LEPIDOPTERAN FOREST DEFOLIATORS IN A CHANGING CLIMATE: PERFORMANCE IN DIFFERENT LIFE-HISTORY STAGES, AND RANGE EXPANSION

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Dedicated to my parents, my sister and my husband, who all tirelessly believe in me when I myself do not.

It is not the strongest or the most intelligent who will survive but those who can best manage change.

> *Charles Darwin*

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LIST OF ORIGINAL PAPERS

This thesis is based on the following articles and manuscripts, referred to in the text by their Roman numerals:

I   Fält-Nardmann J.J.J., Klemola T., Roth M., Ruohomäki K. & Saikkonen K. (2016). Northern geometrid forest pests (Lepidoptera: Geometridae) hatch at lower temperatures than their southern conspecifics: Implications of climate change. — *European Journal of Entomology*, 113: 337–343. doi:10.14411/eje.2016.043

II   Fält-Nardmann J.J.J., Klemola T., Ruohomäki K., Niemelä P., Roth M. & Saikkonen K. (2018). Local adaptations and phenotypic plasticity may render gypsy moth and nun moth future pests in northern European boreal forests. — *Canadian Journal of Forest Research*, 48: 265–276. doi: 10.1139/cjfr-2016-0481

III   Fält-Nardmann J.J.J., Ruohomäki K., Tikkanen O-P. & Neuvonen S. (2018). Cold hardiness of *Lymantria monacha* and *L. dispar* (Lepidoptera: Erebiidae) eggs to extreme winter temperatures: implications for predicting climate change impacts. — *Ecological Entomology*, 43: 422–430. doi: 10.1111/een.12515

IV   Fält-Nardmann J.J.J, Leinonen R., Pöyry J., Ruohomäki K., Saikkonen K., Tikkanen O-P., Otto L-F. & Neuvonen S. (2018). The recent northward expansion of *Lymantria monacha* in relation to realised changes in temperatures of different seasons. — *Forest Ecology and Management*, 427: 96–105. doi: 10.1016/j.foreco.2018.05.053

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Writing the manuscript	JF-N, KR, TK	JF-N, KR, TK	JF-N, SN	JF-N, L-FO O-PT, SN
Coordination of data collection	-	-	-	JP, RL, SN
Commenting on the manuscript	KR, KS, MR, TK	KR, KS, MR, TK, PN	KR, O-PT	JP, KR, KS, RL

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ABSTRACT

Although there are few confirmed records of rising temperatures contributing to range expansions and range shifts of harmful insects so far, the link between climate and insect distribution range is plausible. Temperature is likely the single most important abiotic factor limiting insect survival. Not only average temperatures but also temperature extremes, such as winter cold spells, may play an important role for insect success. As arctic and boreal regions are warming more rapidly than other regions on Earth, insects in these regions can be expected to show the greatest response to climate change. However, a warming climate may also have a negative effect on insect pests by disrupting phenological synchronies between insects and their host plants. Insects may be able to adapt to these changes genetically over generations or, more rapidly, through phenotypic plasticity – the propensity of a genotype to produce different phenotypes under different environmental conditions.

In this thesis, I examine topics of climate change, insect range expansions and adaptive potential of pest insects using five univoltine spring-feeding moth species: the geometrids *Epirrita autumnata*, *Operophtera brumata* and *Erannis defoliaria*, and the lymantriins *Lymantria monacha* and *L. dispar*.

A laboratory experiment revealed that geometrid eggs from southern populations hatch at higher temperature sums than eggs from northern populations. Following the same pattern, *L. monacha* from a continental European core population developed slower than their conspecifics from a boreal edge population in a field experiment. Northern moth strains may thus have genetically adapted to a shorter summer season. No local adaptation in egg supercooling points, which measure winter cold tolerance and survival, was found when comparing northern and southern strains of *L. monacha*.

Phenotypic plasticity of the two lymantriins was studied by rearing individuals originating from the same population in climatically different locations in Germany where both species occur naturally, southern Finland where only *L. monacha* is confirmedly established and northern Finland where neither of the species is naturally present. Continental *L. monacha* appears to be less flexible than boreal *L. monacha* in its phenology, which may indicate that the population living on the edge of the species' distribution range benefits from a high level of adaptive phenological plasticity that facilitates acclimation to varying environments.

A rearing experiment under field conditions confirmed that both *L. monacha* and *L. dispar* can successfully complete their entire life cycle in southern Finland, and that they are not limited by host plant availability. Winter minimum temperatures are unlikely to stop *L. dispar* from expanding its range to southernmost Finland, although they will limit the expansion of both studied lymantriins further north. In climate warming scenarios, the northern boundary of both species' distribution could shift by over 300 km. A recent northwards range expansion and rising abundances of *L. monacha* in Finland is clearly visible in observational data from both an open "Insect Database" and the systematic "Nocturna" monitoring programme. The trend started in the early 1990s and has continued since then, although with fluctuations. The observed range expansions and population growth appear to be connected to less severe winter extreme temperatures, although rising temperatures during the flight period of the species may also have contributed to its recent success.

It is likely that *L. monacha* and *L. dispar* continue expanding their range and increase in abundance in Finland, and there is a risk that they become important forest pests in the country. As a preventive measure, developing a regionally adapted multilevel monitoring programme already today and promoting forest conversion from coniferous to mixed and ecologically stable stands can help reduce defoliation damage in the coming decades.

Tiivistelmä

Vaikka yhteys kohoavien lämpötilojen ja tuhohyönteisten levittäytymisen välillä on toistaiseksi pystytty todentamaan vain harvoissa tapauksissa, on selvää, että ilmasto vaikuttaa hyönteisten levinneisyyteen. Lämpötila on todennäköisesti tärkein hyönteisten selviytymistä rajoittava abioottinen tekijä; keskilämpötilojen lisäksi myös äärilämpötilat, kuten talven minimilämpötilat, voivat rajoittaa hyönteisten levinneisyyttä. Lämpenevä ilmasto voi vaikuttaa tuhohyönteisiin myös negatiivisesti, jos se häiritsee hyönteisten ja niiden isäntäkasvien välistä fenologista synkroniaa. Hyönteiset voivat sopeutua muutoksiin sukupolvien saatossa geneettisillä paikallissopeumilla, tai nopeammin fenotyypin plastisuuden avulla, mikä tarkoittaa genotyypin kykyä tuottaa erilaisia fenotyyppejä erilaisissa olosuhteissa.

Tässä väitöskirjassa tutkin ilmastonmuutosta sekä tuhohyönteisten levittäytymistä ja sopeutumispotentiaalia viiden yöperhoslajin avulla. Sekä mittarit *Epirrita autumnata* (tunturimittari), *Operophtera brumata* (hallamittari) ja *Erannis defoliaria* (pakkasmittari) että villakkaat *Lymantria monacha* (havununna) ja *L. dispar* (lehtinunna) tuottavat yhden sukupolven vuodessa ja talvehtivat munina.

Laboratoriokokeessa eteläisten mittariperhospopulaatioiden munat kuoriutuivat korkeammissa lämpösummissa, toisin sanoen myöhemmin keväällä, kuin pohjoisten populaatioiden munat. Mannereuroopan ydinpopulaation havununnat kehittyivät kenttäkokeissa samoin boreaalisia lajitovereitaan hitaammin. Pohjoiset yöperhoskannat ovat siis mahdollisesti sopeutuneet lyhyisiin kesiin. Talvikaudesta selviämistä mittaavissa munien alijäähtymispisteissä ei sen sijaan ollut havaittavissa paikallisia sopeumia suomalaisten ja saksalaisten havununnapopulaatioiden välillä.

Havu- ja lehtinunnien adaptiivista fenotyyppistä plastisuutta tutkittiin kasvattamalla samasta populaatiosta peräisin olevia yksilöitä ilmastoltaan erilaisilla kenttäalueilla. Keskieurooppalaisten havununnien fenotyyppi osoitti pohjoisten perhosten fenotyyppiä vähemmän joustavuutta, mikä saattaa tarkoittaa, että lajin levinneisyysalueen rajalla elävät populaatiot hyötyvät suuresta fenotyypin plastisuudesta, mikä auttaa sopeutumaan vaihteleviin olosuhteisiin.

Sekä havu- että lehtinunna pystyvät onnistuneesti kehittymään munista lisääntyviksi aikuisiksi Eteläsuomessa, eikä isäntäkasvien saatavuus rajoita lajien leviämistä Suomessa. Talven minimilämpötilat rajoittanevat molempien lajien leviämistä maan pohjoisosiin. Ilmaston lämmetessä molempien lajien levinneisyysalueiden pohjoisraja saattaa siirtyä yli 300 km pohjoisemmas. Havununnan 1990-luvulla alkanut vaihtelevasti edennyt runsastuminen ja levittäytyminen kohti pohjoista näkyvätkin selvästi niin avoimen Hyönteistietokannan kuin systemaattisen seurantaohjelma Nocturnankin havaintotiedoissa. Lajin levittäytyminen ja kannan vahvistuminen vaikuttaisivat olevan yhteydessä talvipakkasten lauhtumiseen, tosin myös kesäisen lentokauden lämpötilojen nousu on saattanut vaikuttaa lajin menestykseen.

Havu- ja lehtinunna todennäköisesti runsastuvat ja levittäytyvät edelleen Suomessa, ja niistä saattaa muodostua merkittäviä tuholaisia. Paikallisiin olosuhteisiin mukautettu monitasoinen seurantaohjelma sekä ekologisesti vakaita sekametsiä suosivien metsänhoidollisten toimenpiteiden käyttöönotto mahdollisimman pian ovat suositeltavia keinoja vähentää tulevaa tuhoriskiä.

SAMMANFATTNING

Trots att det tillsvidare finns få bekräftade fall där stigande temperaturer bidragit till ökad utbredning av skadeinsekter finns det en koppling mellan klimatförändring och insekternas utbredningsområden. Temperatur är troligtvis den viktigaste abiotiska faktorn som begränsar insekternas överlevnad; förutom medeltemperaturer kan extremvärden, såsom vinterköld, också spela en avgörande roll för insekterna. Eftersom arktiska och boreala regioner värms upp snabbare än övriga områden på jorden förväntas insekterna där uppvisa en stark respons till klimatförändringen. Klimatuppvärmningen kan dock också ha negativa effekter på skadeinsekter ifall den leder till att den fenologiska synkroniseringen mellan insekter och deras näringsväxter rubbas. Insekter kan anpassa sig till dessa förändringar genetiskt över flera generationer, eller snabbare genom fenotypisk plasticitet – d.v.s. en genotyps förmåga att producera olika fenotyper i olika miljöförhållanden.

I detta arbete undersöker jag klimatförändring, insekternas utbredning och skadeinsekternas anpassningsförmåga med hjälp av fem nattfjärilsarter. Såväl mätarna *Epirrita autumnata* (fjällhöstmätare), *Operophtera brumata* (mindre frostfjäril) och *Erannis defoliaria* (lindmätare) som tofsspinnarna *Lymantria monacha* (barrskogsnunna) och *L. dispar* (lövskogsnunna) producerar en generation om året och övervintrar som ägg.

Experiment i laboratorium visade att mätarägg från sydliga populationer kläcks vid en högre värmesumma, d.v.s. senare på våren, än ägg från nordliga populationer. Enligt samma mönster utvecklades *L. monacha* från en kärnpopulation i Kontinentaleuropa långsammare än sina artfränder från en boreal population. Det är därmed möjligt att nordliga nattfjärilsstammar genetiskt har anpassat sig till en kort sommar. Vid en jämförelse mellan sydliga och nordliga populationer av *L. Monacha* kunde inga lokala adaptioner påvisas för äggens underkylningspunkter, som vittnar om köldtolerans och vinteröverlevnad.

Adaptiv fenotypisk plasticitet hos *L. monacha* och *L. dispar* undersöktes genom att fjärilar från samma population föddes upp i olika klimatförhållanden i Tyskland, södra Finland och norra Finland. *L. monacha* från Centraleuropa var fenologiskt mindre flexibla än *L. monacha* från en finsk population, vilket kan antyda att populationen som lever på utkanten av artens utbredningsområde drar nytta av en högre anpassningsförmåga som underlättar acklimatisering till varierande förhållanden.

Ett fältförsök bekräftade att både *L. monacha* och *L. dispar* kan överleva och föröka sig i södra Finland och att det finns lämpliga näringsväxter för båda arterna i hela landet. Vinterköld hindrar inte *L. dispar* från att etablera sig i södra delar av landet, men begränsar båda arternas utbredning norrut. I ett klimatscenario med en temperaturökning kan båda arternas nordliga utbredningsgräns flytta sig över 300 km norrut. I observationsdata från både det fritt tillgängliga Insect Database och det systematiska övervakningsprogrammet Nocturna är det tydligt att *L. monacha* har sedan början av 1990-talet både har blivit vanligare och brett ut sig norrut i Finland. Utbredningen verkar hänga ihop med mildare vinterkölder, fastän högre temperaturer under artens flygperioder också kan ha bidragit till dess framgång.

