The Effect of Temperature on Trophic Interactions

Implications for the Population Dynamics of a Forest Pest Insect in a Warmer Climate

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Cover: A group of pine sawfly larvae
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Abstract

Increase in temperature related to climate change will have consequences on the performance of organisms. Insects could be expected to respond more than other organism groups because they are ectotherms. Many herbivorous insects are considered pests and may cause severe damage, therefore, trying to predict the performance of pest insects in a future climate is vital. In order to make predictions about the future we need to better understand the mechanisms and processes that are driving the population dynamics of pest insects. To achieve that all the life stages and the interactions with other trophic levels, such as host plants and natural enemies need to be considered. The European pine sawfly, *Neodiprion sertifer* Geoffr. (Hymenoptera: Diprionidae), is a pest species in boreal pine (*Pinus* spp.) forests. Its populations undergo large fluctuations in densities that may reach very high levels, so called outbreaks. In this thesis the effect of temperature on interactions known to be important for the sawfly population dynamics is evaluated to assess if the risk of outbreaks will increase due to climate warming. Sawfly performance was studied with respect to stage specific mortality factors; i.e. secondary compounds in the food (diterpenes), arthropod predation of the larvae and small mammal predation on the pupae. Climate chambers were used to create different temperatures in the laboratory and in a field study a latitudinal gradient was utilized. The results indicate that survival in the larval stage may decrease but survival in the pupal stage may increase with increasing temperature. The relative importance of the different mortality factors was investigated in a simple population model and the outcome suggests that in warmer temperatures, increased larval mortality outweighs the effects of decreased pupal mortality, which imply that the propensity for sawfly outbreaks to occur will be reduced in a warmer future climate.

Keywords: climate change, herbivore, mortality, natural enemies, outbreak, phytophagous insect, plant-insect interactions, diterpenoid resin acids

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Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Kollberg, I., Bylund, H., Schmidt, A., Gershenzon, J. and Björkman, C. (2013). Multiple effects of temperature, photoperiod and food quality on the performance of a pine sawfly. Ecological Entomology 38, 201-208.

II Kollberg, I., Bylund, H., Schmidt, A., Gershenzon, J. and Björkman, C. Larval survival of a pine sawfly in relation to temperature - the relative role of bottom-up and top-down processes along a latitudinal gradient. (manuscript)

III Kollberg, I., Bylund, H., Laugen, A. and Björkman, C. Effect of increased temperature on larval development and growth in two geographically separated populations of a forest pest insect (*Neodiprion sertifer*): local adaptation and outbreak risk. (manuscript)

IV Kollberg, I., Bylund, H., Huitu, O. and Björkman, C. Small mammal predation on a forest pest insect: enhanced outbreak risks in a warming climate? (manuscript)

V Kollberg, I., Björkman, C. and Bylund, H. Regulation of herbivorous insect populations in a warmer climate: contrasting the role of different mortality factors. (manuscript)

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The contribution of Ida Kollberg to the papers included in this thesis was as follows:

I Developed research questions and design together with HB and CB. Performed data collection. Did the statistical analyses and wrote the paper with assistance from HB and CB. The chemical analysis was done by AS and JG.

II Developed research questions and design together with HB and CB. Performed data collection. Did the statistical analyses and wrote the paper with assistance from HB and CB. The chemical analysis was done by AS and JG.

III Developed research questions and design together with HB and CB. Performed data collection. Did the statistical analyses and wrote the paper together with HB, AL and CB.

IV Developed research questions together with HB and CB and the design together with HB, OH and CB. OH performed the data collection. Did the statistical analyses and wrote the paper with assistance from HB, OH and CB.

V Developed research questions together with HB and CB. Performed the modeling and wrote the paper with assistance from CB and HB.

1 Introduction

"Climate, then, is the ever-present factor in insect life." (Uvarov, 1931)

Global mean air and ocean temperatures are increasing, snow and ice are melting, precipitation patterns are changing, and growing seasons are extending; there is a long list of the observed effects of the Earth's changing climate (IPCC, 2007). One suggested cause of these changes is the increasing amount of greenhouse gases that human activity has released into the atmosphere since the industrial revolution. Changes in the climate affect life on Earth, directly and indirectly. For insects, changes in temperature are thought to be the most important abiotic factor affecting their performance (Bale et al., 2002).

Pest insects are species that share common interest with people. When it comes to herbivores they feed on agricultural and forest crops and are of large economic importance for the society. It is generally believed that apart from invasive species, already established pests might become an increased problem in a warmer climate (Fleming & Candau, 1998; Tenow et al., 1999; Shaver et al., 2000; Logan et al., 2003; Bale, 2010). Insects could be expected to respond more than other organism groups because they are ectotherms, i.e. their body temperature is reliant on the surrounding temperature.

