also been observed in the lowlands of South-east Iceland (Figure 7). Those changes coincide with the recent increase in temperatures in Iceland, which has been more pronounced in the western part of Iceland than the eastern part (Björnsson *et al.*, 2018).

The present PhD study showed that the observed changes in the distribution area of the Broom Moth are unlikely to be explained by higher winter survival of pupae due to higher winter temperatures (Paper II), as a freezing experiment where pupae were exposed to temperatures down to -18°C did not show any significant relationship between temperature and pupal survival rate (Figure 3 in Paper II). There was, however, a highly significant positive relationship between pupal weight and survival rate in the same experiment (Figure 4 in Paper II). Pupal weight in the autumn was found to be significantly linked to larval weight just before pupation (Figure 6 in Paper IV), which again was significantly linked to summer GDD (Figure 5 in Paper IV). These results indicate that higher summer temperatures, rather than milder winters, are likely the explanation for the recent northward expansion of the Broom Moth distribution area in Iceland, and at least partly for the large increase in population levels, as shown by the intense and widespread outbreaks after 1990. Like similar changes in outbreaks of other species feeding on lupin, especially the Satyr Pug and to a lesser extent the Rusty Tussock Moth, that have also occurred after 1990, it is likely that they have also benefited in some way from climate change.

It is well established that pupal and adult weight is significantly related to larval weight just before pupation (Fox & Czesak, 2000; Davidowitz *et al.*, 2003). Hokkanen (1993) found that winter survival of the Rape Beetle (*Meligethes aeanus*) was significantly positively related to the weight of the overwintering beetles and Bradshaw *et al.* (2004) found that the northern population of Plant Mosquito (*Wyeomyia smithii*) benefitted from higher temperatures during larval growth. Other studies have shown that freeze-tolerant insect species that undergo diapause over the wintertime are more likely to benefit from rising summer temperatures during their larval growth period rather than winter temperatures (Bale & Hayward, 2010). The fact that the distribution area of the Broom moth in Iceland before 1990 (Wolff, 1971; Olafsson & Bjornsson, 1997) was confined to areas with the highest GDD sums during 1961-1990 (Björnsson *et al.*, 2007) also supports the conclusion that summer temperature limits the distribution of the Broom Moth in Iceland.

Interactions between introduced plants and native herbivores

Even though summer temperatures seem to be a critical factor limiting population levels and distribution of the native Broom Moth in Iceland, other factors may also have facilitated these changes. Since the species is native and therefore existed before Nootka lupin was introduced, and because Nootka lupin fields and patches are found in lowland areas over most of Iceland (Guðjohnsen & Magnússon, 2019) and Broom Moth is not (Figure 7), it is clear that the Nootka lupin is not the limiting factor of the distribution of the Broom Moth. Nevertheless, the large-scale introduction of the lupin in the 1980s and 1990s may have facilitated the fast changes in the distribution of Broom Moth after 1990, as the Broom Moth is known to favour leguminous plants (Cindea, 1979).

In the present PhD study the Broom Moth larvae grew better on lupin than on tree seedlings (Figure 6). The Nootka lupin has, like other lupins and members of the legume family, a high nitrogen and protein content (Magnusson & Sigurdsson, 1995), which can be beneficial for herbivores (Awmack & Leather, 2002). Many wild legumes also produce Quinolizidine alkaloids as a chemical defence against herbivores (Wink, 1992). Some of the alkaloids found in the Nootka lupin have been shown to affect development and survival of many insect species (Wink, 1992; Þórsson & Hlíðberg, 1997) and studies in Iceland have shown that the Nootka lupin is not suitable for livestock grazing as the sole fodder, due to the high alkaloid content (Guðmundsson, 1986; Þórsson & Guðmundsson, 1993). However, the alkaloid content of the lupin is very variable, varying both between individuals and the time of the growing season (Magnússon *et al.*, 1995; Þórsson & Hlíðberg, 1997), with the alkaloid content decreasing in late summer (Þórsson & Hlíðberg, 1997) when most of the insect herbivory occurs. The clear preference of Broom Moth towards Nootka lupin in Iceland, however, may indicate resistance to its alkaloids.

The reasons for the host shift of native insect herbivores in Iceland over to Nootka lupin around and after 1990 are still unknown. Studies have shown that insects can adapt and increase their herbivory on introduced plants over time (Siemann *et al.*, 2006; Bezemer *et al.*, 2014). Some introduced plant species have lowered their energy usage of defence chemicals and use more energy on other factors like, for instance, growth and higher reproductive output (Siemann & Rogers, 2003; Bossdorf *et al.*, 2005). Cheng *et al.*, (2017) found, for example, that the content of alkaloids in the common groundsel (*Senecio vulgaris*) tended to be lower in their invasive range than in their native range. Similar development might have happened with the Nootka lupin in Iceland. However, further studies are needed to answer that question.

The methods used for large scale establishment of the Nootka lupin in Iceland may have facilitated this process of lowering defence chemicals, as the present lupin fields in Iceland have, to a large extent, their origin in seed harvesting fields that were established by the Soil Conservation Service in 1986 (Arnalds, 1988). The seed used for establishing the harvesting fields was manually collected from relatively few areas (Arnalds, 1988) and represent, therefore, only a small sample of the whole genetic pool of Nootka lupin in Iceland. Mechanical harvesting of lupin seeds from those fields started in 1990, and during 1990-2000 seeds from those fields were annually sown into large areas (Halldórsson *et al.*, 2011). This coincides with the start of large-scale insect outbreaks in Nootka lupin fields and patches.

It is known that plants that use limited resources on the production of defence chemicals often have larger seed outputs than plants that prioritize the production of defence chemicals (Siemann & Rogers, 2003; Bossdorf *et al.*, 2005). Mechanical seed collection from seed fields is, therefore, likely to have favoured plants with high seed output and low defence chemical production, especially since the

Nootka lupin in Iceland is mostly self-pollinated (Baldursson, 1995). The initial collection of seed for establishing the seed harvesting fields may also have favoured plants with the same strategy.

In addition to the above, natural selection within Nootka lupin populations in Iceland towards better adaption to an environment with low herbivory pressure has possibly occurred over time, by reducing their alkaloid production. If this had happened, it would also be likely to have enhanced host shift of native insect herbivores over to Nootka lupin. Such an adaption to an environment with low herbivory pressure is well known (Siemann & Rogers, 2003; Bossdorf *et al.*, 2005; Cheng *et al.*, 2017).

In Greenland, a similar host shift of native insect herbivores over to the non-native Nootka lupin has also occurred, although this involves different insect species (Susanne Harding, personal communication).