Det är sannolikt att både *L. monacha* och *L. dispar* fortsätter att breda ut sig och bli allt vanligare i Finland, och det finns en risk för att de utvecklas till avsevärda skogsskadegörare i landet. Den framtida skaderisken kan dock minimeras genom tidig utveckling av ett regionalt anpassat övervakningsprogram, samt genom gynnande av övergång från barrskogar till ekologiskt stabila blandskogar inom skogsbruket.

1. INTRODUCTION

1.1. Plagues on the move: range shifts and expansions of insect pests

"Dangerous Asian long-horned beetle slipped to Finland" (Tuohinen 2015), "Feared harlequin lady beetle may threaten the ecosystem on Gotland" (Sveriges Radio P4 Gotland 2013), "Dangerous oak processionary spreads out in Berlin" (Berlin.de 2012) [News headlines translated by J.F-N.]. Of the vast number of insect species on Earth, those threatening human health or economic and aesthetic interests – in other words, those regarded as 'pests' – seem to be the ones most beloved by news reporters, especially if they show up somewhere outside of their native distribution ranges. While the alarming headlines may be devised to draw attention, they reflect a real problem: in the United States alone, alien insect pests are estimated to cause US$2.1 billion worth of yearly losses for forestry and US$15.9 billion in agricultural crop losses (here, damage caused by mites is included) (Pimentel *et al.* 2001).

However, not all of the alien invaders that make it to the headlines become economically significant pests in their new range. The "tens rule" states that approximately one tenth of the species arriving at a new area become established and of those only one tenth become pests (Williamson *et al.* 1986, Williamson 1993). While considerable exceptions to this rule exist, it appears to be a useful estimation for diverse regions and for various taxa around the world (Williamson & Fitter 1996; however, Jeschke & Strayer (2005) suggest a considerably higher rate of establishment at least for vertebrates).

1.1.1. What limits insect distribution ranges?

Why does colonization of a new area fail so frequently? If arriving founders are few and far between, it may be due to Allee effects – too low initial population sizes and densities for the species to persist and reproduce in the area (e.g., Courchamp *et al.* 1999, Memmot *et al.* 2005). However, sometimes even one single fertilized female can be enough to successfully settle on a new continent, as most likely happened with a European solitary bee, *Lasioglossum leucozonium* (Schrank), in North America (Zayed *et al.* 2007).

More commonly, insects seem to be restricted by environmental conditions in the new area not matching their requirements for life cycle completion. Environmental variables affect both survival and development rates of insects, and environmental limits of various insect taxa have been studied extensively. The study of range limits integrates many disciplines within biology (Gaston 2009 and references therein), and only a brief summary of the topic can fit within the framework of this thesis.

Temperature is likely the single most important abiotic factor limiting insect survival. However, average yearly or even seasonal temperatures alone are poor predictors of insect distributions, which may depend on extreme temperatures, such as lethal winter cold spells (Ammunét *et al.* 2012, Neuvonen & Virtanen 2015) or summer hot spells (Franco *et al.* 2006). The duration of different temperature ranges within a year can also be crucial for the success of an insect species, whether it needs a sufficiently long warm summer to finish its development (Mousseau & Roff 1989), enough days with temperatures below a certain threshold to trigger hatching in spring (Hibbard & Elkinton 2015), or can only survive for a limited time in very cold or warm temperatures (Persson 1972, Bale 1991).

Insect distributions can also be limited by air or soil humidity and rainfall (Messenger 1959), or – conversely – drought (Morecroft *et al.* 2002). Humidity interacts strongly with temperature and may modify the effects of temperature on insect development and survival, with elevated levels of humidity either improving or deteriorating conditions for insects (Messenger 1959). Wind, in turn, may affect humidity and evaporation (Persson 1972). Snowfall in winter may also play a role, most commonly as an insulator keeping the microclimate of the overwintering locations of insects warmer than surrounding air temperatures (Madrid & Stewart 1981, Bale 1991). Another factor that may act together with temperature is day length. For a nocturnal insect, for example, sufficiently long and warm nights could be essential for foraging or mating (Messenger 1959). Sunshine, a parameter strongly correlated with temperature and day length, may also play a role (Turner *et al.* 1987).

Biotic interactions with other species on the same or different trophic levels are another factor that may strongly limit the distribution of species (Case *et al.* 2005). It is crucial for herbivore insects that suitable host plants, i.e. the right species in the right phase of their development, are available for feeding and oviposition. While generalist herbivores are more flexible in this regard, the requirement for one single host plant species may indirectly limit the distribution range of specialist herbivores (Quinn *et al.* 1997).

Insects may have very different environmental requirements during different phases of their life cycles, narrowing the overall possible distribution range of a species. For example, a given insect species could tolerate temperatures down to -30 °C in mid-winter during diapause but only -10 °C cold spells in the post-diapause phase before hatching in spring (Tenow & Nilssen 1990). Its larvae might be strictly monophagous on a host plant with a narrow distribution range of its own (Krauss *et al.* 2004), the pupae of the species might need sufficiently moist soil to survive (Hulthen & Clarke 2006) and the adults might only be active in darkness (Castrovillo & Cardé 1979). Considering such restrictions, it is easy to understand why so many of the insects arriving in a new area perish. A successful settlement requires either an extraordinarily adaptive species with high tolerances for environmental variation, or a local point of arrival in several ways very similar to the native range of the species.

1.1.2. The effect of climate change on insect pests and their distribution

Changes in the environment constantly provide opportunities for species to invade new areas. Examples for this can be found at diverse scales, ranging from a grand geographical event such as the collision of two continental plates to a highly local one such as when a gardener decides to plant a few square meters of wild flowers. Range shifts of organisms have always occurred naturally (Vermeij 1991, Lodge 1993). However, human activity has accelerated species movements not only by intentional and accidental introductions of species to areas that they would be unlikely to reach by natural means (e.g., Vitousek *et al.* 1997, Lowe *et al.* 2004, McNeely 2001), but also through climate change.

According to the IPCC (Intergovernmental Panel on Climate Change) fifth assessment report the increase in global average land and ocean surface temperatures between 1880 and 2012 was about 0.85 °C and the 30-year period from 1982 to 2012 in the Northern Hemisphere was the warmest in 800 years. In relation to the 1986–2005 period and depending on the emission scenario, temperatures are projected to further rise between 0.3 and 0.7 °C during 2016–2035

and between 0.3 and 4.8 °C before the end of the 21st century (IPCC 2014). These warming rates are spatially heterogenous. The arctic regions have warmed more rapidly than the global mean, and this trend will continue, with a predicted temperature increase of 4–5 °C in the European boreal zone in the next 100 years (Lindner *et al.* 2008, IPCC 2014). The same pattern is also visible on a local scale, for example in Fennoscandia: the winters in northern Finland are warming up faster than in the southern parts of the country (Ruosteenoja 2013).

Average temperatures are not the only climatic parameters that are changing. Temperature extremes – the coldest days of winter and the heat periods in summer – may change relatively more than average temperature values (Alexander *et al.* 2006). Moreover, precipitation, wind intensity and weather patterns are likely changing as well, and although the magnitude and geography of these changes are difficult to predict, a general increase in extreme weather events – such as storm winds and floodings – is very likely (Thorpe 2005, IPCC 2014). The cause behind the climate change, the rising levels of CO_2 and other greenhouse gases, may also directly affect organisms and their interactions (Cannon 1998, DeLucia *et al.* 2008).

All these changes create both opportunities and ultimatums for plant and animal species, including pest insects. Generally, rising temperatures correspond to more time available for exothermic organisms, since their physiology functions faster at higher temperatures, although this assumption only works in a confined temperature range (Beck 1983, Charnov & Gillooly 2003). The ameliorating effect of climate warming is particularly clear for ectotherms living at high latitudes, as the current temperatures tend to be below their physiological optima (Deutsch *et al.* 2008). Rising temperatures may allow for higher winter survival (e.g., Bale *et al.* 2002, Battisti & Larsson 2015), earlier emerging times in spring (e.g., Whittaker & Tribe 1996, Sparks & Yates 1997, Forister & Shapiro 2003), or allow for longer seasonal or diurnal feeding and activity periods (Roy & Sparks 2000, Battisti *et al.* 2006). They may enable a faster development, which can lead to a shortening of vulnerable phases of the lifecycle (Bale *et al.* 2002, Rouault *et al.* 2003), shifting these phases to seasons with less pressure from enemies (Visser *et al.* 1998, Visser & Both 2005) or allow the production of additional generations per year (e.g., Kiritani 2006, Jönsson *et al.* 2007).

However, the current distribution range may also become unsuitable for an insect herbivore due to direct climatic effects such as excessive temperatures or drought, or indirect effects mediated through host plants, competitors, or predators and pathogens (Ayres 1993, Van Nouhuys 2004, Rouault *et al.* 2006). This may lead to range retractions or extinction of the species (e.g., Hughes 2000, McLaughlin *et al.* 2002, Thomas 2006, Walther *et al.* 2009) unless it manages either to adapt to the novel conditions or to shift its distribution range to an area with similar conditions.

On the other hand, new areas may become available for the species, allowing it to expand its distribution range. This, in turn, may enable the species to escape from its natural enemies and grow unchecked in abundance (Menéndez *et al.* 2008). Leaving competitors behind could conceivably achieve the same effect. In new areas herbivorous insects might also encounter "naïve" host plants with less efficient defense mechanisms than the plants in their native range that have coevolved together with their insect antagonists (Rasmann & Pellissier 2015). For species with outbreak dynamics, not only the full distribution range, but also the outbreak range and severity may change (Volney & Fleming 2000, Jepsen *et al.* 2008). Furthermore, it

is possible that migrant species, normally unable to overwinter in an area but regularly recolonizing it, become permanent residents (Cannon 1998).

Range shifts and expansions that can be related to climate change have indeed been reported for insects (e.g., Kleukers *et al.* 1996, Parmesan *et al.* 1999, Hickling 2006, Menéndez 2007, Catling 2016). However, evidence for 'the worst-case scenario', climate change-driven range expansions of serious pest insects, is scarce, though it has been recorded for a handful of prominent species, such as the pine processionary moth (*Thaumetopoea pityocampa*; Denis & Schiffermüller) in Europe and the Mediterranean region and *Dendroctonus* bark beetles in North America (Battisti & Larsson 2015).

It is easy to envision that an insect pest arriving in a new area, without its specialist natural enemies present, may cause great damage to its host plants as well as to the native community of competitors (Redman & Scriber 2000, Davis 2003). There are notorious examples of insects that have caused much more damage in their new ranges than in their native environments, such as the Colorado potato beetle (*Leptinotarsa decemilineata* Say) that was accidentally introduced from North America to Eurasia and the emerald ash borer (*Agrilus planipennis* Fairmaire) that spread in the opposite direction (Lindström & Lehmann 2015, CABI 2016a, 2016b).

However, as the tens rule states, just arriving at a new area does not guarantee successful establishment. *L. decemilineata* and *A. planipennis* represent the rare one percent of species that has succeeded in establishing a permanent population and causes significant harm in the new range – and makes it to the headlines.

1.2. A time to hatch and a time to lay eggs: timing of life cycle events in insects

For many the first peacock butterfly (*Aglais io* (Linnaeus)) fluttering in the sun is an anticipated sign of spring, and for a lepidopterologist a scarce umber moth (*Agriopis aurantiaria* [Hübner]) resting on the wall announces that winter is coming. But how does the peacock butterfly know that it is spring and time to stop hibernating, or the scarce umber sense autumn and emerge from its pupa?

Rathcke and Lacey (1985) define phenology as "the study of the seasonal timing of life cycle events". The more complex a life cycle an insect has, the more events and phases it goes through – eclosion from an egg, several cycles of molting, pupation, adult emergence, mating, ovipositioning, dormancy – all of which need some mechanism to trigger them for the development of the animal to proceed.

In rare cases, such as the obligatory diapause of some insects (Koštál 2006), developmental phases are triggered internally, and sometimes the limited availability of environmental factors such as food or oxygen directly enforce a certain life stage (usually some level of quiescence). More commonly, however, some external *cue* – a predictor of future conditions – is needed for the onset, maintenance or termination of a life cycle phase (Danks 1987). The two most commonly recognized environmental cues that regulate insect phenology are temperature and light.

Temperature triggers insect development with a delay: after reaching a certain temperature limit, a so-called lower developmental threshold, the insect still needs some time to shift from one stage to another. Because insect development is accelerated by high temperatures, the

time is shorter the higher the temperature is. This holds until a certain upper developmental threshold is reached. On the other hand, if the temperature occasionally drops below the lower threshold, the development comes to a halt temporarily. These kinds of temperature dependencies are described with temperature sum models, which measure time in temperature units. In these models, sums of daily average temperatures exceeding the developmental threshold are expressed as d*egree-days* (e.g. Terblanche *et al.* 2015; for a depiction of the relationship between temperatures and degree-days, see **II**: Fig. A1).

Temperature sum models have been widely used for studying development of eggs and larvae (e.g., Buse & Good 1996, van Asch & Visser 2007, Karolewski *et al.* 2007, Jepsen *et al.* 2011, Foster *et al.* 2013). However, while temperature sum models are undeniably useful, the true relationship between temperature and insect development may be nonlinear. Furthermore, different developmental stages, such as the different larval instars, may have different thresholds and the thresholds may vary between populations and locations (e.g., Day & Rowe 2002).