Several pest insects are outbreak species, which means that their populations normally exist at low density, but sometimes in some locations, populations undergo a rapid increase in density and become numerous. Why outbreak happens is connected to one of the big questions in ecology, i.e. "Why is the world green?", and how to prevent them a challenge in plant protection. With global warming, predictions of the success of pest insects in a future climate are especially asked for.

In this thesis, the link between population dynamics and climate is explored by studying how trophic interactions are affected by temperature. In order to make predictions about the future we need to understand the mechanisms and processes driving the population dynamics of pest insects. We need to consider all the life stages (Radchuck et al., 2013) and the interactions with other trophic levels, such as host plants and natural enemies (Tylianakis et al., 2008).

The study species in this thesis, the European pine sawfly, *Neodiprion sertifer* Geoffr. (Hymenoptera: Diprionidae), is a well-studied outbreak species in boreal pine (*Pinus* spp.) forests. The larvae feed on pine needles and during outbreaks the growth and economical value of pines is substantially reduced. The biology and trophic interactions affecting the dynamics of the species are well studied and it seems that both bottom-up, i.e. food quality, and top-down effects, i.e. natural enemies, are important. In this thesis the importance of these factors for the population dynamic of the sawfly is evaluated in a climate change perspective. The temperature effect on larval performance was studied in paper I, II and III, taking into account bottom-up and top-down effects. In paper IV the role of small mammals (voles) as important cocoon predators is considered as these are thought to control sawfly populations at low densities. In paper V the combined response to temperature by mortality factors in the larval and pupal stages is examined in a simple population model to assess the risk of outbreaks in a warmer climate. Improved knowledge of the relative role of bottom-up and top-down effects in the European pine sawfly may generate general insights for understanding the population dynamics of other herbivorous insects in a warmer climate.

1.1 A Changing Environment

1.1.1 Direct Effects of Temperature

Many studies have shown that an increase in temperature benefits insects in terms of increased rates of survival, growth and development (Uvarov, 1931; Atkinson, 1994; Bale et al., 2002). For example may a reduced time spent in early developmental stages be favorable for the survival, as these stages are typically exposed to predation (Bale et al., 2002). Moreover, increased temperatures at the beginning of the year imply an earlier start of spring and consequently an extension of the growing season. Under these circumstances, some insect species may benefit as they are able to have a second generation within a single year (Jönsson, 2009; Altermatt, 2010). Furthermore, increasing winter temperatures can decrease overwintering mortality and hence affect population sizes (Ayres & Lombardero, 2000; Bale & Hayward, 2010). Therefore, if an insect is considered to be a pest, problems associated with that particular species are anticipated to increase due to the expected increase in its abundance.

The potential of a population to rapidly increase in number is linked to individual fitness, i.e. the contribution of offspring to the next generation. For long lived species survival may have a larger impact on the population dynamics than fecundity, but for short lived species (shorter than a year) fecundity may be more relevant (Crone, 2001). For many invertebrate species there is a positive correlation between fecundity and body size (Stearns, 1992; Roff, 2002). Atkinson (1994) observed that size at maturity decreases with higher temperatures, which would mean lower fecundity. The reason for this change is not clear but can be partly explained by physiological effects. The mechanisms behind cell differentiation are thought to respond more strongly to increased temperature (through faster cell division) than the mechanisms responsible for cellular growth, resulting in a smaller average cell size and smaller individuals (Van der Have and de Jong, 1996). As a result of the same physiological mechanisms however, eggs produced at higher temperatures are more numerous but smaller in size (Ernsting and Isaaks, 1997). Hence, the impact of temperature on fecundity could results in females having more eggs despite a lower weight.

Generally, species in colder environments tend to be larger than their conspecifics in warmer environments, a pattern referred to as Bergmann’s rule (James, 1970). For insects, a converse Bergmann’s rule, i.e. a decreased body size at higher latitudes, is also suggested to be common (Blanckenhorn and Demont, 2004). That the same species differ in size depending on locality suggest adaptive plasticity. Smaller species with shorter development times tend to follow Bergmann’s rule, whereas larger species with longer development times typically follow the converse Bergmann’s rule. This pattern is probably explained by the constraining effects of a shorter season length at higher latitudes for species with long development times (Blanckenhorn and Demont, 2004).

When assessing and comparing different species responses to temperature we need to consider that species with different life strategies may respond differently. For species being able to have several generations per year, it may be a good strategy to grow fast at the expense of weight in warmer temperatures, such that the species can have more generations; but for species with only one generation per year resources are better invested in a larger body size (Fischer and Fiedler, 2002).