Effects of insect herbivory on Nootka lupin fitness

The late summer herbivory did not affect the Nootka lupin survival but did, however, affect the seed production negatively in older Nootka lupin fields, though not in the younger fields (Table 4 in Paper III). Those results are partly in line with studies where Nootka lupin was cut at different times in a middle-aged lupin field during the growing season. There cutting the lupin in late summer or autumn did not affect its survival but did lower its seed production the following year (Sigurdsson *et al.*, 1995; Björnsson & Dalmannsdóttir, 2004).

The Nootka lupin forms a large energy storage root system in late summer (Sigurdsson *et al.*, 1995), and cutting at that time has been shown to affect the root biomass negatively the following year (Björnsson & Dalmannsdóttir, 2004). It has also been shown that late summer cutting affects the number of stems negatively the next year (Björnsson & Dalmannsdóttir, 2004). Seed production was significantly related to the number of flowering stems, but no effect of herbivory was found on the number of pods per flowering stem or seeds per pod (Table 4 in Paper III). It is therefore likely that herbivory during late summer and/or autumn, has negative effects on the buildup of resources in roots leading to negative effects on the number of flowering stems, especially when the lupin gets older and less viable. In the present PhD study, the older lupin was found to have lower seed production than the younger lupin, and this difference was caused by the number of flowering stems (Figure 4 in Paper III). Those results are in line with Sigurdsson & Magnusson, (2004) who also found that older Nootka lupin plants produced fewer flowering stems.

Baldursson (1995) showed that fewer flowers develop into seeds on older Nootka lupin plants than younger plants when he studied age-gradients from patch edges into their older central areas. However, this last observation of Baldursson (1995) seems not to be the case in the current study, as there were no significant differences in number of pods per stem between lupin sites or treatments (Table

4 in Paper III). Since the Nootka lupin is, to a large extent, self-pollinated (Baldursson, 1995), this pattern could also be caused by more windy conditions at Nootka lupin patch edges and more movements of the stem, leading to more self-pollination there compared to the inner parts of the patches. In the present study, all observations took place within larger lupin fields/patches, and such 'edge effects' are therefore not to be expected.

These results indicate that insect herbivory on the Nootka lupin in Iceland could have a substantial effect on the dynamics of lupin-associated communities through reduced seed production, as has been shown for other lupin bioregions (Bishop *et al.*, 2005). The present study showed that three-year protection from insect herbivory had a significant positive effect on the seed production of older Nootka lupin, which reflects a reduced fitness of the older Nootka lupin under the current herbivory conditions. Insect outbreaks in Nootka lupin frequently reoccur for several years in the same areas in Iceland (Brynja Hrafnkelsdóttir, unpublished results). Such reoccurring outbreaks are likely to cause long term reduction of fitness, which could affect the vitality of the lupin and have negative effects on its competition with other plants and thereby speed up the successional cycle. Other studies have shown that a smaller chronic herbivory can greatly affect plants and ecosystems over time (Zvereva *et al.*, 2012).

Effects of insect's herbivory on tree growth

Soon after Broom Moth outbreaks started on Nootka lupin in Iceland, the larvae started to cause more damage in forestry in the south part of the country (Sigurðsson *et al.*, 2003; Hrafnkelsdottir & Oddsdóttir, 2010). There are no records of Broom Moth causing severe damage in forestry before that time and it, was not listed as important forest pest in Ottósson, for instance (1983). Broom Moth herbivory does not affect all trees in the same way, as young tree seedlings are more vulnerable than older trees (Sigurðsson *et al.*, 2003) and there may even be clonal differences within the same tree species as to how likely the Broom Moth is to attack them (Gudmunsdottir, 2008). Also, some tree species seem to be more affected by Broom Moth herbivory than others. in the present PhD study, a massive Broom Moth herbivory negatively affected Sitka spruce height growth (Figure 8) but did not affect the black cottonwood's height growth in the following year (Figure 9). These results are in line with Sigurðsson *et al.* (2003) where conifer trees were more affected by Broom Moth herbivory than deciduous trees. The conifers may be more sensitive because they are likely to lose many age classes of needles, while deciduous trees are able to regrow all leaves the following year, if their energy resources allow. Sigurðsson *et al*. (2003) also found that trees that survive a Broom Moth outbreak can benefit from the effects that follow massive defoliation as the insect faeces and dead insects can accelerate the nutrient cycling (Hunter, 2001).

The Broom Moth larvae also preferred Sitka spruce over the black cottonwood as the Broom Moth defoliation ranged from 25-100% on Sitka spruce but from 0-75% on the black cottonwood. Polyphagous insects often prefer special host plants over others, and that is frequently connected to host plant suitability (Lechowicz & Mauffette, 1986; Bernays & Chapman, 2007). For instance, the Gypsy Moth (*Lymantria dispar*) is highly polyphagous and lives on many tree species but prefers oak (*Quercus* spp.) as a host over other known host species (Lechowicz & Mauffette, 1986; McCormick *et al*., 2019). Studies have shown that if the Gypsy Moth larvae feed on oak, their survival and pupal weight is higher and development rate faster than if they feed on other known host species (Hough & Pimentel, 1978; Montgomery, 1991). Further studies on the host preference (on lupin and tree species) and larval weight are necessary to answer if this is also true for the Broom Moth in Iceland.

Conclusions

The present PhD study showed that climate change has had considerable effects on the population dynamics and distribution potential of native herbivores on exotic Nootka lupin and trees. A case study showed that summer temperatures are a key factor in the population dynamics and distribution potential of the Broom Moth but that winter temperatures seem to be of little importance. Host shift of native herbivores over to lupin has not been explained, but adaptation of the lupin to a low herbivore environment is a possible explanation. Insect herbivory was found to have a significant effect on the fitness of Nootka lupin, using seed production as a proxy for fitness. It also had a significant effect on Sitka spruce growth, but not on black cottonwood. Increasing population levels of native insect herbivores, due to climate change and new resources due to host shift over to lupin, have therefore the potential to cause a long-term reduction in the invasiveness of Nootka lupin in Iceland.

The main findings were:

- Higher temperatures have both affected the number of new introductions and the intensity of outbreaks of forest herbivores in Iceland.
- The Broom Moth distribution in Iceland has greatly expanded since 1990, especially in western Iceland, concurrent with changes in temperatures.
- Low winter temperatures did not affect the Broom Moth pupae survival rate.
- High summer temperatures did affect the Broom Moth larval and pupal size positively and bigger pupae had higher winter survival rates.
- Broom Moth larvae grew faster on lupin than on trees.
- Heavy Broom herbivory affected growth of Sitka spruce and black cottonwood in opposite ways.
- Insect herbivory affected the seed production of older lupin, but not the younger lupin.