Temperatures below the lower developmental threshold may also play a role in insect development. *Chilling* of insect eggs, i.e. exposing them to low temperatures, in many cases has been proven to accelerate subsequent development once the temperatures rises above the developmental threshold. Chilling may even change the developmental threshold itself. Both the severity and the duration of the cold period may matter in the chilling process (Kimberling & Miller 1988, Bell 1996, Hibbard & Elkinton 2015).

Insect phenology may also be influenced by day length or photoperiod – the duration of the light phase of a day – or conversely night length (Masaki & Kimura 2001, Bradshaw & Holzapfel 2010). Any light periods longer than a certain critical photoperiod may, for example, terminate diapause in some insect species, while in others the absolute day length determines the rate of diapause development (Tauber & Tauber 1976). Day length also controls processes such as the production of sexual forms of some aphids and the migration of lady beetles in autumn (deWilde 1962). Arthropods may sense the length of the photoperiod with ocelli, compound eyes or even directly with the brain (Bradshaw & Holzapfel 2007). It is thus not surprising that photosensitivity has been found in all insect life stages; however, not all stages of a species are usually photosensitive (deWilde 1962, Reznik 2011). Furthermore, a developmental event in one life stage can be dependent on photoperiods encountered in an earlier stage (deWilde 1962, Denlinger 2002).

Cyclic changes in day length provide a long-term calendar, predicting seasonal changes long before they occur. Day length and its seasonal variation are reliable cues even over evolutionary time spans (Bradshaw & Holzapfel 2007). Temperature, on the other hand, gives precise information on the present conditions. Thus, many insects use a combination of both cues to optimize their phenology (Valtonen *et al.* 2011). For example, the egg hatch of a spring-feeding insect may be initiated at a certain temperature, but only if the photoperiod is long enough; this way the eggs do not accidentally hatch in autumn when days are short, even if the season happens to be unusually warm.

Why is the exact timing of life cycle events so important that such sophisticated – and potentially costly – mechanisms for detecting environmental cues and translating them into physiological changes has evolved to ensure that everything happens exactly at a certain moment? Time windows imposed by the abiotic environment of insects are usually wide: during a long summer, a butterfly could emerge at any time during an interval of several

months and still encounter enough days with high temperatures that allow flight and reproduction. Biotic interactions, however, require great precision.

1.2.1. The importance of synchrony

For many insects, it is crucial to match their phenology with that of other species. A parasite can only survive and reproduce in the presence of the right life stage of its host species (Godfray *et al.* 1994, Van Nouhuys 2004). Pollinators are equally dependent on ephemeral flowers (Memmott *et al.* 2007). Likewise, spring-feeding folivore larvae need to hatch in synchrony with the budburst of their host plant to be able to feed on the soft new leaves before the leaves develop a hard surface or a chemical defense (Visser & Holleman 2001; for further examples, see reviews by Harrington *et al.* 1999, Visser & Both 2005, and Miller-Rushing *et al.* 2010). However, there is little if any proof of insects directly tracking the phenology of the species that they are dependent on (Buse & Good 1996, Harrington *et al.* 1999). Instead, they use abiotic cues for controlling their phenology. While the control mechanism has evolved to produce a synchrony with their host or mutualist partner, it rarely functions in the exact same way as that of the host (van Asch & Visser 2007). As a simplified example, a tree may time its budburst according to day length in spring (Häkkinen *et al.* 1998, Caffarra *et al.* 2011a, Caffarra *et al.* 2011b), while a folivorous moth may track temperatures to time egg hatch (Visser & Holleman 2001).

Two species using different phenological control systems may still be synchronized, if the different cues correlate with each other predictably. In the example above this would imply that the day length needed for tree budburst is reached in spring at the same time as the temperature sum required for the moth egg hatch. However, when the relationship between the cues changes, the synchrony of the species may be threatened. Potential mismatches between species have been studied extensively, and examples of asynchrony have been recognized in many taxa and in many different kinds of biotic interactions (review by Donnelly *et al.* 2011).

While asynchrony can be devastating for an insect population, there are also strategies for coping with it. Some insect species mitigate the problem of asynchrony by producing eggs that hatch at different times, thus ensuring that at least a small fraction of the eggs hatch in synchrony with the host plant's budburst. It has even been suggested that, for certain species, such asynchrony rather than synchrony may be a stable state (Singer & Parmesan 2010).

Temperature and light, the two cues most relevant for the plant-herbivore systems studied in this thesis (van Asch & Visser 2007), both change at different rates with latitude (for an example, see **II**: Fig. A1). Moreover, day length is not affected by climate change. Thus, a herbivore insect does not only risk mismatch with its host plant if it moves across latitudes to new areas, a mismatch may also occur in its original distribution range due to climate change (Fig. 1, Visser & Both 2005, Saikkonen *et al.* 2012). On the other hand, the same changes may also lead to new couplings between previously asynchronous species (Jepsen *et al.* 2011). Asynchrony between species may also have large-scale implications on species distribution. For example, it has been proposed that intercontinental differences in photoperiod may explain the greater success of European insects in America than vice versa (Mattson & Niemelä 1996, Mattson *et al.* 2007, Saikkonen *et al.* 2012).
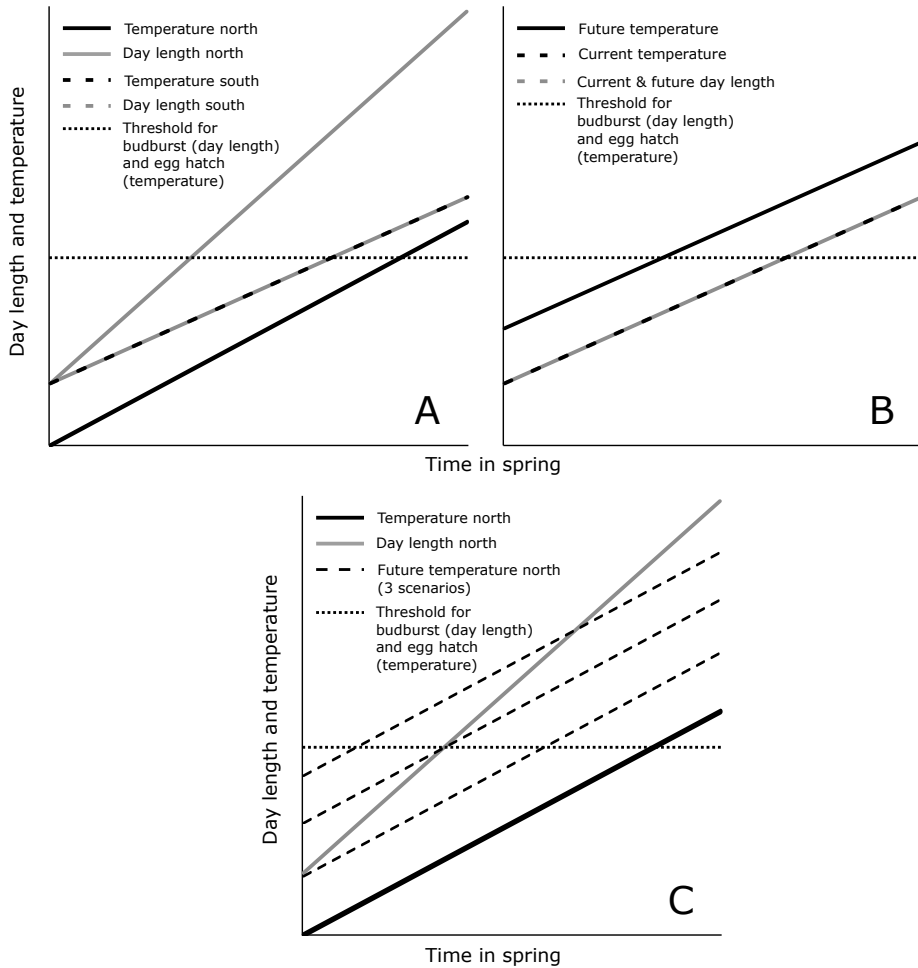
Figure 1. A highly simplified model of the synchrony between a tree that uses day length for timing budburst and an herbivore insect that uses temperature for timing egg hatch. Grey lines depict day length, black ones depict temperature. The dotted horizontal line marks both the threshold day length where budburst happens and the threshold temperature for egg hatch. A – Here solid lines depict northern conditions and dashed lines southern conditions. In the current southern location eggs hatch in synchrony with budburst (the two dashed lines overlap and cross the threshold at the same point in time). If the insect moves northwards the synchrony breaks, as budburst happens before hatch (the difference in time between the two solid lines). B – Here the dashed lines depict the current conditions, while the black line depicts the temperature in the future. Note that the day length remains the same even if the temperature rises. Thus, if the climate becomes warmer, egg hatch happens before budburst. C – Here solid lines depict current conditions in the north. The dashed lines depict different temperature scenarios in the north. This illustrates a case where the insect moves northwards as the temperature rises. Depending on the climate scenario, this might lead to a mismatch in either direction or, by chance, to a synchrony (the middlemost dashed line). The graphs do not account for situations where the required threshold of the insect or the tree changes with latitude.

Despite these challenges, insects – even specialists requiring a strict synchrony with other species – have succeeded in invading new areas and appear, at least in some cases, to be coping with asynchrony (Kerslake & Hartley 1997, Hunter & Elkinton 2000, Dixon 2003, Benadi *et al.* 2014). The key to their success lies in their capability to change their phenology and adjust control mechanisms to match new environmental conditions. This is possible through evolutionary adaptation, or more rapidly through phenotypic plasticity.

1.3. Local adaptation and adaptive phenotypic plasticity – keys to survival in changing environments

Insects with short generations and large broods seem obvious candidates for fast genetic diversification and adaptations to fluctuating conditions, and there is ample experimental and observational evidence for rapid changes in various insect traits as a response to artificial or natural selection (e.g., Fellowes *et al.* 1998, Huey *et al.* 2000, Ooik & Rantala 2010). However, it is debated whether even insect adaptation is fast enough to cope with the speed of current climate change and especially the resulting potential asynchrony between insects and their host or prey species. Insect fossil records show little evidence for adaptation waves in times of previous significant periods of climate change (Coope 1995). Instead, insects appear to be *niche conservative*, as defined by Hill and Thomson (2015), and move with the climate zones, shifting their ranges in order to stay within optimal climatic conditions. However, new molecular methods have revealed connections between prehistoric changes in climate and species diversification rates in, for example, butterflies (e.g., Peña & Wahlberg 2008, Müller & Beheregaray 2010, van Velzen *et al.* 2013). This suggests that insects – or at least butterflies – can be *niche shifting*, that is, they may move to new areas with conditions that differ from those on their native range, which may require special adaptations (definition by Hill *et al.* 2015). There are also many examples of locally adapted insect populations that differ physiologically or phenologically from their sister populations up to the point of reproductive isolation (Masaki 1967, Tauber *et al.* 1986, Korol *et al.* 2000, Bradshaw *et al.* 2001, Tikkanen *et al.* 2006), although it is rarely known how much time the development of such adaptations has required.

Evolutionary transitions driven by climate change may also be present in niche conservative species. There is evidence for climate change creating a natural selection pressure towards greater dispersal and genotypes that are more successful at colonizing new areas (Hughes *et al.* 2003, Simmons *et al.* 2004).

The current distribution range of a species may give hints of its capability to adapt to changing environments. For genetic adaptation to happen, enough variation in a trait, for example growth rate in relation to summer temperatures, must exist in a population for natural selection to act on. Butterfield and Coulson (1997) argue that widespread species that already exist in a variety of climates are "preadapted" to climate change due to genetic variety already present in the species and are thus more likely to quickly adapt to new conditions than species that have specialized in living in a certain climate.

However rapid it may be, genetic adaptation always takes several generations. Phenotypic plasticity, on the other hand – the propensity of a genotype to produce different phenotypes under different environmental conditions (Nylin & Gotthard 1998) – makes it possible for an individual insect to match its own phenology or that of its direct offspring (via maternal effects, Mousseau & Dingle 1991) to new conditions it may encounter. If, for example, a spring folivore can adjust its time of egg hatch in spring (as opposed to always rigidly

hatching at a certain temperature sum, Fig.1) it can retain synchrony with its host plant even if the climate changes or if it moves to a new location (Nylin & Gotthard 1998, Asch & Visser 2007, Valtonen *et al.* 2011, Saikkonen *et al.* 2012, Valladares *et al.* 2014). Genetic adaptation may follow, but *adaptive phenotypic plasticity* buys it time to develop. However, it has also been proposed that short-term survival of a population through adaptive phenotypic plasticity may in fact prevent genetic adaptation as there is no strong selection pressure towards change. A negative long-term effect would occur once change surpasses the buffering capacity of phenotypic plasticity (Valladares *et al.* 2014).

It is important to note here that not all phenotypic plasticity is necessarily adaptive. For instance, the pupal mass of a butterfly could be lower at low temperatures than at high ones not because of any advantage of small size at low temperatures but because the exotherm larva simply is not able to feed and grow to full size at suboptimal temperatures before some environmental cue triggers pupation (e.g., Esperk *et al.* 2013).