1.1.2 Indirect Effects of Temperature

The latest report from the IPCC (2007) states that ‘there is very high confidence, based on more evidence from a wider range of species, that recent warming is strongly affecting terrestrial biological systems, including such changes as earlier timing of spring events, such as leaf-unfolding, bird migration and egg-laying; and poleward and upward (altitudinal) shifts in ranges in plant and animal species.' An ecosystem shifting from one type to another is a major indicator of climate change and means that new areas become suitable for species to invade (Williams and Liebhold, 1995; Parmesan, 1996). It also means that new arriving species into an ecosystem may affect the native species, which could have a larger effect than the temperature rise itself (Berggren et al., 2009).

It is not only the spatial distribution of species that are affected by climate change, it also affects the temporal associations between species interacting at different trophic levels, particularly in the relative timing of coevolved or otherwise intimately-linked species (Parmesan, 2007; Van Asch, 2007; Dell et al. 2013). Synchrony in phenology between different species may be disrupted if an increase in temperature affects the phenology of one of the interacting species more than the other (Dewar and Watt, 1992; Jamieson et al., 2012). For many herbivores a mismatch with their host plant could be crucial for their survival, but a mismatch with natural enemies could enable the herbivore to escape control.

1.1.3 Temperature Affects Trophic Interactions

Species are embedded in systems with nearly endless biotic and abiotic interactions. To understand how population growth of a certain species responds to warming temperatures it may therefore be of larger importance to assess how the interactions are affected by increasing temperatures rather than the individual components (Dell et al., 2013). It means that higher temperatures will not only affect a pest insect but will also have an effect on its host plant and its natural enemies which makes predictions about insect population dynamics more complicated. It has been suggested that the same level of climate change will have different influences on plants, herbivorous insects and their natural enemies (Berggren et al., 2009; Jamieson et al., 2012) and that the relative importance of bottom-up processes (host traits) and top-down processes (natural enemies) in a system will determine the effect of temperature on the population dynamics. If regulatory processes respond to increased temperature in different directions the outcome might not be easily foreseen. Regulatory processes from below may become of greater importance if enhanced temperatures strongly affect plant quality, e.g. contents of nitrogen and secondary compounds. If increasing temperatures on the other hand have a strong effect on the efficiency of natural enemies, regulatory processes from above may become of increased importance. However, if the herbivore at the same time responds by developing faster due to an increased metabolism, the increased top-down effect could be reduced since the "window" for predation/parasitism decreases (Benrey and Denno, 1997). The net effect of climate change will depend on the relative strengths of bottom-up and top-down processes. The general finding seems to be that there is an increased sensitivity to climate change moving up through the trophic hierarchy, i.e. top-down effects strengthen and natural enemies can better control the herbivores (Voigt et al., 2003; Barton et al. 2009; O'Connor, 2009).

1.1.4 Thermal Adaptation

Species may vary in their response to increasing temperatures and to what degree may depend on their ability to adapt to new environments, either through rapid evolution or high plasticity (Gotthard and Nylin, 1995; Lande, 2009). An increase in temperature will therefore have a larger effect on species that have a restricted climatic range, because they are not pre-adapted to cope with temperature variation (Bale et al., 2002). A high level of genetic variability within a species can help buffer it against potential effects through the selection of appropriate genotypes (Harrington et al., 1999). Populations adapted to warmer temperatures tend to have higher temperature optima and seem to respond stronger to an increase in temperature than colder adapted populations. However, the level of species or system adaptability depends on both the size of the change and on the rate of the change (Leemans and Eickhout, 2004).

1.2 Pest Insects and Climate Change

1.2.1 Outbreaks

Herbivorous insects can cause severe damage by defoliating plants. The reason why the world stays green is that herbivorous populations are regulated by intraspecific competition (Denno et al., 1995), interactions with their host plants (Mattson and Addy, 1975) and predators, parasites and pathogens (Hairston et al., 1960). These factors respond to herbivore density and provide negative feedback loops as they reduce herbivore survival and reproduction. However, for reasons that are not well understood, populations sometimes escape these regulating control mechanisms and reach high densities. Most outbreak species have some degree of cyclic fluctuations in their densities which are probably driven by delayed density dependent factors (Myers, 1988). The frequency and intensity of an outbreak is often associated with exogenous factors, such as climatic variables (Martinat, 1987). Endogenous and exogenous factors however, cannot be totally separated because they are linked, e.g. higher temperatures may alter the efficiency of a predator or the quality of the food.