Future work

- To get a better understanding of the long-time effects of insect herbivory on the Nootka lupin in Iceland, herbivory study over a longer time is needed.
- To see if selection has occurred in the Nootka lupin in Iceland toward better adaption to an environment with low herbivory pressure, further research on the lupin alkaloid content is needed. This could be possible by comparing the alkaloid content of Nootka lupin from its native range (Alaska) to lupin growing in Iceland. To connect that to insect herbivory, both lupins that have experienced heavy herbivory and no herbivory are needed for this study.
- Comparing Broom Moth larvae weight gain fed on Nootka lupin from Alaska or Iceland might answer some questions as to whether the Nootka lupin in Iceland is better suited for insect herbivores after being in an herbivory free environment for many years. Field studies on Broom Moth larval weight gain on different tree species in Iceland could give us a better understanding of the Broom Moth larvae preference.
- To get a better understanding of the effects of higher summer temperatures on the distribution of the Broom Moth in Iceland, further comparison of changes of GDD (meteorological data) and the Broom Moth distribution changes over the years are needed.
- Not much is known about natural enemies on insect herbivores in Iceland. Better understanding of natural enemies (if they exist) of the Broom Moth would give a better understanding on the development of the moth.
- It would be useful to do a similar freezing and larval weight study on the other insect herbivores species in Iceland.

References

Adamski, D., Apple, J.L. & Bishop, J.G. 2009. A New Filatima Busck (Lepidoptera: Gelechiidae) Associated with Lupine and Early Herbivore Colonization on Mount St. Helens. *Proceedings of the Entomological Society of Washington* 111: 293-304.

Altermatt, F. 2010. Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences* 277: 1281-1287.

Aradottir, A.L. 2004. Does the Nootka lupin facilitate or impede colonization and growth of native birch in Iceland? In Santen E.v. (eds.), *Wild and cultivated lupins from the tropics to the poles. Proceedings of the 10th International Lupin Conference, Laugarvatn Iceland, 19-24 June 2002*. International Lupin Association, Canterbury, New Zealand, pp. 184-90.

Arnalds, A. 1988. Lúpínan og landgræðslan [The Nookta lupin and land reclamation]. In Arnalds A. (eds.), *Græðum Ísland, Landgræðslan 1907-1987*. Landgræðsla ríkisins, pp. 193-196 [In Icelandic].

Arnalds, A. & Runolfsson, S. 2004. The role of Nootka lupin (Lupinus nootkatensis) for revegetation in Iceland. In Santen E.v. (eds.), *Wild and cultivated lupins from the tropics to the poles. Proceedings of the 10th International Lupin Conference, Laugarvatn Iceland, 19-24 June 2002*. International Lupin Association, Canterbury, New Zealand, pp. 94-6.

Ayres, M.P. & Lombardero, M.J. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of the Total Environment* 262: 263-286.

Ayres, M.P. & Scriber, J.M. 1994. Local adaptation to regional climates in *Papilio canadensis* (Lepidoptera: Papilionidae). *Ecological Monographs* 64: 465-482.

Awmack, C.S. & Leather, S.R. 2002. Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology* 47: 817.

Baldursson, S. 1995, Frjóvgun og fræsenting alaskalúpínu [Fertilization and seed set in Nootka lupin]. In Magnússon B. (eds.), *Líffræði alaskalúpínu (Lupinus nootkatensis). Vöxtur, fræmyndun, efnainnihald og áhrif sláttar.* Rannsóknastofnun landbúnaðarins, Reykjavík, pp. 38-43 [In Icelandic].

Bale, J. & Hayward, S. 2010. Insect overwintering in a changing climate. *Journal of Experimental Biology* 213: 980-994.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D. & Whittaker, J.B. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8: 1-16.

Barton, B.T. 2010. Climate warming and predation risk during herbivore ontogeny. *Ecology* 91: 2811-2818.

Battisti, A., Stastny, M., Netherer, S., Robinet, C., Schopf, A., Roques, A. & Larsson, S. 2005. Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecological Applications* 15: 2084-2096.

Bayes, J., Dawson, M. & Potts, G. 1964. The food and feeding behaviour of the great skua in the Faroes. *Bird Study* 11: 272-279.

Bejer-Petersen, B. 1962. Peak years and regulation of numbers in the aphid *Neomyzaphis abietina* Walker. *Oikos* 13:155-168.

Benediktsson, K. 2015. Floral hazards: Nootka lupin in Iceland and the complex politics of invasive life. *Geografiska Annaler: Series B, Human Geography* 97: 139-54.

Bernays, E.A. 1997. Feeding by lepidopteran larvae is dangerous. *Ecological Entomology* 22: 121-3.

Bernays, E.A. & Chapman, R.F. 2007. *Host-plant selection by phytophagous insects*. vol. 2, Springer Science & Business Media, New Yourk 312 p.

Bezemer, T.M., Harvey, J.A. & Cronin, J.T. 2014. Response of native insect communities to invasive plants. *Annual review of entomology* 59: 119-141.

Bishop, J.G., Fagan, W.F., Schade, J. & Crisafulli, C. 2005. Causes and consequences of herbivory on Prairie Lupine (Lupinus lepidus) in early primary succession. In Dale V., Swanson F. & Crisafulli C. (eds.), *Ecological Responses to the 1980 Eruption of Mount St. Helens*, Springer New York, pp. 151-161.

Bishop, J.G. 2002. Early primary succession on Mount St. Helens: Impact of insect herbivores on colonizing lupines. *Ecology* 83: 191-202.

Bjarnason, H. 1957. Um innflutning plantna [On import of plants]. Ársrit Skógræktarfélags Íslands 24: 64-79 [In Icelandic].

Björnsson, D. 2011. Hörfar lúpínan? Dæmi úr Heiðmörk [Does the Nootka lupin retreat? Example from Heiðmörk]. *Skógræktarritið* 2011: 12-7 [In Icelandic].

Björnsson, H. & Dalmannsdóttir, S. 2004, Yield potential of the Nootka lupin. In Santen E.v. (ed.), *Wild and cultivated lupins from the tropics to the poles. Proceedings of the 10th International Lupin Conference, Laugarvatn Iceland, 19-24 June 2002*. International Lupin Association, Canterbury, New Zealand, pp. 97-100.

Björnsson, H., Sigurdsson, B.D., Davíðsdóttir, B., Ólafsson, J., Ástþórsson, Ó.S., Ólafsdóttir, S., Baldursson, T. & Jónsson, T. 2018. *Hnattrænar loftslagsbreytingar og áhrif þeirra á Íslandi. Skýrsla vísindanefndar um loftslagsbreytingar. [Global climate change and its effects in Iceland. Report from the national scientific panel on climate change]*, Veðurstofa Íslands, Reykjavik, pp. 238 [In Icelandic].