Not all species and populations have equal levels of phenotypic plasticity, and those with less capacity for fast adjustments of phenology are in greater danger of (local) extinction (Valtonen *et al.* 2011). Valladares *et al.* (2014) summarize that species encountering much environmental variation within one generation or having wide fundamental niches should have a higher level of phenotypic plasticity that helps individuals retain high fitness under many different conditions. Particularly interesting cases are populations at the edges of a species' distribution range, as colonization of new areas and, on the other hand, extinctions due to environmental changes are most likely to happen along these margins. Any universal patterns of the level of plasticity in edge populations compared to core populations are however yet to be confirmed. Plasticity in edge populations may be low due to little genetic variation within small founder populations or, as stated by an alternative hypothesis, higher than average if populations on the edge encounter higher climatic variability than core populations (Valladares *et al.* 2014 and references therein).

Genetic adaptation and adaptive phenotypic plasticity can also be interlinked: local adaptation does not necessarily mean a narrowing down of phenotypic responses to one optimized pattern, it may also lead to an increase of phenotypic plasticity, a genotype that is programmed to perform differently in different environments and able to react to fast changes (Valtonen *et al.* 2011). Both rapid genetic adaptation and adaptive phenotypic plasticity help populations overcome the challenges of climate change: novel conditions in current and new locations, more frequent weather extremes and continuous change itself.

1.4. Aims of the thesis

As temperatures in the boreal zone continue to rise, the question of the effects of climate change on insect pest species is a topical one in Finland and other northern countries. There are already signs that a warming climate in the north benefits resident pest insects, for example by improving egg survival in winter of the European pine sawfly (*Neodiprion sertifer* (Geoffroy)), or by allowing for additional generations during a summer as is the case with the spruce bark beetle (*Ips typographus* Linnaeus) (Virtanen *et al.* 1996, Lange *et al.* 2010, Vapaavuori *et al.* 2010, Økland *et al.* 2015). An additional threat are potential new invasive species arriving from the south.

In my thesis I examine the topics of insect range expansions and adaptive potential using two groups of univoltine spring-feeding moth species (see chapter 2.1). The geometrids *Epirrita autumnata* (Borkhausen), *Operophtera brumata* (Linnaeus), and *Erannis defoliaria* (Clerck)

are all species with wide distribution ranges in Europe. The first two are abundant well beyond the polar circle. The two lymantriins, *Lymantria monacha* (Linnaeus) and *L. dispar* (Linnaeus), have a more southern distribution, but both are accredited with the potential to rapidly move northwards (Vanhanen *et al.* 2007) .

Phenological synchrony with their host plants is important for all these species, although their polyphagous diet facilitates finding at least some suitable plants throughout the spring season. In the north, they are additionally challenged by bright but short and relatively cool summers during which they have to complete their life cycle, and harsh winter cold spells that threaten egg survival.

Using these five moth species as examples, I concentrate on the following four main themes:

Local adaptations. Individuals that are well adapted to local conditions tend to have a higher fitness in their home range than "Jack-of-all-trades"-representatives of the same species, but developing a local adaptation requires time and a certain degree of isolation. My first goal was to examine if there are any signs of local adaptations in egg hatch timing of geographically separated populations of the three geometrid species. I also investigated whether all three species have similar geographical variation in egg hatch timing, or whether the magnitude of adaptation varies with species. Great variation in a species across locations could imply that a precise adaptation to local conditions – in this case most importantly host plant budburst – is important for the species. Small differences between different populations could on the one hand indicate that the species is more robust in coping with mismatches (for example due to guaranteed availability of alternative host plants). It could, on the other hand, also mean that the population has not been isolated enough or had enough time for genetic changes to occur (**I**). The same approach was extended to encompass further life history traits – timing of pupation and adult emergence, pupal mass, duration of pupal period and egg supercooling points (i.e. the freezing temperature of eggs) – of *L. monacha* to investigate whether a population on the edge of the distribution range of the species differs from a population in the core range (**II, III**).

Adaptive phenotypic plasticity. For species facing climate change and potentially expanding their ranges polewards, such as *L. monacha* and *L. dispar*, the ability of genetically similar individuals to display different phenotypes when exposed to different conditions helps to cope with change and extreme conditions at the expansion frontier. My aim was to investigate whether core and edge populations of *L. monacha* display similar levels of phenotypic plasticity when reared along a natural climate gradient in northern Europe. I also aimed to study how plastic *L. dispar* is in its response to the same gradient, which for this more southern species is more extreme than for *L. monacha* (**II**).

Potential for a northwards range expansion. Whether a species is able to settle permanently in a new location that it arrives at depends on many abiotic and biotic factors. In a field experiment with near-natural conditions where the insects were exposed to local climatic and light conditions and feed on local host plants, I evaluated survival and success of *L. monacha* and *L. dispar* at and beyond the northern border of their current distribution range (**II**).

Because extreme winter cold spells can limit insect distribution range, I determined the supercooling points of *L. monacha* and *L. dispar* eggs. I compared these values with winter minimum temperatures of the original distribution areas of the species as well as those of areas north of their current ranges. A further aim was to compare my results with previous

observations and predictions of *L. monacha* and *L. dispar* cold hardiness and range expansion potential (**III**).

Evidence for a northwards range expansion. Certain evidence of established *L. dispar* populations in Finland is yet to be published. While *L. monacha* is also absent or extremely rare in earlier records, it is now a common species along the southern coast of the country. In manuscript **IV** I investigate how *L. monacha* has spread and grown in abundance in Finland. I further parallel the development of the *L. monacha* population with climate parameters during different life-stages of the species in order to reveal any links between climate change and *L. monacha* distribution in Finland.

2. MATERIALS AND METHODS

2.1. Study species

2.1.1. Geometridae

Geometrid moth outbreaks leading to defoliation of vast mountain birch (*Betula pubescens* var. *pumila* (L.) Govaerts; syn. *Betula pubescens* subsp. *czerepanovii* (N. I. Orlova) Hämet-Ahti, which was the scientific name used in original articles **I**–**II**) forests in northern Fennoscandia have been the focus of research projects since the 1970s (Haukioja *et al.* 1988, Ammunét *et al.* 2015). In the more recent studies, invasive geometrid species new to the region and their relationships with resident species have gained increased attention (e.g., Jepsen *et al.* 2011, Ammunét *et al.* 2012).

The autumnal moth, *Epirrita autumnata* (Borkhausen) (Fig. 2 I–K), is a common Holarctic species, native even to northernmost Fennoscandia (Tenow 1972, Tammaru *et al.* 2001). The winter moth, *Operophtera brumata* (Linnaeus) (Fig. 2 L–N), is a Eurasian species, common in most of Europe and introduced to North America (Embree 1966, Gillespie *et al.* 1978, Tenow *et al.* 2013). It is slightly less cold tolerant than *E. autumnata* (MacPhee 1967, Nilssen & Tenow 1990, Ammunét *et al.* 2012), but the warming climate has recently allowed it to increase in abundance in the more continental areas of northern Fennoscandia, outside its earlier native outbreak ranges along the coast. Both species display cyclic population dynamics, with *O. brumata* having regular outbreaks throughout its distribution range and *E. autumnata* mainly in the northern parts of its range (e.g., Tenow 1972, Bylund 1999, Ruohomäki *et al.* 2000, Tenow *et al.* 2013). The mottled umber, *Erannis defoliaria* (Clerck) (Fig. 2 O–Q), is a widespread Eurasian species. It is not as cold-hardy as the other two species, and its northern range limit crosses central Finland. However, it has been suggested that the species may potentially expand its range northwards with the warming climate (Ammunét *et al.* 2012).

All three species are univoltine with overwintering eggs that hatch in early spring and adults emerging in autumn. *Epirrita autumnata* females are relatively poor flyers although they have fully developed wings (Tammaru *et al.* 1995) (Fig. 2 I), while *O. brumata* and *E. defoliaria* females are flightless, the former having strongly reduced wings (Fig. 2l) and the latter no wings at all (Fig. 2 O). However, early-instar larvae of all three species can disperse by ballooning, i.e. using thin silk strands to float with the airflow to a new location (Edland 1971, Bylund 1999, Bell *et al.* 2005, Glavendekić 2010).

The larvae of all three species are polyphagous spring-feeding defoliators of deciduous trees and shrubs. During outbreaks *E. autumnata* can cause severe damage to mountain birch forests, and the same is true for *O. brumata*, which together with *E. defoliaria* also counts as a serious pest of orchards, parks and gardens (Tenow 1972, Holliday 1977, Tomiczek & Perny 2005 Jepsen *et al.* 2008.) The synchrony between egg hatching and budburst in spring has been extensively studied in *E. autumnata* and *O. brumata*; both species are highly dependent on young leaves of mountain birch in northern Fennoscandia (Tenow 1972, Buse & Good 1996, Bylund 1999, Visser & Holleman 2001, Jepsen *et al.* 2011).
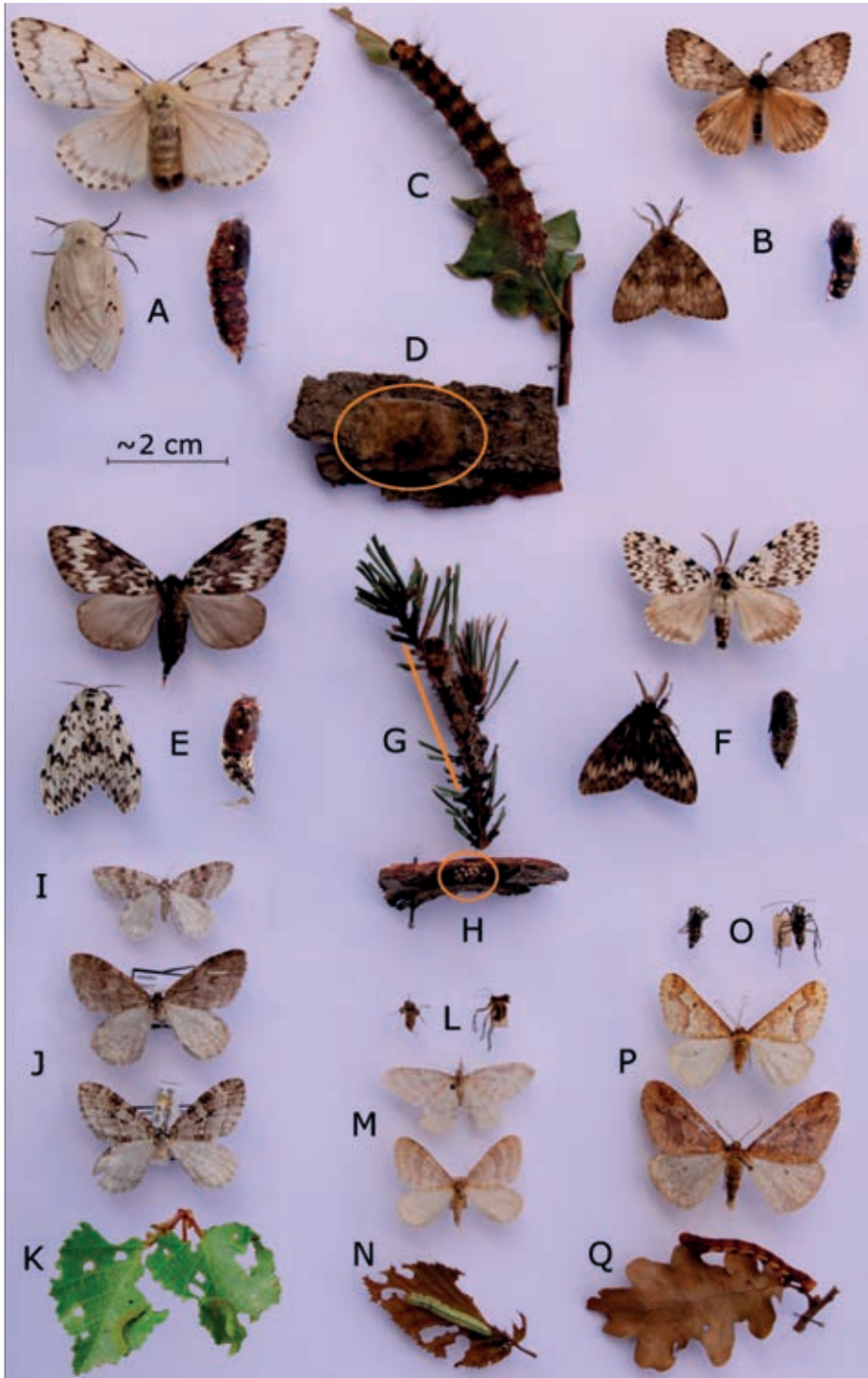
Figure 2. Overview photo of the study species. The scale bar is approximate: because the figure is a composite of several photographs, the scaling between the different objects may vary up to 5 mm. A – *Lymantria dispar* females: 2 imagines (lower one in natural-like resting position) and pupa, B – *L. dispar* males: 2 imagines (lower one in natural-like resting position) and pupa, C – late-instar *L. dispar* larva, D – *L. dispar* egg batch, covered with hair by the female, on a piece of bark (the position of the batch is marked with an orange circle) E – *L. monacha* females: 2 imagines displaying different colour variations (lower one in natural-like resting position) and pupa, F – *L. monacha* males: 2 imagines displaying different colour variations (lower one in natural-like resting position) and pupa, G – late-instar *L. monacha* larva on a partly defoliated pine twig (the position of the larva is marked with an orange line), H – *L. dispar* egg batch on a piece of bark (the position of the batch is marked with an orange circle), I – *Epirrita autumnata* female, J – 2 *E. autumnata* males, K – 2 late-instar *E. autumnata* larvae on leaves, L – 2 *Operophtera brumata* females, M – 2 *O. brumata* males, N – late-instar *O. brumata* larva on a leaf, O – 2 *Erannis defoliaria* females, P – 2 *E. defoliaria* males, Q – late-instar *E. defoliaria* larva on the edge of a leaf. Figure K, the only figure above showing live animals, is courtesy of the autumnal moth project of the University of Turku.