1.2.2 Occurrences of Outbreaks

The classical way of detecting causes to fluctuations in population densities is to look for correlation between population growth rates and possible explanatory variables. One way to evaluate the role of climate on species' population dynamics is to compare time series of population densities with weather data. Such correlative studies can give valuable insights in demography and patterns. Looking at a global scale temperature increases towards the equator and many studies have focused on whether biomass consumption by herbivores is larger in the tropics. In general, herbivory is thought to be more intense at lower latitudes. In a review by Coley and Barone (1996), the annual rates of herbivory were on average 7% in temperate forests compared to 11% in tropical forests. In the tropics, the more constant climate conditions are favorable to herbivores allowing them to feed throughout the year. When seasonality and percentage damage per unit time were included in the calculations, herbivory in the tropics was shown to be much less intense than in temperate regions (Adams et al., 2009). Studies have also shown that herbivory is more intense towards the north, which contradicts the general pattern (Adams and Zhang, 2009), while other studies show no differences between latitudes (Andrew and Hughes, 2005). However, to compare levels of herbivory on a global scale may be difficult because the different climatic conditions also have an effect on the other trophic levels, the plants and the natural enemies (Björkman et al., 2011). Even if changes in environmental factors, for instance, improve the quality of food from an individual herbivore's perspective it does not always increase the herbivore population, because the improved conditions also affect higher trophic levels (i.e. predators and parasitoids).

Long-term data is not always accessible, and even if it is, it does not tell us about the mechanisms behind the patterns observed. To understand the mechanisms behind the patterns discerned in correlative studies, we need to perform experiments. A drawback with experiments in the field is that they can be hard to evaluate since many unwanted factors interfere with the factors of interest and affect the results. Modelling can then be a good complimentary approach to understand more complex interactions. The optimal approach however, must be to combine field studies with lab experiment, long-term data and modeling (Jamieson et al., 2012). By doing so, there would be good chances to be able to predict outbreak risks in a future warmer climate.

2 Thesis aims

> "Regulation of populations must be known before we can understand and predict its behavior." (Hairston et al., 1960)

The general aim of this thesis was to estimate how increasing temperatures affect trophic interactions and from that evaluate future outbreak risks of the European pine sawfly in pine forests. The specific questions addressed in each paper were:

I How do multiple effects of temperature, day length and food quality affect the performance of sawfly larvae?

II How does temperature affect interactions between the sawfly larvae, its host plant and natural enemies along a latitudinal field gradient?

III Which role plays local adaptation on thermal reaction norms in the European pine sawfly?

IV How do temperature, local habitat and alternative food affect sawfly pupal predation rates by small mammals?

V What effect has different responses to temperature by different mortality factors on the population growth of the European pine sawfly?

3 The Study System

3.1 The European pine sawfly

The European pine sawfly, *Neodiprion sertifer* Geoffr. (Hymenoptera: Diprionidae) is an herbivorous insect, considered to be one of the major pest species in boreal forests. Its native range is in Eurasia but it is also common in North America, where it has been introduced. It exhibits rapid but irregularly occurring population explosions, so called outbreaks (Kolomiets et al., 1979; Pschorn-Walcher, 1965).

Most commonly it has a univoltine life cycle, i.e. one generation per year (Figure 1), but the life cycle can be extended over more than one year under unfavorable weather conditions. The eggs are laid in the autumn and the female insert them in pockets of the pine needles. The larvae are gregarious and feed primarily on older needles in the summer (June-July in Fennoscandia). Males pass four larval instars and females five. After finishing feeding, the larvae drop to the ground and spin a cocoon in the upper humus layer, often within the crown projection of the tree (Kolomiets et al., 1979). The larva pupates within a cocoon and adults emerge after about two months (Wallace & Sullivan 1963).

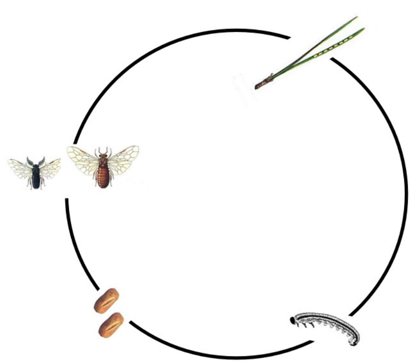

Figure 1. The life cycle of the European pine sawfly. Eggs are laid in pine needles in the autumn and hatch in the following spring. The larvae feed on the needles for about 1-2 months before pupating in the ground. Adults emerge after another 2 months, mate and die.