Bjornsson, H., Olason, E.O., Jónsson, T. & Henriksen, S. 2007. Analysis of a smooth seasonal cycle with daily resolution and degree day maps for Iceland. *Meteorologische Zeitschrift* 16: 57-69.

Blossey, B. & Notzold, R. 1995. Evolution of increased competitive ability in invasive nonindigenous plants: A hypothesis. *Journal of Ecology* 83: 887-889.

Bossdorf, O., Auge, H., Lafuma, L., Rogers, W.E., Siemann, E. & Prati, D. 2005. Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* 144: 1-11.

Bradshaw, W.E. & Holzapfel, C.M. 2010. Light, time, and the physiology of biotic response to rapid climate change in animals. *Annual Review of Physiology* 72: 147-166.

Bradshaw, W.E. & Lounibos, L.P. 1977. Evolution of dormancy and its photoperiodic control in pitcher-plant mosquitoes. *Evolution* 31: 546-567.

Bradshaw, W.E., Zani, P.A. & Holzapfel, C.M. 2004. Adaptation to temperate climates. *Evolution* 58: 1748-1762.

Capinera, J.L. 2001. Handbook of Agricultural Pests, Academic Press, 420-422.

Cheng, D., Nguyen, V.-T., Ndihokubwayo, N., Ge, J. & Mulder, P.P. 2017. Pyrrolizidine alkaloid variation in Senecio vulgaris populations from native and invasive ranges. *PeerJ* 5: 1-22.

Ciesla, W. 2011. *Forest Entomology: A Global Perspective*. John Wiley & Sons, Oxford, UK, 416 p.

Cindea, E. 1979. Investigations on the biology and control of some pests of edible pea crops. *Probleme de Protectia Plantelor*, 7, 87–96

Constantineanu, I., Constantineanu, R. & Ştefan, C. 2009. Ichneumonidae (Hymenoptera) new or rare for the Romanian fauna in some grassland ecosystems in the lower flow of the Prut water meadow (Romania). *Buletin de Informare Sociatatea Lepidopterologica Romana* 20: 27-38.

Coviella, C.E. & Trumble, J.T. 1999. Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Conservation Biology* 13: 700-712.

Crozier, L. 2003. Winter warming facilitates range expansion: cold tolerance of the butterfly Atalopedes campestris. *Oecologia* 135: 648-656.

Crozier, L.G. 2004. Field transplants reveal summer constraints on a butterfly range expansion. *Oecologia* 141: 148-157.

Davidowitz, G., D'Amico, L.J. & Nijhout, H.F. 2003. Critical weight in the development of insect body size. *Evolution & Development* 5: 188-197.

Davis, J.B. 2007. *Statistics using SAS enterprise guide*. SAS Institute, Cary.

Davíðsdóttir, B. 2013. *The Effect of vegetation Reclamation on Birds and Invertebrates in Iceland*. M.Sc. thesis from the Acricultural University of Iceland, 89 p.

Dukes, J.S., Pontius, J., Orwig, D., Garnas, J.R., Rodgers, V.L., Brazee, N., Cooke, B., Theoharides, K.A., Stange, E.E. & Harrington, R. 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? *Canadian Journal of Forest Research* 39: 231-248.

Edvardsen, Ø.M., Guðleifsson, B.E. & Skúlason, B. 2000. Kalstofan á Möðruvöllum: kynning á aðstöðu og rannsóknum [The Low Temperature Laboratory at Mödruvellir: Introduction to the facilities]. *Rit Mógilsár* 1: 16 [In Icelandic].

Einarsson, M.Á. 1984. *Veðurfar á Íslandi* [The climate of Iceland]. Iðunn, Reykjavík, 150 p. [In Icelandic].

Ekholm, A., Tack, A.J., Bolmgren, K. & Roslin, T. 2019. The forgotten season: the impact of autumn phenology on a specialist insect herbivore community on oak. *Ecological Entomology* 44: 425-435.

Elton, C.S. 1958. *The Ecology of Invasions by Animals and Plants*. University of Chicago Press, Methuen, London.

Emison, W.B. & White, C.M. 1988. Foods and weights of the Rock Ptarmigan on Amchitka, Aleutian Islands, Alaska. *The Great Basin Naturalist* 48: 533-540.

Erhardt, E. 2013. Distribution of three species of insect herbivores within Nootka lupine (Lupinus nootkatensis) in South and West Iceland. B. Sc. thesis, Albert-Ludwigs Universität Freiburg, 70 pp.

Fagan, W.F. & Bishop, J.G. 2000. Trophic interactions during primary succession: herbivores slow a plant reinvasion at Mount St. Helens. *The American Naturalist* 155: 238-251.

Fagan, W.F., Lewis, M., Neubert, M.G., Aumann, C., Apple, J.L. & Bishop, J.G. 2005. When can herbivores slow or reverse the spread of an invading plant? A test case from Mount St. Helens. *The American Naturalist* 166: 669-685.

Fox, C.W. & Czesak, M.E. 2000. Evolutionary ecology of progeny size in arthropods. *Annual Review of Entomology* 45: 341-369.

Grabenweger, G., Hopp, H., Jaeckel, B., Balder, H., Koch, T. & Schmolling, S. 2007. Impact of poor host-parasitoid synchronisation on the parasitism of *Cameraria ohridella* (Lepidoptera: Gracillariidae). *European Journal of Entomology* 104: 153-158.

Graves, S.D. & Shapiro, A.M. 2003. Exotics as host plants of the California butterfly fauna. *Biological Conservation* 110: 413-433.

Guðjohnsen, S.K. & Magnússon, B. 2019, *Útbreiðsla og flatarmál lúpínubreiða á Íslandi 2017 [The distribution and area of lupin fields in Iceland 2017], NI-19001*, Náttúrufræðistofnun, Gardabær Iceland. 31 pp. [In Icelandic].

Gudmundsdottir, H. 2008. *Ertuygla. Áhrif ertuyglu á mismunandi afkvæmahópa alaskaaspar[The effects of Broom Moth herbivory on different clones of black cotttonwood].* B.Sc. thesis from the Acricultural University of Iceland, 38pp. [In Icelandic].

Guðmundsson, Ó. 1986. Fóður- og fóðrunargildi belgjurta [Nutritive and feeding value of legumes]. In Helgadottir, A. (ed.) Nýting belgjurta á Íslandi. Agricultural Research Institute, Iceland, *Rala Report* 121: 71–93 [In Icelandic].