2.1.2. Lymantriinae

The nun moth (*Lymantria monacha* (Linnaeus), also known as black arches) (Fig. 2 E–H) and the gypsy moth (*L. dispar* (Linnaeus; Fig. 2 A–D) have historically been two of the most feared forest pest species in temperate Europe and not without good reason: both species are serious defoliators that frequently though irregularly reach extreme outbreak population densities (although Haynes *et al.* (2014) found some evidence of earlier cyclic outbreaks of *L. monacha,* at least in Bavaria, Germany). During its most notorious outbreak in 1978–1984 *L. monacha* infested and partly defoliated over 2 million ha of coniferous forest in Poland alone, corresponding to one-quarter of Poland's forests (CABI 2015a, Schönherr 1985). *L. dispar* outbreaks, though intense, are generally more localized and of shorter duration (CABI 2015b).

Both species are highly polyphagous. *Lymantria monacha* prefers, but is not restricted to, conifers such as Norway spruce (*Picea abies* (L.) H. Karst.) and Scots pine (*Pinus sylvestris* L.) (Keena 2003), while *L. dispar* is known to feed on over 300 host plants of different genera, though it prefers broadleaf trees such as *Quercus, Betula, Fagus,* and *Populus* (Doane & McManus 1981, Lechowicz & Mauffette 1986).

Lymantria monacha and *L. dispar* are univoltine and both overwinter in diapause as small, fully developed larvae in eggs that hatch in spring. The adult moths emerge in late summer. The females of *L. monacha* and the Western European subspecies of gypsy moth – *L. dispar dispar* are considered poor flyers that rarely move from the tree trunk where they pupated (Majunke *et al.* 2004, Pogue & Schaefer 2007, Keena *et al.* 2008). The first instar larvae are, however, capable of ballooning.

The distribution range of *L. monacha* comprises most of temperate Europe – including southern Finland – and Asia (Vanhanen *et al.* 2007). *Lymantria dispar* is a more southern species that occurs in most of Asia and Europe (except the British Isles) as north as southern Sweden. A permanent Finnish *L. dispar* population has not yet been officially confirmed but the species has been sighted more frequently in Finland during the past decade than earlier

(Insect Database'). A relatively recent and accurate distribution map of both species is found in Hydén 2006. In the mid-19th century, *L. dispar* was also introduced to North America where it rapidly established as a significant pest species (Forbush & Fernald 1896, Liebhold *et al.* 1992, Liebhold *et al.* 2000). The potential of both *L. monacha* and *L. dispar* to expand their distribution ranges with further accidental introductions or naturally with a warming climate, as well as the possible damage they may cause in new areas, are of interest both in northern Europe and on other continents (Withers & Keena 2001, Vanhanen *et al.* 2007, Heit *et al.* 2014). *Lymantria monacha* has recently also gained some publicity in Finland, where for the first time it contributed to significant defoliation on at least two islands in the southwestern archipelago of the country (Heino & Pouttu 2014; Jaakko Kullberg, personal communication). *Lymantria dispar* also gained some news coverage as the largest migration to date of the species was observed as recently as August 2017 (Mankkinen 2017).

2.2. Experimental set-up

The following is intended as a brief overview of the methods used in my research. Detailed descriptions of the experiments and the statistical analyses are given in the original articles and manuscripts.

2.2.1. Studying the timing of egg hatch of geometrid moths in the laboratory (**I**)

Synchrony between egg hatch and budburst of the host plant is often crucial for spring-feeding folivores such as many geometrid moths. As host-plants and their phenology vary between locations, moth eggs from different populations may have to hatch at different times.

To study whether there are differences that could point towards local adaptation in egg hatch timing in geographically different populations of geometrid defoliators, eggs of *E. autumnata*, *O. brumata* and *E. defoliaria* from different populations were incubated under the same laboratory conditions. *Epirrita autumnata* eggs were obtained from populations in Germany, southern Finland and northern Finland, *O. brumata* eggs from Germany and northern Finland and *E. defoliaria* from Germany and southern Finland, yielding a total of seven test groups, each with three replicates (**I**: Fig. 1). After keeping the eggs at sub-zero temperatures over the winter, they were transferred to a climate chamber in April.

Temperature in the climate chamber was changed weekly to simulate the progressing of spring in southern Finland. Average weekly temperatures for the chamber were calculated from data collected at a weather station in Turku, southern Finland. Daylight lamps mounted in the climate chamber were set weekly to match average weekly sunrise and sunset times of the same region (**I**: Fig. 2).

Eclosed larvae were counted daily and the hatch dates were recorded. Hatch dates were translated to degree-days above 5 °C (DD>5 °C), i.e. the cumulative sum of daily average temperatures exceeding the base level of 5 °C. The threshold value of 5° Celsius is commonly used in various studies (e.g., Pöyry *et al.* 2009) and marks the onset of the growing season. Here it was used for being able to compare the hatch time of the different species. The true developmental thresholds are most likely different for each of the three species and somewhat lower than 5 °C (Embree 1970, Kimberling & Miller 1988, Nilssen & Tenow 1990, Jepsen *et al.* 2011). The data were analysed using linear mixed models with temperature sum at

hatching as a response variable and test group as a fixed explanatory factor. Replicate was set as a random factor.

2.2.2. Field experiment on life cycles of *L. monacha* and *L. dispar* (**II**)

As stated earlier, *interpopulation* differences in phenology between moth eggs or larvae that are reared under the same conditions but originate from geographically different populations may hint at adaptations to local conditions. Correspondingly, *intrapopulation* differences between moths of the same population reared in different locations may reveal adaptive phenotypic plasticity – the ability of an individual to rapidly modify its life cycle to match the surrounding conditions.

To study the prevalence of these two adaptation strategies in *L. monacha* and *L. dispar*, eggs and larvae from a continental and a boreal *L. monacha* population, originating from Germany and southern Finland respectively, and *L. dispar* from a continental German population were reared at three climatically different field sites in 2014 (Fig.3, **II**: Fig.1, A1). The southernmost site was located in Tharandt, Germany (50°58'N 13°50' E), the second site was in Turku in southern Finland (60°26'N 22°10'E) and the northernmost site at Kevo near the northern border of Finland (69°44'N 27°00'E). A further aim of the field experiment was to evaluate *L. dispar* success beyond the northern boundary of its natural distribution range and on different host plants.
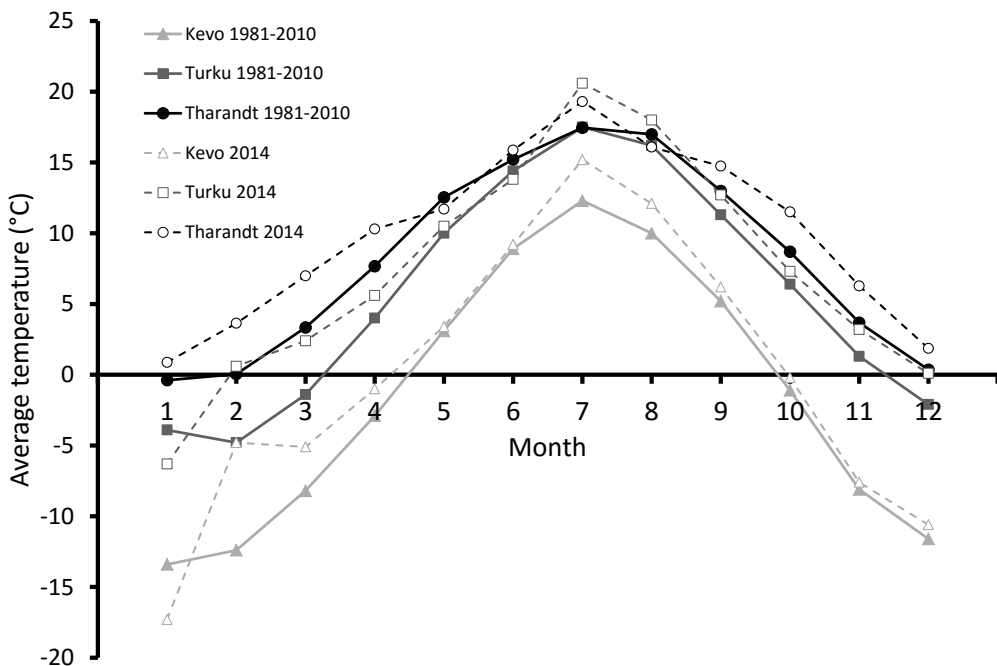

Figure 3. Monthly average temperatures in the field experiment year 2014 and during the 30-year period 1981–2010 in the three locations where field experiments were conducted. Data provided by the Finnish Meteorological Institute and the Chair of Meteorology at Technische Universität Dresden.

As in the geometrid experiment, eggs were stored in sub-zero temperatures over the winter before transferring them to the three field sites in spring: early April in Tharandt, mid-May in Turku and late May at Kevo. At the study sites eggs (and later the developing larvae) were kept on tree branches enclosed in mesh bags. *Lymantria monacha* was reared on Scots pine, *Pinus sylvestris* L., while *L. dispar* was reared both on oak, *Quercus robur* L., and silver birch, *Betula pendula* Roth in Tharandt, on *Q. robur* in Turku and on mountain birch, *Betula pubescens* var. *pumila* at Kevo.

The pupation dates of the larvae were recorded and the pupae sexed, weighed and stored in an open shed where they were checked for emerging adults. Times for pupation and adult emergence were translated to local temperature sums (DD>5 °C) in order to better be able to compare the results from the different field sites (Fig. 3, **II**: Fig. A1). Using a different threshold value than the one actually utilized by the developing larvae may however lead to erranneous interpretations of the data. To control for this, additional complementary temperature sums using threshold values between 2 and 10 °C were calculated and used in the subsequent analyses.

Linear mixed models with test group as the fixed factor were used to explain temperature sum at date of pupation, temperature sum at date of adult emergence, pupal mass and duration of pupal period. Test group was calculated by merging field site, sex and population of origin of each larvae/pupae. Significant differences between the test groups were determined using *a priori* contrasts. Egg batch and mesh bag were set as a random factor and a likelihood-ratio test was used to test for the variation accounted for by the parents of the eggs in the experiment and for the two mesh bags that each egg batch was divided into.

2.2.3. Investigating the potential of *L. monacha* and *L. dispar* eggs to survive extreme winter cold spells in Finland (**III**)

Winter minimum temperatures can limit insect distribution where average winter temperatures would still allow a population to survive (Nilssen & Tenow 1990, Virtanen *et al.* 1998, Neuvonen *et al.* 1999, Ammunét *et al.* 2012, Neuvonen & Virtanen 2015). To determine how cold winter minimum temperatures *L. monacha* and *L. dispar* can survive and whether there is a difference in cold hardiness between eggs from continental and boreal *L. monacha* eggs (from Germany and Finland, respectively), supercooling points for eggs from all three test populations were determined with differential thermal analysis. The egg batches were put in tubes attached to thermal sensors in a controlled chamber and the temperature was lowered gradually. Temperature differences between the tube with eggs and an empty control tube were recorded. Sudden peaks in the temperature differences indicate release of energy associated with the freezing of eggs. Medians of egg batches were recorded for statistical analyses.

Supercooling points of continental and boreal *L. monacha* eggs were compared with each other using an independent samples t-test. A non-parametric Mann-Whitney U test was used for comparing the supercooling points of continental *L. monacha* and *L. dispar* eggs. The supercooling point medians were also compared with winter minimum temperatures between year 1991 and 2000 in southwestern Finland and eastern Germany, the areas from which the eggs in the experiment originated, as well as with winter minimum temperatures at other sites in Finland. This helps to estimate whether extreme cold spells might limit *L. monacha* and *L.*

dispar distribution in the country in the current climate and under different climate change scenarios. In addition, old literary sources on *L. monacha* and *L. dispar* cold hardiness were reviewed, with the particular aim to track down a common claim that *L. monacha* eggs can survive temperatures as low as -40 °C (Schwenke 1978, Hydén *et al.* 2006).