3.2 Trophic interactions

The sawfly is a frequently studied species and its biology and interactions with both its host plant, *Pinus* spp., and its natural enemies, primarily arthropods and small mammals, are well understood (Figure 2). Earlier studies have demonstrated the importance of plant quality (Larsson & Tenow, 1984; Larsson et al. 2000) and small mammals (Holling, 1959; Hanski, 1990; Olofsson, 1987; Kouki et al., 1998) to maintain the species at endemic densities. Thus, changes in food quality in combination with changes in densities or efficiency of natural enemies can affect sawfly population growth rate and the likelihood to it reaching outbreak densities.

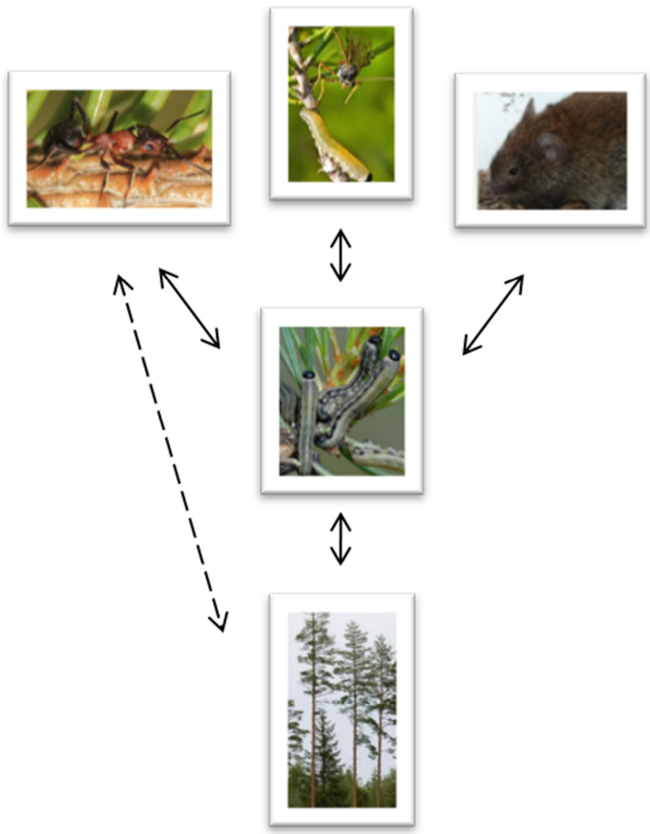

Figure 2. Some of the trophic interactions suggested to be important for the survival of the European pine sawfly. The larvae (middle) feed on pine needles (bottom). Predation by mainly arthropods (top left, here represented by an ant) and parasitoids (top middle) decreases the survival in the larval stage and predation by mainly small mammals (top right, a bank vole) further decreases the survival in the pupal stage. (photos: V. Manak, C. Björkman, and A. Zimmer)

3.2.1 Bottom-up processes

Plant nutrition, allelochemicals and morphological traits (e.g. the thickness of the epidermis and the number of resin ducts determining resin quantity) are important factors affecting herbivore performance (Schoonhoven et al. 2005). It is likely that such plant characteristics will change in response to climate change (Ayres and Lombardero, 2000). It is also possible that herbivore responses to increased temperatures may be affected by plant traits. Among plant traits, needle contents of nitrogen and secondary metabolites as diterpenes seem to be the most important, affecting sawfly larval performance both directly (Larsson and Tenow, 1984; Larsson et al. 1986) and indirectly (Björkman & Larsson 1991). The most obvious effect of nitrogen is probably in drought stressed pines. Pines stressed by drought have been shown to have increased nitrogen concentrations and decreased concentrations of defensive chemicals which make them more vulnerable to herbivory (Larsson and Tenow, 1984; White, 1984). However, a meta-analysis conducted by Koricheva et al. (1998) found that stressed trees in general did not increase insect performance. Since climate change is associated with warmer summer temperatures and in some locations summer drought, a concern about increasing risks of sawfly outbreaks in the future may be justified.

Needle content of diterpenes influences sawfly performance as the larvae use the diterpenes in their own defense against natural enemies (Eisner et al., 1974; Björkman & Larsson, 1991) (Figure 3). Larvae have been shown to have an improved survival when feeding on needles with high amounts of diterpenes but the cost of detoxifying the food comes as early increased mortality and longer developmental times (Larsson et al., 1986; Björkman & Larsson, 1991).