Halldórsson, G. & Kjartansson, B.Þ. 2005. Sitkalús [Green Spruce Aphid]. In Ægisson S. (ed.), Á sprekamó. Afmælisrit tileinkað Helga Hallgrímssyni sjötugum, pp. 107-115. [In Icelandic].

Halldórsson, G., Svavarsdóttir K., Þórarinsdóttir, E.F. & Runólfsson, 2011. Vistheimt á vegum Landgræðslu ríkisins [Ecological restoration actions of the Soil Conservation Service of Iceland]. In Aradóttir Á. L. & Halldórsson G.(eds.) *Vistheimt á Íslandi* [Ecological restoration in Iceland]. Landbúnaðarháskóli Íslands og Landgræðsla ríkisins, Reykjavík, Iceland, pp. 40-48.

Hallgrímsson, H., Halldórsson, G., Kjartansson, B.Þ. & Heiðarsson, L. 2006. Birkidauðinn á Austurlandi 2005 [The birch death in East Iceland in 2005]. *Skógræktarritið* 2006 (2): 44-53 [In Icelandic].

Hanna, E., Jónsson, T. & Box, J.E. 2004. An analysis of Icelandic climate since the nineteenth century. *International Journal of Climatology: A Journal of the Royal Meteorological Society* 24: 1193-1210.

Harrison, S. 1995. Lack of strong induced or maternal effects in tussock moths (*Orgyia vetusta*) on bush lupine (*Lupinus arboreus*). *Oecologia* 103: 343-348.

Harrison, S., Hastings, A. & Strong, D.R. 2005. Spatial and temporal dynamics of insect outbreaks in a complex multitrophic system: tussock moths, ghost moths, and their natural enemies on bush lupines. *Annales Zoologici Fennici* 42: 409-419.

Harrison, S. & Maron, J.L. 1995. Impacts of defoliation by tussock moths (*Orgyia vetusta*) on the growth and reproduction of bush lupine (*Lupinus arboreus*). *Ecological Entomology* 20: 223-229.

Harting, A.L. & LeFranc, M.N. 1987. *Grizzly Bear Compendium*. National Wildlife Federation.

Helgason, H.H. 2008. Fæða refa (*Vulpes lagopus*) á hálendi Íslands að vetrarlagi [The food of foxes (*Vulpes lagopus*) in the highlands of Iceland during the winter]. 3 ects Thesis, Universitiy of Iceland, Reykjavík, 12 pp. [In Icelandic].

Herms, D.A. 2004. Using degree-days and plant phenology to predict pest activity. *IPM (integrated pest management) of Midwest Landscapes* 49-59.

Herms, D.A. & McCullough, D.G. 2014. Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. *Annual Review of Entomology* 59: 13-30.

Hierro, J.L., Maron, J.L. & Callaway, R.M. 2005. A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology* 93: 5-15.

Hill, J., Thomas, C. & Huntley, B. 2003. Modeling present and potential future ranges of European butterflies using climate response surfaces. *Butterflies: Ecology and Evolution Taking Flight* 149-167.

Hiltbrunner, E., Aerts, R., Bühlmann, T., Huss-Danell, K., Magnusson, B., Myrold, D.D., Reed, S.C., Sigurdsson, B.D. & Körner, C. 2014. Ecological consequences of the expansion of N 2-fixing plants in cold biomes. *Oecologia* 176: 11-24.

Hokkanen, H. 1993. Overwintering survival and spring emergence in Meligethes aeneus: effects of body weight, crowding, and soil treatment with Beauveria bassiana. *Entomologia Experimentalis et Applicata* 67: 241-6.

Holzmueller, E.J. & Jose, S. 2011. Invasion success of cogongrass, an alien C 4 perennial grass, in the southeastern United States: exploration of the ecological basis. *Biological Invasions* 13: 435-42.

Hough, J.A. & Pimentel, D. 1978. Influence of host foliage on development, survival, and fecundity of the gypsy moth. *Environmental Entomology* 7: 97-102.

Hrafnkelsdottir, B. & Oddsdóttir, E. 2010. Ertuygla [The Broom Moth]. Ársrit Skógræktar ríkisins 2009. pp 18-19 [In Icelandic].

Hrafnkelsdottir, B., Oddsdóttir, E., Halldórsson, G. & Sverrisson, H. 2016. Rannsóknir á ertuyglu [Studies on the Broom Moth]. Ársrit Skógræktar ríkisins 2015 12-4 [In Icelandic].

Hunter, M.D., 2001. Insect population dynamics meets ecosystem ecology: Effects of herbivory on soil nutrient dynamics. *Agricultural and Forest Entomology*, *3*(2), pp.77-84.

Icelandic Institute of Natural History & Soil Conservation Service 2010. Alaskalúpína og skógarkerfill á Íslandi: útbreiðsla, varnir og nýting [Nootka Lupin and wild parsley in Iceland: distirbution, control and usage: Report for minister of the environment]. *Skýrsla til umvhverfisráðherra*, Náttúrufræðistofnun Íslands og Landgræðsla ríkisins, Reykjavík, 30 pp. [In Icelandic].

Ikemoto, T. 2005. Intrinsic optimum temperature for development of insects and mites. *Environmental Entomology* 34: 1377-1387.

IPCC 2007. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* In Solomon S., Qin D., Manning M., Chen Z., Marquis M., Averyt K., Tignor M. & Miller H (eds.). Cambridge University Press, Cambridge, United Kingdom & New York, USA, 996 p.

IPCC 2013. *Climate change 2013: the physical science basis: Working Group I contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. In Stocker T.F., Qin D., Plattner G.-K., Tignor M., Allen S.K., Boschung J., Nauels A., Xia Y., Bex V. & Midgley P.M. (eds.), Cambridge University Press, United Kingdom and New York , USA, 1552 pp.

IPCC 2014. *Climate Change 2014: Impacts, Adaptation and Vulnerability*. In Klein R.J., Midglev G., Preston B., Alam M., Berkhout F., Dow K. & Shaw M. (eds.), Cambridge University Press, United Kingdom and New York, USA, 1132 p.

Jamieson, M.A., Trowbridge, A.M., Raffa, K.F. & Lindroth, R.L. 2012. Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions. *Plant Physiology* 160: 1719-1727.

Jepsen, J.U., Hagen, S.B., Ims, R.A. & Yoccoz, N.G. 2008. Climate change and outbreaks of the geometrids Operophtera brumata and Epirrita autumnata in subarctic birch forest: evidence of a recent outbreak range expansion. *Journal of Animal Ecology* 77: 257-264.

Jepsen, J.U., Kapari, L., Hagen, S.B., Schott, T., Vindstad, O.P.L., Nilssen, A.C. & Ims, R.A. 2011. Rapid northwards expansion of a forest insect pest attributed to spring phenology matching with sub-Arctic birch. *Global Change Biology* 17: 2071-2083.