2.2.4. Revealing changes in *L. monacha* distribution range using entomological records (**IV**)

Lymantria monacha is predicted to expand its range northwards in Europe (Karolewski *et al.* 2007, Vanhanen *et al.* 2007). Temporal trends in *L. monacha* numbers as well as changes in the northern distribution limit of the species were analysed using data from two entomological databases. The records were compared with climate data to reveal possible connections between climate change and *L. monacha* populations.

The Insect Database ("Hyönteistietokanta") is maintained by Luomus, the Finnish Museum of Natural History at the University of Helsinki, and it includes insect observations with data on species, observation date and location. To reduce biases caused by temporal variation in observation and reporting intensity in this large open database only records from 1961 onwards (i.e. from a time when light-trapping was well established among Finnish lepidopterologists) were used. Records from the Insect Database were used to describe temporal trends in *L. monacha* numbers. Moreover, observations from both the Insect database and a similar database from Sweden, ArtPortalen, were used to analyse changes in the northern distribution limit of the species.

L. monacha records from Nocturna, a systematic countrywide light trap monitoring programme for night-flying moths, (Söderman 1994, Söderman *et al.* 1999, Leinonen *et al.* 2016), were used to examine the abundances of the species at different trapping sites during the years 1993–2013. To calculate an estimate for how fast the species has spread northwards the data was divided into three 7-year periods, and the median latitudes of the northernmost traps that caught *L. monacha* were compared between periods. Moreover, 20 long-running trapping sites from southern Finland were chosen and divided into three 150 km wide latitudinal zones for a closer analysis of the northwards expansion rate of *L. monacha*.

Yearly climatic parameters for the egg-stage (minimum temperatures for November – March, EminT), larval stage (average temperatures for May – June, LT) and pupal/adult stage (average temperatures for July – August, PAT) of *L. monacha* were calculated for the distribution range of *L. monacha* in Finland. Three information criteria methods – Akaike's Information Criteria (AICc, with correction for small sample size), Sawa's Bayesian Information Criteria (BIC) and Schwarz Bayesian Criteria (SBC) were then used to rank models with 1–3 of these temperature variables explaining *L. monacha* numbers in the Insect Database and Nocturna datasets during different time periods.

Information criteria methods compare the goodness of fit of multiple competing linear models. They are used to estimate the parsimony of alternative models, with the aim to find the model with the best balance between explanatory power and complexity (number of parameters), that is, between underfitting and overfitting a model (Burnham & Andersson 2003).

3. RESULTS AND DISCUSSION

In the following, I will return to the four main research topics of chapter 1.4 – *local adaptations*, *adaptive phenotypic plasticity* and *potential* as well as *evidence for a northwards range expansion* of geometrid and lymantriin example species. Moreover, I offer an outlook on the future of *L. monacha* and *L. dispar* in Finland, highlighting a few questions that remain unanswered.

3.1. Differences between geographically separated populations of the same moth species as indicators of local adaptation

3.1.1. Egg hatch in geometrid moths

Eggs of *E. autumnata*, *O. brumata* and *E. defoliaria* from southern populations all hatched at higher temperature sums than eggs from northern populations of the same species (**I**: Fig. 3). This matches the observation that bud burst frequently happens at higher temperature sums in southern trees than in their northern conspecifics (Worrall & Mergen 1967, Myking & Heide 1995). It might thus point at local adaptations aiding the moth to retain synchrony between host plant phenology and larval development (Visser & Holleman 2001, van Asch & Visser 2007). However, as there were slight differences in the experiment in how the northern (Finnish) and southern (German) eggs were stored over winter, it is possible that they have experienced different lengths of sub-zero chilling periods, which may have affected the results (Kimberling & Miller 1988, Visser & Holleman 2001, Hibbard & Elkinton 2015). Thus, it is not possible to entirely rule out the option that the observed differences in hatch times were larger than they would naturally be.

For *E. autumnata*, hatch times of three geographical populations – one from northern Finland, one from southern Finland and one from Germany – were compared. Although the differences in temperature sum accumulation and, for example, day length are greater between the two locations in Finland than between the locations in southern Finland and Germany, the differences in hatch times displayed the opposite pattern: there was little difference between hatch times of the Finnish populations, but a great difference between eggs from southern Finland and Germany (**I**: Fig. 3). Assuming that this discrepancy is not only caused by the abovementioned difference in egg storage, it could indicate that the Finnish populations of *E. autumnata* – a species present in the entire country – are genetically interconnected to such a degree that the formation of distinct local adaptations is not possible. However, Snäll *et al.* (2004) have discovered moderate levels of genetic differentiation between *E. autumnata* populations in southern and northern Fennoscandia, although female dispersal does indeed appear to cause continuous gene flow on a local level. Alternatively, the highly polyphagous *E. autumnata* may feed on a different set of host plants in Central Europe than in Finland and may synchronize its egg hatch to match the phenology of the dominant host plant at both these locations.

The pattern of temperature sum requirements for egg hatch in the three species resembled requirements of the different populations within species: *E. defoliaria*, a species restricted to the southern parts of Fennoscandia, hatched at higher temperature sums than *O. brumata* and *E. autumnata*, which both have more northerly distribution ranges (**I**: Fig. 3). A difference in hatch timing between *E. autumnata* and *O. brumata* from the same region in northern Finland is surprising, as both species are assumed to depend on the young leaves of mountain birch in that area. However, previous observations (e.g., Mjaaseth *et al.* 2005, Jepsen *et al.* 2011)

confirm that *E. autumnata* hatches earlier than *O. brumata* in the north. It is unlikely that interspecific competition has caused this difference in hatch timing (Ammunét *et al.* 2010); it may simply be that synchronizing egg hatch with the youngest birch leaves is more important for *E. autumnata* than *O. brumata*, or that *O. brumata* larvae actually prefer slightly larger birch leaves, as they feed on leaves that are loosely spun together with silk (Tenow, 1972).

The magnitude of latitudinal differences in egg hatch timing varied considerably among the three species. Where *E. autumnata* displayed a large difference in hatch times between northern and southern populations, the difference was much smaller in *E. defoliaria* (**I**: Fig. 3). This could be explained by local adaptations to budburst being more important for some species than for others. *Erannis defoliaria* lives among numerous alternative host plants, which flush at different times in spring. It is possible that the the species is not as dependent on synchrony with any one host plant as is *E. autumnata* in northern Fennoscandia where mountain birch is practically the only readily available host plant. *E. defoliaria* also has slightly larger eggs and neonate larvae than the other two species and hence perhaps is able to process older and tougher leaf material directly after hatching.

3.1.2. Life history traits of *L. monacha*

Rearing *L. monacha* under field conditions revealed that larvae originating from a population on the boreal edge of the distribution range of the species pupated at a lower temperature sum than larvae from a continental core population (**II**: Fig. 2a, b, Table A1). Similarly, adult boreal *L. monacha* emerged at a lower temperature sum than continental ones (**II**: Fig. 5a, b, Table A1). This result resembles the abovementioned pattern found in egg hatch timing in northern and southern populations of geometrid moths. The fast development of the boreal *L. monacha* may indicate a local adaptation to short northern summers, and it may have developed rapidly, as the species was probably established in the country only after the 1950s (Grönblom & Suomalainen 1950).

The benefit that the boreal *L. monacha* gains in development time may be a trade off against a smaller size: boreal females had a lower pupal mass than continental ones (**II**: Fig. 3a, Table A1). This may be due to a shorter larval period where the boreal larvae simply have less time to feed between eclosion and pupation than continental ones. However, as eclosion times of larvae were not recorded it is not known how long the actual duration of the larval phase was. If the hypothesis about a shorter larval period of the boreal *L. monacha* females is true, the question arises what the female gains from pupating earlier and at a smaller size? In capital breeders, i.e. species that do not feed as adults (such as *L. monacha*), the pupal mass of females correlates with the number of eggs they are able to produce (Hough & Pimentel 1978, Gilbert 1984, Honěk 1993, Tammaru & Haukioja 1996). A large size thus indicates higher fitness. However, it is possible that in the north earlier timing of pupation and emergence is more important for the fitness than large size. In *L. monacha*, adult emergence, reproduction and egg development happens in autumn, and the risk of too cold temperatures during this reproductive period may be too high if pupation is postponed.
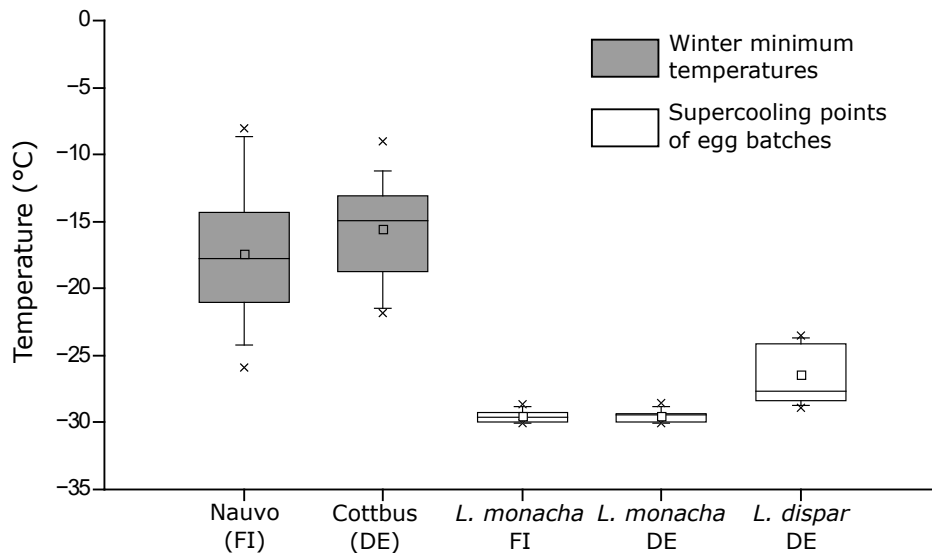
Figure 4. Winter minimum temperatures during 1991–2014 in Nauvo, Finland and Cottbus, Germany, two measuring stations adjacent to the areas of origin of the moth populations in the supercooling experiment, and median supercooling points of lymantriin egg batches (*L. monacha* FI *n*=6, *L. monacha* DE *n*=7, *L. dispar* DE *n*=7). Box outlines mark 50th percentile values, whiskers mark 90th percentile values. The median is marked with a horizontal line dividing the box, the average is marked with a square and minimum and maximum values are marked with "x".

No difference was found between eggs of boreal and continental *L. monacha* populations when comparing median supercooling points (Fig. 4), which are indicative of cold hardiness. However, as the measured supercooling points of both populations had a large safety margin, being well below even the colder (boreal) winter minimum temperatures, there has been no selection pressure towards a local adaptation or divergence of a more cold-hardy strain on the southern coast of Finland.

3.2. Adaptive phenotypic plasticity observed between moths from the same population reared in different climate zones

When measuring temperature sum at pupation and at adult emergence, duration of the pupal period, and pupal mass, very few differences between the continental *L. monacha* reared in Turku, southern Finland and Tharandt, Germany were found – only the pupal period of males was longer in Turku than in Tharandt (**II**: Figs. 2–5a–b, Table A1). Reaching a certain point in larval development at the same temperature sum in Tharandt and Turku means that it is reached at an earlier calendar date in Tharandt than in Turku, where temperature sum accumulation is slower (**II**: Fig. A1). It thus appears that the continental *L. monacha* was not able to adjust its life cycle timing within one generation to optimally follow the short northern summer season. Instead, the larvae attempted to pupate at a similar temperature sum as in their region of origin. This lack of plasticity was fatal for continental *L. monacha* at the northernmost experimental location, Kevo in northern Finland, where only four individuals succeeded in pupating at all.

This experiment covered only one generation of continental *L. monacha*, the parents of which had been reared in Tharandt. Investigating any possible maternal effects – a special type of adaptive phenotypic plasticity (Mousseau & Dingle 1991) – by comparing the offspring of a parent generation reared in Tharandt and of one reared in Turku would certainly be an interesting topic for a follow-up experiment.

Boreal *L. monacha* and continental *L. dispar* both displayed a somewhat higher degree of plasticity in response to environmental conditions than continental *L. monacha*, although certain effects were only discernible in one of the sexes or only between two of the three locations (**II**: Figs. 2–5, Table A1). They both had a tendency to pupate and emerge at lower temperature sums and to have a shorter pupal period in the north than in southern sites. It is possible that *L. monacha* displays *high margin plasticity* or *high leading edge plasticity*, as defined by Valladares *et al.* (2014). This would imply that the boreal population – which struggles at the northern limit of the distribution range of the species – would benefit from a high level of adaptive phenological plasticity that facilitates acclimation to varying environments. However, such flexibility is clearly also present in the core distribution range of *L. dispar*.

Pupal mass was only affected by location in *L. dispar* females, which grew heavier at Kevo than in Tharandt (**II**: Fig. 4b, Table A1). An explanation for this could be a prolonged larval period, with more time to feed and grow at Kevo, if the environmental cues that trigger pupation were delayed (too cold, too long days). However, as discussed earlier in relation to local adaptations, this hypothesis cannot be verified based on this experiment. A nutritional difference between silver birch used as host plant in Tharandt and mountain birch used at Kevo can also not be entirely ruled out (Valkama *et al.* 2005). The fact that the effect is only present for females may reflect the greater advantage of a higher mass for females than for males. In other words, there might be a selection pressure on females to have a plastic ability to grow larger if the opportunity offers itself, while the body mass of males may be more "fixed". A similar effect of female size responding stronger to environmental changes than male size has also been documented in a meta-analyis by Teder & Tammaru (2005).