Figure 3. A sawfly defense droplet. (photo: C. Björkman)

There are only a few studies that have investigated how terpenoids are influenced by elevated temperatures. Sallas et al. (2003) and Holopainen and Kainulainen (2004) were able to detect higher concentrations of some foliage terpenes in Scots pine and Norway spruce under warmer conditions, but specific compounds responded differently in these studies, which makes it difficult to identify any general patterns. Higher levels of emissions of volatile organic compounds as temperature increases have been shown by other studies (e.g. Constable et al., 1999; Loreto et al., 2006). However, Constable et al. (1999) were unable to detect any changes in the amount of monoterpenes in the needles.

3.2.2 Top-down processes

Herbivore performance, in particular survival, is strongly influenced by natural enemies (Hairston et al., 1960). Because predators and parasitoids are also likely to respond to changing weather conditions, increasing temperatures may indirectly affect a herbivore's performance through the altered behavior of its enemies. All life stages of an insect can be susceptible to predation and parasitism. Predation by other arthropods, especially ants, can cause high mortality among many insect species whose larvae feed on plant tissue (Hawkin et al., 1997). Olofsson (1992) recorded unusually high mortality of newly emerged sawfly larvae due to ants during an exceptionally warm spring. Ant activity is known to increase with higher temperatures and ants can become more efficient pest regulators in a warmer climate (Virtanen and Neuvonen, 1999). Increasing temperatures are also likely to increase the reproductive ability of parasitoids (Colinet et al., 2007) and thereby parasitism rates.

Predators other than arthropods may have large influence on the population dynamics of insect herbivores. Unlike poikilothermic animals, homoeothermic animals are expected to decrease their metabolism as temperatures become warmer and thereby predation rates. However, indirect effects of temperature, such as drought and winter mortality, strongly influence the densities of mammals. Reduced predation rates caused by lower densities of mammals may have a larger effect on the insect population than reduced predation rates caused by decreased metabolism. The predator group that is thought to constitute the most regulating top-down force on the European pine sawfly is small mammals, e.g. shrews and voles, which predate on cocoons buried in the ground (Hanski and Parviainen, 1985; Olofsson 1987). Sawfly outbreaks are often related to forests growing on poor soils, which may suggest an interaction between climate and habitat on small mammal predation (Hanski & Parviainen 1985).

When an outbreak of the European pine sawfly ends, and the population density abruptly declines, virus may be a causal factor (Juutinen, 1967). The virus has several possible transmission pathways and some of these pathways may be affected by increased temperature and precipitation. The virus can be transmitted directly through contact with infected needles or larvae or indirectly by raindrops or insects moving within or between trees (Olofsson, 1989). If larvae eat more due to an increased metabolism, they will potentially be more exposed to virus. It is also possible that increased ant activity can spread virus more effectively, since ants are believed to be a vector, transferring virus from the ground to the foliage where the virus may be ingested by the larvae (Olofsson, 1989).

4 Methods

4.1 Studies using climate chambers

In paper I, II and IV, sawfly performance and survival were studied at different temperatures under controlled lab conditions in climate chambers. Two different temperatures were used; 15°C and 20°C. The lower temperature treatment (15°C) was chosen to represent the mean temperature during the larval feeding period at current conditions. The higher temperature of 20°C was chosen as it is within the span of the predicted increase in temperature. In Sweden, the mean annual temperature is expected to increase by 3°C-5°C by the end of the 21st century, compared to the period 1960-1990 (Lind and Kjellström, 2008). In paper I, the effect of photoperiod on larval performance was also assessed. The different day length treatments were chosen to reflect the light situation in the southern and the northern part of Sweden in the beginning of the summer, when the larvae are active. At this time of the year the days are longer in the northern parts, therefore a photoperiod of L18:D6 was used to represent light conditions in the south and L20:D4 to represent light conditions in the north.

4.2 Studies using a latitudinal gradient

Latitudinal studies are often used as a proxy for temperature gradients for the purpose of estimating performances of various species in relation to climate warming (De Frenne et al., 2013).

A latitudinal gradient (Figure 3) was used in paper II to study the effect of temperature on interactions between sawfly larvae, its host plant and natural enemies. Two sites at each of three different latitudes throughout Sweden was used for this purpose; Asa (N 57°11', E 14°47'), Faringe (N 60°00', E 18°18') and Vindeln (N 64°12', E 19°50'). Within the latitudes, the two sites were 500-

1000 m apart. The sites consisted of naturally generated *Pinus sylvestris* dominated forests of an age of 15 years. At each site 12-15 young pines in a manageable working size of approximately 2-3 meters were haphazardly selected. Eggs or newly hatched sawfly larvae were transferred to the experimental trees, either to a branch selected to host larvae within a fine-meshed cage or to a branch to host larvae without a cage. Caged and uncaged larvae were on the same tree whorl which has similar host qualities. The larvae normally stay on a branch as long as there is food available and it was therefore easy to keep track of the uncaged larvae. After five weeks, when larvae feeding on the open branch were in their later instars, they were also caged to prevent them from escaping from the tree. Once a week during the study period the larvae were visited and their survival and development were followed by counting the number of larvae in each larval stage. The disappearance of larvae in the cages was assumed to be due to host quality. The disappearance of the uncaged larvae was assumed to be due to both host quality and natural enemies. The difference in disappearance between caged and uncaged larvae was assumed to be due to predation.