Johnson, S.N. & Jones, T.H. 2017. Introduction to Global Climate Change and Terrestrial Invertebrates. In Johnson S.N. & Jones T.H. (eds.), *Global climate change and terrestrial invertebrates*, Wiley, Hoboken, pp. 1-8.

Jónsson, J.Á. & Halldórsson, G. 2009 *Varnir gegn brandyglu í Þorlákshöfn* [Control of the Red-backed Cutworm]. Landgræðsla Ríkisins, 20 p. [In Icelandic].

Karban, R. & Strauss, S.Y. 2004. Physiological tolerance, climate change, and a northward range shift in the spittlebug, *Philaenus spumarius*. *Ecological Entomology* 29: 251-254.

Keane, R.M. & Crawley, M.J. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* 17: 164.

Kerr, E.D., Phelan, C. & Woods, H.A. 2013. Subtle direct effects of rising atmospheric CO^2 on insect eggs. *Physiological entomology* 38: 302-305.

Kolb, T.E., Fettig, C.J., Ayres, M.P., Bentz, B.J., Hicke, J.A., Mathiasen, R., Stewart, J.E. & Weed, A.S. 2016. Observed and anticipated impacts of drought on forest insects and diseases in the United States. *Forest Ecology and Management* 380: 321-34.

Leather S. R. and Kidd N. A. C. 1998. The quantitative impact of natural enemies and the prospect for biological control. In Day K.R., Halldórsson G., Harding S. & Straw N.A. (eds.), *The Green Spruce Aphid in Western Europe; ecology, status, impacts and prospects for management. Forestry Commission, Technical Paper* 24:61-70.

Lechowicz, M. & Mauffette, Y. 1986. Host preferences of the gypsy moth in eastern North American versus European forests. *Revue D'entomologie Quebec.* 31: 43-51.

Lehmann, P., Ammunét, T., Barton, M., Battisti, A., Eigenbrode, S.D., Jepsen, J.U., Kalinkat, G., Neuvonen, S., Niemelä, P. & Terblanche, J.S. 2020. Complex responses of global insect pests to climate warming. *Frontiers in Ecology and the Environment* 18: 141-150.

Lindroth, R., Arteel, G. & Kinney, K. 1995. Responses of three saturniid species to paper birch grown under enriched CO 2 atmospheres. *Functional Ecology* 306-311.

Liu, Z., Gong, P., Wu, K., Wei, W., Sun, J. & Li, D. 2007. Effects of larval host plants on over-wintering preparedness and survival of the cotton bollworm, *Helicoverpa armigera* (Hübner)(Lepidoptera: Noctuidae). *Journal of Insect Physiology* 53: 1016-1026.

Logan, J.A., Régniére, J. & Powell, J.A. 2003. Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment* 1: 130-137.

Lombardero, M., Ayres, M.P., Lorio Jr, P.L. & Ruel, J.J. 2000. Environmental effects on constitutive and inducible resin defences of Pinus taeda. *Ecology Letters* 3: 329-339.

Louda, S.M. & Rand, T.A. 2003. Native thistles: expendable or integral to ecosystem resistance to invasion. *The Importance of Species* 5-15.

Luoto, M., Heikkinen, R., Pöyry, J. & Saarinen, K. 2006. Determinants of the biogeographical distribution of butterflies in boreal regions. *Journal of Biogeography* 33: 1764-1778.

McCormick, A.C., Arrigo, L., Eggenberger, H., Mescher, M.C. & De Moraes, C.M. 2019. Divergent behavioural responses of gypsy moth (*Lymantria dispar*) caterpillars from three different subspecies to potential host trees. *Scientific Reports* 9: 1-12.

Magnússon, B. 2010. *NOBANIS—Invasive Alien Species Fact Sheet—Lupinus nootkatensis.* viewed 22 April, 2020 on Online database of the European Network on invasive alien species–www.nobanis.org.

Magnusson, B., Magnusson, S.H. and Sigurdsson, B.D., 2004. Plant succession in areas colonized by the introduced Nootka lupin in Iceland. In Santen E.v. (ed.), *Wild and cultivated lupins from the tropics to the poles. Proceedings of the 10th International Lupin Conference, Laugarvatn Iceland, 19-24 June 2002*. International Lupin Association, Canterbury, New Zealand, pp. 170-177 [In Icelandic].

Magnússon, B., Magnússon, S.H. & Sigurðsson, B.D. 2018. *Langtímaáhrif alaskalúpínu á gróður og jarðveg á Íslandi [Long-term effects of the introduced Nootka lupin (Lupinus nootkatensis) on vegetation and soils in Iceland]*, Náttúrfræðistofnun Íslands, Garðabær [In Icelandic].

Magnusson, B. & Sigurdsson, B.D. 1995. Efnasamsetning alaskalúpínu [Protein, mineral, fiber and alkaloid content of Nootka lupine]. In Magnússon B. (ed.), *Líffræði alaskalúpínu (Lupinus nootkatensis). Vöxtur, fræmyndun, efnainnihald og áhrif sláttar [Biological studies of Nootka lupine (Lupinus nootkatensis) in Iceland. Growth, seed set, chemical content and effect of cutting]* vol. 178, Rannsóknastofnun landbúnaðarins, Reykjavík, 82 pp. [In Icelandic].

Magnússon, B., Sigurðsson, B.D. & Magnússon, S.H. 2001. Gróðurframvinda í lúpínubreiðum [Vegetation succession in areas colonized by the introduced Nootka lupin (Lupinus nootkatensis) in Iceland]. *Fjölrit RALA* 207:100 p.

Magnússon, B., Sigurðsson, B.D., Magnússon, S.H. & Baldursson, S. 1995. *Líffræði alaskalúpínu (Lupinus nootkatensis). Vöxtur, fræmyndun, efnainnihald og áhrif sláttar [Biological studies of Nootka lupine (Lupinus nootkatensis) in Iceland. Growth, seed set, chemical content and effect of cutting]*. In Magnússon B.(ed.), Rannsóknastofnun landbúnaðarins, Reykjavík, pp. 9-27 [In Icelandic].

Maron, J.L. & Gardner, S.N. 2000. Consumer pressure, seed versus safe-site limitation, and plant population dynamics. *Oecologia* 124: 260-269.

Maron, J.L. & Jefferies, R.L. 1999. Bush lupine mortality, altered resource availability, and alternative vegetation states. *Ecology* 80: 443-54.

Maron, J.L. & Vilà, M. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95: 361-373.