3.3 Potential of *L. monacha* and *L. dispar* for northwards range expansion

3.3.1. Development from egg to adult in southern and northern Finland

Both continental *L. monacha* and *L. dispar* successfully completed their life cycle in Turku, southern Finland. In fact, 72 % of the *L. dispar* eggs developed to pupal stage, which is considerably more than the 51 % of the local boreal *L. monacha* eggs. The continental *L. monacha* performed worse than the two other groups with only 18 % of the eggs developing to pupae. Success in developing from pupa to adult stage ranged from 55 % in *L.* dispar to 62 % in boreal and 65 % in continental *L. monacha*. In comparison with the field site in Tharandt, in the core distribution range of both species, *L. monacha* performed slightly worse and *L. dispar* better in Turku (**II**: Table 1). The results suggest that *L. dispar*, which has been observed frequently in southern Finland in recent years (Insect Database), could establish as a new species in the region, if it has not already.

In contrast, all *L. monacha* and *L. dispar* failed to emerge as adults at the extremely northern site at Kevo, where pupation success was also considerably lower than at the southern sites (**II**: Table 1). The result was expected, as the chosen field site lies well beyond the current distribution range of either species and has a harsh, short summer. However, a few of the

pupae of both species hatched considerably later in mid-October when transferred to room temperature (and a more southern, longer daylight period). This suggests that adult emergence in these species is regulated by temperature. Either the pupal development slowed down considerably in the low outdoor temperatures and the process was not yet finished by the time the experiment was cancelled due to onset of autumn, or some threshold temperature or temperature sum crucial for pupal development was not reached. Although no conclusions about the adaptive nature of this delay can be drawn based on the data used here, it is conceivable that such a temperature dependent delay in pupal development would allow the pupae to "wait out" temporary unfavourable cold periods in late summer, postponing adult emergence to a time more favourable for flight.

Host plant availability would not limit *L. dispar* range in Finland, as the larvae successfully pupated on both the northern mountain birch and silver birch which is readily available in most of the country. Larval development was slightly faster on *Q. robur* than on *B. pendula* in Tharandt, and the larve reared on *Q. robur* were heavier than larvae reared on *B. pendula*. *Pinus sylvestris*, one of the main host plants of *L. monacha*, grows throughout Finland. While a preference of the small *L. monacha* larvae for male cones with pollen is recorded in the literature (e.g., Keena 2003), pollen is not an obligatory food source for the species (personal observation) and thus a precise synchrony with the host plant is not necessary.

3.3.2. Cold hardiness of eggs

Median supercooling points of *L. monacha* egg batches from a boreal population in southern Finland and a continental one from Germany ranged from -28.6 to -30.1 °C. These temperatures are much lower than recent winter minimum temperatures at the sites of origin of the eggs in the experiment, yet considerably higher than the -40 °C frequently quoted in literature as a cold-tolerance limit for *L. monacha* eggs (Schwenke 1978, Hydén *et al.* 2006) (Fig.4, **III**: Fig S1a-b). The -40 °C limit was traced back to a somewhat dubious observation from the winter 1928/29 (Knoche 1932), and several more plausible tolerance limits for *L. monacha* eggs were discovered in old entomological literature (**III**: Table S2). It is, however, quite possible that *L. monacha* eggs endure winters with measured air temperature extremes lower than the supercooling point of eggs, as local topography and snow conditions may ameliorate microclimatic conditions that the eggs actually experience. In fact, *L. monacha* has already been observed in Finland in areas where measured temperatures occasionally drop below the supercooling point (compare Fig. 5 and **IV**: Fig. 2). Especially in eastern Finland, where the "too cold" *L. monacha* observations are most common, this may be explained by a thick and long-lasting snow cover (Finnish Meteorological Institute 2017) insulating the overwintering eggs. At the same time, there is more topographical variation in eastern compared to western Finland (Aalto *et al.* 2017), and *L. monacha* eggs laid at higher altitudes than the weather stations may have experienced less severe winter temperatures than recorded.
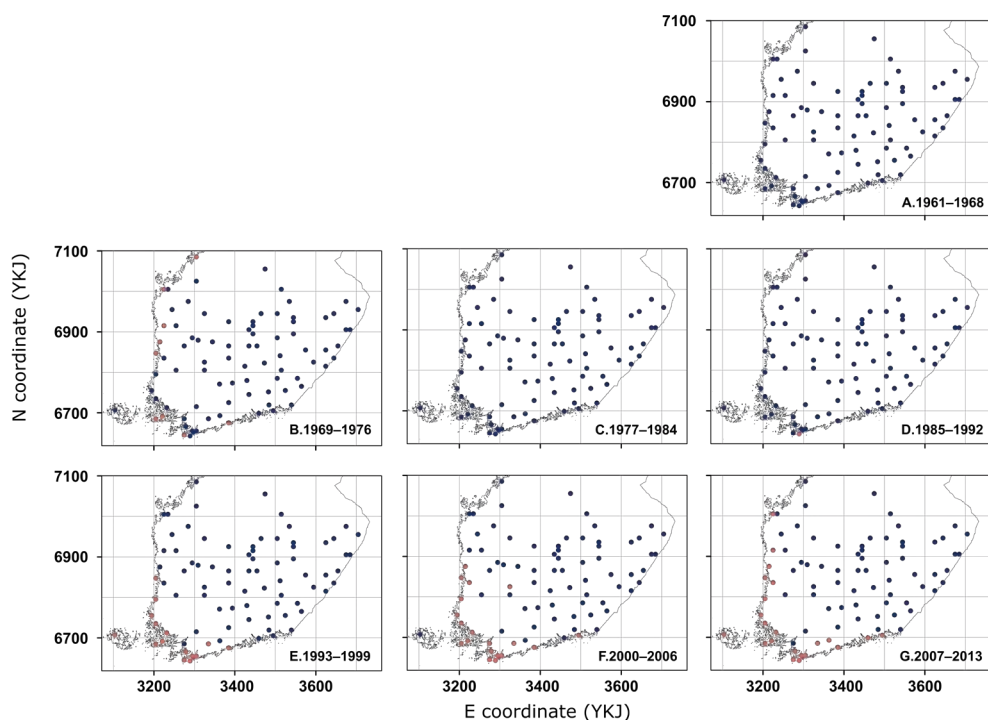
Figure 5. Weather stations with temperatures constantly above -29 °C, which is the median supercooling point of *L. monacha* eggs, (light red) and stations with temperatures dropping below -29 °C at least once (dark blue) in four 8-year and three 7-year periods between the years 1961 and 2013. The coordinates are values in the Finnish YKJ-coordinate system; the N coordinate shows the distance from the equator in km. Compare with **IV**: Fig. 2.

The median supercooling points of the *L. dispar* egg batches showed bimodal variation, with medians of one group ranging from -23.6 to -24.4 °C and the other from -27.7 to -28.9 °C (**III**: Fig. S1 c). Also in this species the "safety margin" between median winter minimum temperatures of its core distribution range and median egg supercooling points was several degrees. Only during four winters between 1991 and 2014 the coldest winter temperatures in Nauvo, southern Finland were lower than the median supercooling points of the most freezing-sensitive egg batches of German *L. dispar* (Fig. 4). The range of median supercooling points corresponded well with results in the literature reviewed in manuscript **III**.

These results suggest that *L. monacha* and *L. dispar* are well adapted to the winter temperature within their current distribution ranges, and that winter cold spells would not limit *L. dispar* from expanding its range to southernmost Finland. However, it should be kept in mind that the supercooling point and mortality are not synonymous as low temperatures might cause the death of insect eggs even before these reach their supercooling point and freeze, with the duration of the cold period often being at least as important as the temperature limit itself (Sinclair *et al.* 2003).

A comparison between egg supercooling points and winter minimum temperatures between 1991 and 2000 at 101 sites in Finland revealed that winter minimum temperatures would limit

the latitudinal distribution of *L. monacha* to about 60.5 °N and *L. dispar* to about 59.9 °N. This matches recently published distribution maps well (**III**: Figs 1–2, Hydén 2006).

Under climate warming scenarios of +3.6 and +5.8 °C based on the B2 scenario of the third IPCC assessment report (IPCC 2001) the northern boundaries of the two moth species' distribution would shift on average 190 and 307 km northwards respectively (**III**: Fig. 1). This is considerably less than the predicted shift of over 500 km modelled by Vanhanen *et al.* (2007) using a CLIMEX model that did not consider extreme winter temperatures.

The cold-dependent northern distribution limit of *L. monacha* and *L. dispar* would not cross the country evenly: instead, it would be affected by local topography, geography and climatic conditions, such as snow cover. For example, both at current temperatures and under the two temperature scenarios the distribution limits of both species would be further north along the coast than inland (Fig. 6) – a pattern already visible in other species, such as *O. brumata* and *A. aurantiaria*, currently spreading in Fennoscandia (Jepsen *et al.* 2008, 2011).
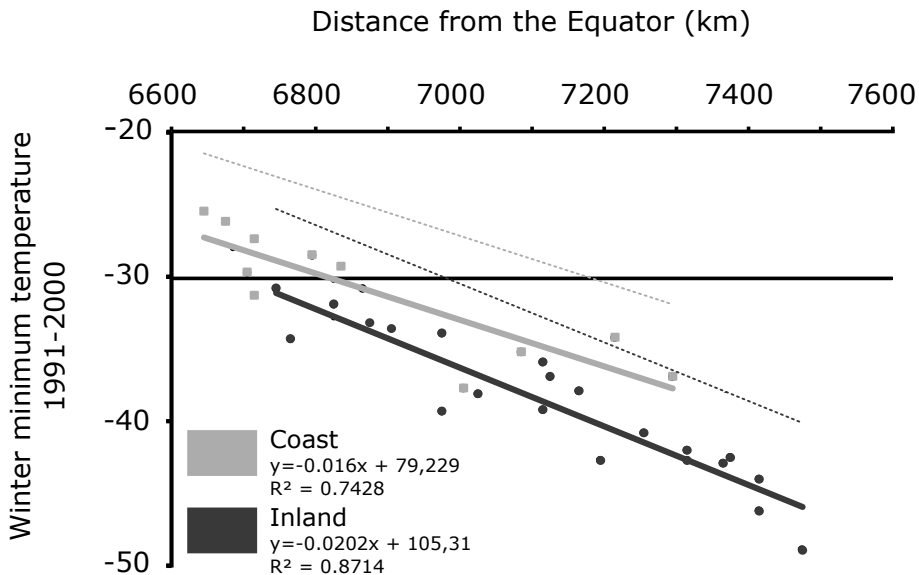

Figure 6. Winter minimum temperatures in 11 coastal and 21 inland locations in Finland during 1991–2000. Compare with **III**: Fig. 1. Solid regression lines show the relationship between winter minimum temperature and latitude, dashed lines show corresponding lines for a warming scenario of +5.8 °C. A horizontal black line shows the median supercooling point of the most cold resistant egg batch of *L. monacha*. A similar line for *L. dispar* as well as markings for the intermediate warming scenario are omitted to retain clarity.

3.4 Observed population growth and northwards range expansion of *L. monacha*

The first confirmed observation of *L. monacha* in Finland was made in 1899, but the species appears to have been scarce, maybe not even permanently established in Finland until recent years (**IV**). Observations from the open Insect Database reveal that *L. monacha* numbers on the southern coast of Finland varied without a significant trend from 1961 to 1989 but have been strongly rising since 1990. The increase was about three orders of magnitude from 1991 to 2010. While a similar pattern of observations is discernible for other lymantrids and

noctuids, the recent increase in these groups has been less steep (**IV**: Fig. 3), confirming that the observed increase in *L. monacha* is real rather than caused by temporal variation in recording intensity. Observations from the Insect Database also show a range expansion from the southern coastline of Finland northwards and inland (**IV**: Fig. 2). A comparison of observations from the Insect Database and the corresponding Swedish ArtPortalen reveals great similarities in the development of the northern distribution limit of *L. monacha* in both countries, clearly showing that the species has been moving northwards since the 1990's despite periods of withdrawal in between (**IV**: Fig. 1).

A trend of rising *L. monacha* abundances as well as a range expansion northwards and inland could also be seen in the records of the standardized Nocturna monitoring programme. Before the year 2000 only 1–2 *L. monacha* individuals were recorded yearly per light trap, and almost exclusively on the southern coast (**IV**: Fig. 5a). Between 2000 and 2006 the numbers of yearly records rose above 10 on the southernmost sites (**IV**: Fig. 5b). In 2007–2013 over 60 *L. monacha* moths were recorded from some of the coastal traps and several inland traps yielded a yearly average of 1–9 *L. monacha* individuals (**IV**: Fig. 5c).

Although the northwards expansion rate based on the median latitude of traps with *L. monacha* depended on how many of the northernmost traps with *L. monacha* were used for the calculation, the species had in general spread northwards faster during the time period from 2000–2006 to 2007–2013 than during the earlier period from 1993–1999 to 2000–2006. The average rate was 5.7 km/year (0.7–19.5 km/year) during the earlier period and 12.9 (0.0–20.1) km/year during the later period.