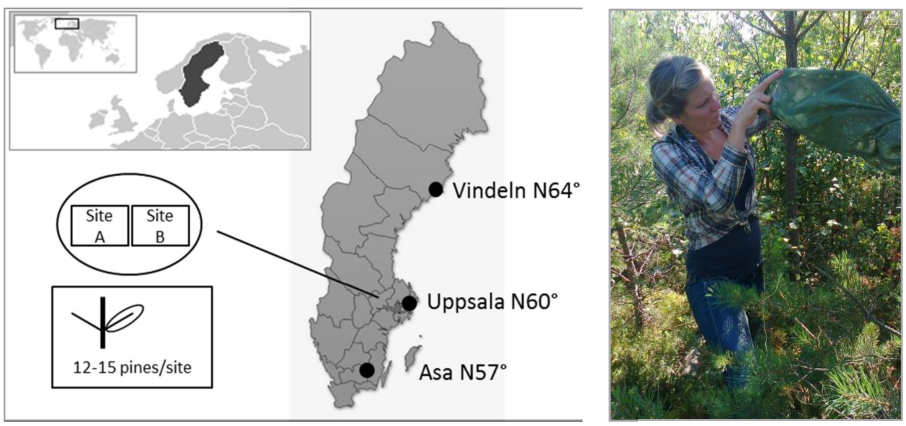

Figure 4. Map showing the study areas and an indication of the method used in the latitudinal gradient study. In each of the three areas (Asa, Uppsala and Vindeln), 12-15 pines at each of two sites (A and B) hosted larvae. Host quality effects on larval survival were measured for caged larvae and predation effects on larval survival for uncaged (exposed) larvae.

4.3 Bottom-up and top-down

In paper I direct bottom-up effects were studied by raising larvae in the laboratory on needles with two different levels of diterpenes collected in a pine seed orchard. In paper II the combined effects of bottom-up and top-down effects were studied in the field. Needles were collected from each individual tree and analyzed for content of nitrogen, carbon and diterpenes to assess bottom-up effects. Top-down effects, i.e. predation rates, are likely to be associated with both the efficiency and the abundance of natural enemies. The efficiency was measured indirectly through estimating the rate at which the larvae disappeared from the experimental pines. Since it is difficult to get an accurate figure on the abundances of predators we chose to instead measure the amount of pines and deciduous trees surrounding the experimental trees and refer to the hypothesis that natural enemies are more abundant in diverse habitats (Root 1973, Russell 1989, Jactel 2005).

When trying to assess climatic impact on a population it is important to consider all life stages. Previous studies have highlighted the importance of predation in the larval stage and the pupal stage. Therefore, the influence of temperature on larval survival was estimated in paper II and on pupal survival in paper IV. The relative importance of the stage specific mortality was assessed in paper V by a simple population model.

Predation rates of the small mammals were measured by offering one vole a fixed amount of cocoons and after a time, the number of eaten and intact cocoons was counted (Figure 5 left). Sometimes, small mammals relocate their food and eat it at a safer place and therefore number of lost cocoons was also counted. Pupal predation was estimated both in the laboratory and in a semi-natural field experiment. In the laboratory the purpose was to estimate predation rates in relation to temperature. In the field the role of microhabitat was evaluated for small mammal behavior and predation. Outdoor enclosures were manipulated to mimic open, barren habitats and rich, sheltered habitats (Figure 5 right) and pupal predation rates were measured over a number of feeding trials.