Menéndez, R., González-Megías, A., Lewis, O.T., Shaw, M.R. & Thomas, C.D. 2008. Escape from natural enemies during climate-driven range expansion: a case study. *Ecological Entomology* 33: 413-421.

Montgomery, M.E. 1991. Variation in the suitability of tree species for the gypsy moth. In Gottschalk, K. W., Twery, M. J., Smith, Shirley I., (eds.)*, Proceedings, US Department of Agriculture Interagency Gypsy Moth Research Review 1990; East Windsor,US.* Department of Agriculture, Forest Service, Northeastern Forest Experiment Station 146:1-13.

Murray, M. 2008. Using degree days to time treatments for insect pests. *Utah pests fact sheet* 1-5.

Neven, L.G. 2000. Physiological responses of insects to heat. *Postharvest Biology and Technology* 21: 103-111.

Nigam, S., Thomas, N.P., Ruiz-Barradas, A. & Weaver, S.J. 2017. Striking seasonality in the secular warming of the northern continents: Structure and mechanisms. *Journal of Climate* 30: 6521-6541.

Oddsdóttir, E., Hrafnkelsdotti, B. & Sverrisson, H. 2014. Ástand trjágróðurs á árinu 2013 [Status of tree health in 2013]. Ársskýrsla Skógræktar ríkisins 2013 10-13 [In Icelandic].

Oddsdóttir, E.S., Hrafnkelsdóttir, B. & Sverrisson, H. 2017. Heilsufar trjágróðurs á árinu 2016 [Status of tree health in 2016]. Ársrit Skógræktarinnar 2016 22-25 [In Icelandic].

Oddsdóttir, E.S., Svavarsdóttir, K. & Halldórsson, G. 2008. The influence of land reclamation and afforestation on soil arthropods in Iceland. *Icelandic Agricultural Science* 2: 3-13.

Olafsson, E. 2020. *Skógbursti (Orgyia antiqua)* [Rusty Tussock Moth]. Náttúrufræðistofnun Íslands, viewed 22 April 2020, https://www.ni.is/biota/animalia/arthropoda/hexapoda/insecta/lepidoptera/erebidae/skogbursti-orgyia-antiqua [In Icelandic]

Olafsson, E. & Bjornsson, H. 1997, *Fiðrildi á Íslandi 1995 [Lepidoptera i in Iceland 1995]*, Náttúrufræðistofnun Íslands Reykjavík, Vol. 32:135 p. [In Icelandic].

Olafsson, H., Furger, M. & Brummer, B. 2007. The weather and climate of Iceland. *Meteorologische Zeitschrift* 16: 5-8.

Olafsson, S. 1988. Brandygla í kartöflugörðum. *Freyr* 240 - 241.

Orlova-Bienkowskaja, M.J. & Bieńkowski, A.O. 2016. The life cycle of the emerald ash borer Agrilus planipennis in European Russia and comparisons with its life cycles in Asia and North America. *Agricultural and Forest Entomology* 18: 182-188.

Óskarsson, H. & Sigurgeirsson, A. 2004, Effects of fertilization on tree seedling establishment and growth in a lupin field in southern Iceland. In Santen E.V. (ed.), *Wild and cultivated lupins from the tropics to the poles. Proceedings of the 10th International Lupin Conference, Laugarvatn Iceland, 19-24 June 2002*. International Lupin Association, Canterbury, New Zealand, pp. 203-205.

Ottósson, J. 1983. Íslensk skordýr á trjám og runnum [Icelandic insects on trees and shrubs]. *Ársrit Skógræktarfélags Íslands 1983* 14-42 [In Icelandic].

Parker, J.D., Burkepile, D.E. & Hay, M.E. 2006. Opposing effects of native and exotic herbivores on plant invasions. *Science (New York, N.Y.)* 311: 1459-1461.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J. & Tammaru, T. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399: 579-583.

Parmesan, C. & Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42.

Pálmason, F., Gudmundsson, J. & Sverrisson, H. 2004. Estimates of symbiotic nitrogen fixation in two lupin species in Iceland. In Santen E.V. (ed.), *Wild and cultivated lupins from the tropics to the poles. Proceedings of the 10th International Lupin Conference, Laugarvatn Iceland, 19-24 June 2002*. International Lupin Association, Canterbury, New Zealand, pp. 118-120.

Pincebourde, S., Van Baaren, J., Rasmann, S., Rasmont, P., Rodet, G., Martinet, B. & Calatayud, P.-A. 2017. Plant–insect interactions in a changing world. *Advances in Botanical Research* 81: 289-332.

Pitkin, B., Ellis, W., Plant, C. & Edmunds, R. 2012. The leaf and stem mines of British flies and other insects. Viewed 22 April 2020, *http://www. ukflymines. co. uk/Flies/Chyliza_vittata. Php.*

Preble, E.A. 1923. *A biological survey of the Pribilof Islands, Alaska: I. Birds and Mammals*. US Government Printing Office.

Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N. & Weis, A.E. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual review of Ecology and Systematics* 11: 41-65.

Pureswaran, D.S., Roques, A. & Battisti, A. 2018. Forest insects and climate change. *Current Forestry Reports* 4: 35-50.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G. & Romme, W.H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *Bioscience* 58: 501-17.

Reynolds, L.V., Ayres, M.P., Siccama, T.G. & Holmes, R.T. 2007. Climatic effects on caterpillar fluctuations in northern hardwood forests. *Canadian Journal of Forest Research* 37: 481-91.

Régnière, J. 2009. Predicting insect continental distributions from species physiology. *Unasylva* 60: 37-42.

Riege, D.A. 2004. The use of Lupinus nootkatensis in a revegetation and afforestation program in Southwest Iceland. In Santen E.V. (ed.), *Wild and cultivated lupins from the tropics to the poles. Proceedings of the 10th International Lupin Conference, Laugarvatn Iceland, 19-24 June 2002*. International Lupin Association, Canterbury, New Zealand, pp. 206-207.

Riege, D.A. & Sigurgeirsson, A. 2009. Facilitation of afforestation by Lupinus nootkatensis and by black plastic mulch in south-west Iceland. *Scandinavian Journal of Forest Research* 24: 384-393.

Robinson, E.A., Ryan, G.D. & Newman, J.A. 2012. A meta-analytical review of the effects of elevated CO2 on plant–arthropod interactions highlights the importance of interacting environmental and biological variables. *New Phytologist* 194: 321-36.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421: 57-60.

Roy, D. & Sparks, T. 2000. Phenology of British butterflies and climate change. *Global Change Biology* 6: 407-16.