A closer examination of 20 long-running traps in southern Finland reveals that *L. monacha* numbers started to rise in the mid-1990s in the southernmost parts of the country, first at an even but moderate rate but steeply and with considerable fluctuations after 2003. Further north a moderate steady rise in *L. monacha* numbers can be observed starting around 2004, but beyond 62.2 °N a total of only two *L. monacha* were recorded in the chosen traps during 1993–2013 (**IV**: Fig. 6). Dividing the traps into 150 km wide latitudinal zones and comparing when an annual capture rate of 0.5, 1 and 5 *L. monacha* per traps was reached in the two southernmost zones yielded estimates for a northwards expansion rate between 13.7 and 17.1 km/year. This can be considered the most robust estimate of the expansion rate in this study, as it is based on systematic standardized observations, which minimizes the error caused by variation in recorder effort.

Information criteria methods ranked high models where *L. monacha* numbers from the Insect Database and Nocturna were explained with winter minimum temperatures (EminT) and average temperatures during the pupal/adult stage (PAT). While these two parameters are strongly correlated in both datasets (**IV**: Table A1), they can both biologically plausibly affect *L. monacha* success. In addition to the direct effects of temperature on *L. monacha* survival and success described here, temperature may, naturally, also effect the species indirectly through biotic interactions with both lower and higher trophic levels.

Higher temperatures during the flight period may have facilitated dispersal and improved reproduction success of the adult *L. monacha*, as higher temperatures may increase flight activity (Skuhravý 1987). However, high temperatures during flight may also reduce the life span of the adult moths and thus affect reproduction success negatively (e.g., Nadgauda & Pitre 1983, Mironidis & Savopoulou-Soultani 2008). Milder winter minimum temperatures, on the other hand may have improved winter survival of the eggs. A comparison with the

experimentally confirmed median supercooling point of *L. monacha* eggs, -29.5 °C, and minimum winter temperatures on the southwestern coast of Finland revealed that the temperature has not dropped below this lethal limit since 1987 (Fig.5; **IV**: Figs. 7, A1). This is temporally well matched with the *L. monacha* upswing starting in the 1990s.

3.5. Future prospects of *L. monacha* and *L. dispar* in Finland

Based on the findings presented above, an establishment of *L. dispar* and a continued northwards range expansion and population growth of *L. monacha* in Finland appear likely. Especially *L. monacha* could become an important forest pest in the country, considering that it is a polyphage that prefers conifers, the most important trees in Finnish forestry (Luke 2017).

Future damage risk especially from *L. monacha* and later possibly also from *L. dispar*, should be considered in forest management decisions already today (**IV**). Integrated Pest Management (IPM; Wainhouse 2005) defines three action levels which could be used as a framework for mitigating the risk from new pest species. First, appropriate silvicultural management practices can increase the resistance of forests against outbreaks and enhance mechanisms of natural population control of pest species. Studies on insect diversity in different forest stands (Heiermann & Füldner 2006) suggest that risk reduction, in the case of *L. monacha*, can be reached through appropriate thinning, ecologically stable forest stands and forest conversion from coniferous to mixed (coniferous/deciduous; Castagneyrol *et al.* 2013). This is corroborated by models estimating the risk for *L. monacha* damage in different forest management scenarios (Hentschel *et al.* 2017). The second level consists of risk area mapping and population monitoring. To this end, a multilevel monitoring programme based on pheromone trapping is already in use in Denmark (Jensen 1991) and several federal states in Germany (Möller *et al.* 2016). The programme could also be adapted to Finnish conditions and would deliver valuable data on defoliator populations. The third IPM level, possible control methods and related cost-benefit analyses, may become relevant in the future. Furthermore, there is a need for continued research on species-specific defoliator-tree-interactions, which helps recognize the high-risk combinations of tree species, site conditions and effects caused by a changing climate.

Knowledge gaps in our understanding of lymantriin physiology and phenology hinder our understanding of their geographical expansion. While *L. monacha* and *L. dispar* are well-known and relatively well-studied species, knowledge of many of their life history traits connected with range expansion potential and invasiveness – especially in northern latitudes – is lacking. The experiments presented in this thesis were not designed to reveal the environmental cues and their threshold values triggering different phenological events in the two species (although the few *L. monacha* and *L. dispar* pupae from Kevo hatching later indoors imply that adult emergence is regulated by temperature as discussed above in chapter 3.3). Temperature sum was used as a response variable that enabled biologically meaningful comparisons of spring and summer conditions at different sites. In reality, the moths may rely at least partly on other cues, such as day length, which is estimated to be the most important environmental cue for the timing of phenology in temperate insects (deWilde 1962, Bale *et al.* 2002; however, see Valtonen *et al.* 2011 & 2014 concerning the commonness of thermal control of phenology in Lepidoptera). It is conceivable that differences in day length, which are significant even between southern and northern Finland, could hamper the range expansion of *L. monacha* and *L. dispar* across latitudes and require special adaptations or

adaptive phenotypic plasticity in the same way as temperature differences do. Further carefully designed rearing experiments under controlled laboratory conditions and especially in the field could help with separating the effects of day length – or other environmental cues – from those of temperature on the phenology of *L. monacha* and *L. dispar*.

4. CONCLUSIONS

The present work adds to our knowledge about the phenology and life history traits of lepidopteran insect pests as well as the potential shifts and expansions of their distribution ranges in a changing climate. It is based on studying five different species, the geometrids *E. autumnata*, *O. brumata* and *E. defoliaria* and the lymantriins *L. monacha* and *L. dispar*, each with slightly different distribution ranges and histories, ranging from *E. autumnata*, which is a long-time resident species of even the northernmost parts of Fennoscandia, to *L. dispar*, which probably is in an ongoing process of establishing on the Finnish side of the Baltic Sea. Although many other insect species resemble at least one of these five study species, transferring these results to other potential invasive pest species should be done with caution. Already within this study, comparisons between seemingly similar species revealed significant differences.

Both the geometrids and *L. monacha* from northern strains tended to develop faster and or earlier than their conspecifics from southern strains. This could reflect a genetic adaptation of northern moth populations to a short summer season. In the case of geometrid egg hatch, local adaptations may help the eggs to hatch in synchrony with host plant budburst, which is vital for the survival of neonate larvae and is also known to happen at a lower temperature sum, i.e. earlier, in the north than in the south. However, the differences in egg hatch timing between geometrid populations were not equally large for all species, but instead more extreme in the northern *E. autumnata* than in the more southern *O. brumata* and *E. defoliaria*. This could indicate that local adaptations leading to synchrony with certain host plants are more crucial in the north than in the south.

For *L. monacha*, a gain in development rate in the northern population (from boreal southern Finland) appears to be connected with a decrease in pupal mass of females. It is possible that in the north a fast development is even more important for female fitness than a large size.

Phenotypic plasticity – the ability of genetically similar individuals to display different phenotypes when exposed to different conditions – can be revealed by rearing individuals originating from the same population in different conditions. *L. monacha* from Central Europe appear to have less such flexibility in their phenology than *L. monacha* from southern Finland, which may indicate that the population living on the edge of the species' distribution range benefits from a high level of adaptive phenological plasticity that facilitates acclimation to varying environments. In *L. dispar*, however, similar plasticity is clearly also present in the population originating from the species' core distribution range in Central Europe.

Host plant availability does not limit the range of *L. monacha* or *L. dispar* in Finland. Both species can successfully complete their entire life cycle in southern Finland, the latter even slightly more successfully than in its core distribution range in Germany. While winter minimum temperatures will not stop *L. dispar* from expanding its range from continental Europe to southern Finland, they will limit the expansion of both studied lymantriins further north in the country. Dismissing all other abiotic and biotic variables, current winter minimum temperatures would limit the latitudinal distribution of *L. monacha* to about 60.5 °N and *L.*

dispar to about 59.9 °N. In climate warming scenarios of maximally +5.8 °C, the northern boundary of both species' distribution could shift by over 300 km, which is still less than predicted earlier by models not considering winter minimum temperatures.

L. monacha has both become more frequent and expanded its range in Finland since the early 1990s. The observed range expansions and population growth appear to be connected to less severe winter extreme temperatures, although rising summer temperatures during the flight period of the species may also have contributed to its recent success.

As *L. monacha* and *L. dispar* become more frequent and expand their range in Finland, they may develop into considerable forest pests in the country the way they are in their core distribution ranges. Multilevel monitoring programmes have proven efficient in current *L. monacha* outbreak areas, and could be deployed for risk areas in Finland. Defoliating risk can also be reduced through forest conversion to mixed and ecologically stable stands.

ACKNOWLEDGEMENTS

My Phd-studies have by no means been a solo venture. From the very beginning, I have been advised, supported and encouraged by colleagues, friends and family both in Finland and in Germany, and only with the help of these people have I been able to design and carry out my experiments and develop as a scientist. First of all, I am grateful to all of them for being patient and flexible with the challenges of work and communication over long distances.

I was extremely fortunate in my choice of supervisors, whom I hardly knew before it was time to sign the appropriate forms and embark together on the road towards a thesis. Pekka Niemelä has guided me with his immense experience on the field of forest ecology and helped me to see my studies in a larger context. I also thoroughly enjoyed our discussions after our meetings, where entomology encountered etymology and biogeography merged with renaissance art history. Kari Saikkonen's ability to spot relationships in natural systems helped me both in experiment design and in interpreting my tangled results. I am also grateful for Kari's great help and experience with publications and presentations, and for his through and through positive, encouraging attitude. Mechthild Roth, my supervising professor at Technische Universität Dresden, has been a wonderful support in a new research environment, creating for me a free space to work on my project and warmly welcoming me to her team, well earning the German title of "Doktormutter". I also thank my research directors, Erkki Korpimäki and Ilari Sääksjärvi, for their help with all the formalities of a PhD-project.

I had the honour to work on my experiments and articles with great colleagues towards whom I feel deep gratitude and respect. Kai Ruohomäki accompanied me in every study, and always quickly had a reply ready to any question I had. Without Tero Klemola's skills in both doing and patiently explaining statistics, this thesis simply would never have happened. Seppo Neuvonen with his great knowledge of the study systems and impeccable analytical skills contributed more than "significantly" to the latter two articles, and I thank him for thoroughly explaining again and again his ideas for analyses and methodology previously unknown to me. I thank Olli-Pekka Tikkanen for contributing with his expertise on the Finnish forest pest situation and current research on the field, and Reima Leinonen, Lutz-Florian Otto and Juha Pöyry for their assistance with the last article.

Special thanks goes to all the people who helped me with the practical experiments and work – they got wet in a thunder storm counting pupae, housed hairy larvae on their balconies and cleaned caterpillar boxes during late evening hours. I warmly thank Tommi Andersson and Marjo Myllyrinne as well as the staff on the research station at Kevo and at the botanical garden in Ruissalo, and my technical assistants at TU-Dresden. My thanks also go to all those who assisted me with translations and language checks of the articles, and to Tapani Hopkins and Sonja Vidjeskog for proofreading the language of this thesis.

Furthermore, I am very grateful to all my colleagues and friends at the Chair of Forest Zoology in Tharandt. You have made working in a new country and a new institute easy and enjoyable. Nobody is able to keep all the loose threads in her hands as Cornelia Scheibner, the enthusiasm for entomology of Ingo Brunk is without compare and very infectious, and Jana

Zschille is a role model for me as an academic teacher constantly striving to develop and improve her work.

Great thanks goes out to all my friends. You have been up for something fun on brief notice when I visit Finland, you have encouraged me online regardless of distance, and you have made me feel welcome in Germany. Ella, Hanna, Jenni, Tarja and Tuuli – we started our journey into the world of biology together, and I could not have wished for better travel company for the long road. Let's celebrate with some doughnuts!

One special group of friends that I want to thank are all the scouts worldwide that I know – the ones that taught me many practical skills that have been useful during my research, the ones I in turn have been able to teach something new, and of course the ones with whom I have experienced amazing adventures and friendship throughout the years. Particular thanks goes to Pia-Maria Grandell, Mikaela Korin and Hedda Mether who helped me find the correct scientific terms in Swedish, and to Marieke Frassl who not only read through the final manuscript with great enthusiasm and made valuable comments, but also adviced me not to leave the writing of the aknowledments last. Too late for that, I am afraid.

Finally, my deepest gratitude goes to my extended family. My mother Carola and father Kalevi, together with my grand parents, aunt and uncles, have lovingly raised me to awareness of nature and been unwaiveringly supportive throughout my studies. They have also very concretely played a crucial role in my research by hunting for nun moth (both in the nightly forest and in their own living room) and by driving me hundreds of kilometres by car and boat around the country. At some point, I must have switched places with my little sister Stefania, because during the past years it has been she who is the grown-up, the shoulder to lean on and the listening ear (and the one with full-time employment). Thank you, Nia. And Tobi… I am so very grateful to have you on my side. You have helped me to see scientific work from totally new angles, encouraged me in every phase of my research and – more importantly – dragged me away from it when needed!

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