Runólfsson, S. 2018. Lúpínan hefur lokið hlutverki sínu [The lupin has now ended its role]. viewed 22 April 2020, https://www.mbl.is/frettir/innlent/2018/08/16/lupinan_hefur_lokid_hlutverki_sinu/ [In Icelandic]

Schierbeck, H.J.G. 1886. Skýrsla um nokkrar tilraunir til jurtaræktunar á Íslandi [report on several plant growing attempts in Iceland]. *Tímarit hins íslenzka bókmentafélags* 7:1-66 [In Icelandic].

Schultz, E.L., Eckberg, J.O., Berg, S.S., Louda, S.M. & Miller, T.E. 2017. Native insect herbivory overwhelms context dependence to limit complex invasion dynamics of exotic weeds. *Ecology Letters* 20:1374-1384.

Siemann, E. & Rogers, W.E. 2003. Reduced resistance of invasive varieties of the alien tree Sapium sebiferum to a generalist herbivore. *Oecologia* 135:451-457.

Siemann, E., Rogers, W.E. & Dewalt, S.J. 2006. Rapid adaptation of insect herbivores to an invasive plant. *Proceedings of the Royal Society B: Biological Sciences* 273:2763-2769.

Sigurdardottir, H. 2004. Earthworm activity in a lupin patch in Heidmörk, Southern Iceland. In Santen E.V. (ed.), *Wild and cultivated lupins from the tropics to the poles. Proceedings of the 10th International Lupin Conference, Laugarvatn Iceland, 19-24 June 2002*. International Lupin Association, Canterbury, New Zealand, pp. 191-4.

Sigurdsson, B.D. & Magnusson, B. 2004. Seed ecology of the Nootka lupin (*Lupinus nootkatensis*) in Iceland. In Santen E.V. (ed.), *Wild and cultivated lupins from the tropics to the poles. Proceedings of the 10th International Lupin Conference, Laugarvatn Iceland, 19-24 June 2002*. International Lupin Association, Canterbury, New Zealand, pp. 195-8.

Sigurdsson, B.D., Magnusson, B. & Magnusson, S.H. 1995. Áhrif sláttar á vöxt alaskalúpínu [Regrowth of Nootka lupine after cutting]. In Magnússon B. (ed.), *Líffræði alaskalúpínu (Lupinus nootkatensis). Vöxtur, fræmyndun, efnainnihald og áhrif sláttar.* Rannsóknastofnun landbúnaðarins, Reykjavík [In Icelandic].

Sigurðsson, B.D. 1993. *Fræforði alaskalúpínu (lupinus nootkatensis) á uppgræðslusvæðum í Heiðmörk og í Öræfasveit*. B.Sc Thesis, Háskóli Íslands, Reykjavík [In Icelandic].

Sigurðsson, B.D., Halldórsson, G. & Heiðarsson, L. 2003. Ertuygla. „Nýr" vágestur í skógrækt í nánd við lúpínubreiður [Broom Moth causes problems on afforestation sites in S and SE Iceland]. *Skógræktarritið* 2003: 87-92 [In Icelandic].

Sinclair, B.J., Vernon, P., Klok, C.J. & Chown, S.L. 2003. Insects at low temperatures: an ecological perspective. *Trends in Ecology & Evolution* 18: 257-62.

Svavarsdóttir, K., Pétursdóttir, T. & Gísladóttir, G. 2004. Distribution dynamics of exotic Nootka lupin (Lupinus nootkatensis) on a braided river plain in Skaftafell National Park, Iceland. In Santen E.V. (ed.), *Wild and cultivated lupins from the tropics to the poles. Proceedings of the 10th International Lupin Conference, Laugarvatn Iceland, 19-24 June 2002*. International Lupin Association, Canterbury, New Zealand, pp. 199-202 [In Icelandic].

Systat Software, I. 2008. SigmaPlot for Windows, version 11.0, Systat Software, Inc San Jose, California.

Tauber, M.J., Tauber, C.A. & Masaki, S. 1986. *Seasonal adaptations of insects*. Oxford University Press on Demand.

Thomson, L.J., Macfadyen, S. & Hoffmann, A.A. 2010. Predicting the effects of climate change on natural enemies of agricultural pests. *Biological Control* 52: 296-306.

Trân, J.K., Ylioja, T., Billings, R.F., Régnière, J. & Ayres, M.P. 2007. Impact of minimum winter temperatures on the population dynamics of Dendroctonus frontalis. *Ecological Applications* 17: 882-899.

Ungerer, M.J., Ayres, M.P. & Lombardero, M.J. 1999. Climate and the northern distribution limits of *Dendroctonus frontalis Zimmermann* (Coleoptera: Scolytidae). *Journal of Biogeography* 26: 1133-1145.

van Asch, M., Salis, L., Holleman, L.J., van Lith, B. & Visser, M.E. 2013. Evolutionary response of the egg hatching date of a herbivorous insect under climate change. *Nature Climate Change* 3: 244-248.

Veteli, T., Kuokkanen, K., Julunen-Tiitto, R., Roininen, H. & Tahvanainen, J. 2002. Effects of elevated CO2 and temperature on plant growth and herbivore defensive chemistry. *Global Change Biology* 8: 1240-1252.

Vetter, V., Tjaden, N.B., Jaeschke, A., Buhk, C., Wahl, V., Wasowicz, P. & Jentsch, A. 2018. Invasion of a legume ecosystem engineer in a cold biome alters plant biodiversity. *Frontiers in Plant Science* 9: 715.

Visser, M.E. & Holleman, L.J. 2001. Warmer springs disrupt the synchrony of oak and Winter Moth phenology. *Proceedings of the Royal Society of London B: Biological Sciences* 268: 289-294.

Wink, M. 1992. The role of quinolizidine alkaloids in plant-insect interactions. *Insect-plant interactions* 4: 131-166.

Wolff, N.L. 1971. *The Zoology of Iceland*, Vol. 45 Munksgaard, Copenhagen, 193 p.

Yamamura, K. & Kiritani, K. 1998. A simple method to estimate the potential increase in the number of generations under global warming in temperate zones. *Applied Entomology and Zoology* 33: 289-298.

Zvereva, E.L., Zverev, V. & Kozlov, M.V. 2012. Little strokes fell great oaks: minor but chronic herbivory substantially reduces birch growth. *Oikos* 121: 2036-2043.

Þórsson, J. & Guðmundsson, Ó. 1993. Fóðrun á alaskalúpínu [Feeding with the Nootka lupin]. *Ráðunautafundur* 1993: 295-306 [In Icelandic].

Þórsson, J. & Hlíðberg, K. 1997. Beiskjuefni í alaskalúpínu, Lupinus nootkatensis [Alkaloids in Nootka lupin]. *Icelandic Agricultaral Science*, 11: 75-89 [In Icelandic].