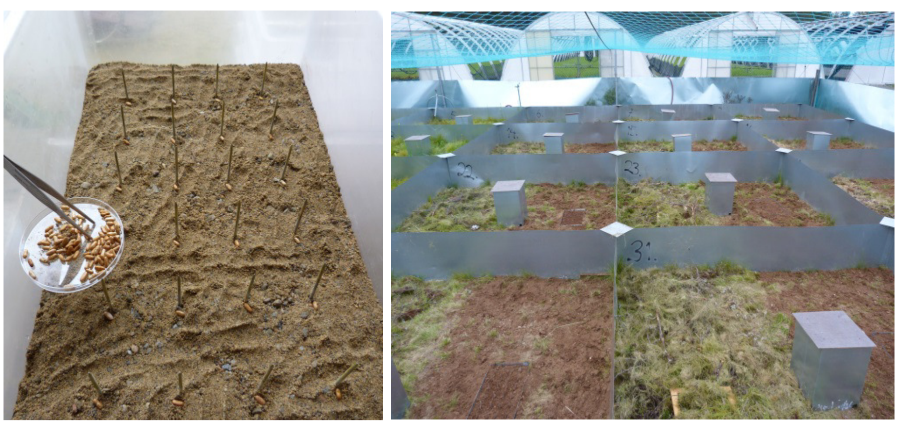

Figure 5. Method of measuring small mammal predation on sawfly cocoons in lab (left) and field (right) enclosures. (photos: A. Zimmer)

4.4 Origin of sawfly populations

Larvae and pupae of the European pine sawfly used in the studies were collected in areas where they could be found in sufficient numbers during the specific years. In 2010, eggs were collected in an outbreak area close to Skultuna (N59°46’, E16°16’), and in 2011 eggs were collected in a an outbreak area close to Mönsterås (N57°1’, E16°4’). Egg batches were collected by cutting off the branch on which the eggs where situated, protect it by a plastic bag to prevent the spread of potential virus infection and stored in 5°C in the lab. Pupae were collected by caging late instar larvae with a thin mesh material and allowing the larvae to pupate within the cage out in the field.

The response to temperature can be altered due to local adaptation which was studied in paper III. Larvae origin from the populations in Skultuna and Mönsterås were reared in different temperatures (15°C and 20°C) and their performance was estimated.

5 Results and Discussion

In this thesis the effect of temperature on trophic interactions is estimated to assess their relative importance for the population dynamics of the European pine sawfly in a climate change perspective. A basis to be able to predict the risk of future outbreak events is an understanding about factors behind present outbreak events. In the sawfly system the influence of food quality and predators seem to be the important factors determining population growth at low densities. Therefore interactions between the sawflies, its host plant and natural enemies were chosen to be studied further. Results derived from the studies allowed discussion about the impact of climate warming on future outbreak risks.

5.1 Top-down vs. bottom-up

Although both food resources and natural enemies play important roles in regulating natural populations (Hairston et al. 1960), their relative importance may differ depending on the spatial and temporal context. The relative strength of trophic interactions may also change due to a changing climate. More and more studies emphasize the importance of incorporation more than two trophic levels when determining species performance in relation to increasing temperatures (Tylianakis et al., 2013). In this thesis the effect of temperature was assessed on sawfly performance in relation to 1) food quality and 2) predation. How temperature may affect sawfly performance in relation to 3) anti-predator defense derived from the host plant and 4) development is discussed.

5.1.1 Food quality

When studying the effect of temperature on the interaction between the larvae and its host plant in the laboratory (paper I), there was no direct significance of food quality on larval performance. However, there was an unexpected indirect effect; the larvae showed reduced virus susceptibility when feeding on pines rich in diterpenes compared to larvae feeding on low diterpene pines. The direct effect of food quality was however evident in the field experiment (paper II) in which the results suggest that direct bottom-up effects will become of greater importance in a warmer climate, especially when it comes to diterpenes. The larval survival decreased as temperatures increased which could be related to an enhanced intake of toxic compounds. Even though sawfly larvae have evolved with pines for long times, it is known that larvae suffer increased early mortality when feeding on pines with high levels of resin acids (Larsson et al., 1986). The reason that bottom-up effects yielded such strong response on larval survival in the field and not in the laboratory may be due to the wider range of diterpene content among trees and a larger variation in temperature in the field. In the lab experiment there was a twofold difference in needle diterpenes among the pines used while in the field experiment the difference was 20-fold. Regarding variation in temperature, it is known that using constant temperatures in laboratory studies is not always accurate (Fischer et al., 2011). Constant temperatures do not reflect the large fluctuations that occur in the field, particularly during early summer when the experiment took place. Even though the overall mean temperature for the five weeks when the experiment was running was 14 °C, the minimum temperature registered was −4 °C and the maximum 39 °C. Since insect metabolism is known to be highly sensitive to even fast changes in temperature (Uvarov, 1931), the variation (and perhaps especially the warm temperatures) may explain the different outcomes between the lab and field experiments.

5.1.2 Predation

Different kinds of natural enemies, e.g. mammals and arthropods, are thought to respond differently to an increase in temperature because of fundamental differences in temperature response. The metabolism of insects increase with surrounding temperatures, therefore insects are likely to be more efficient predators in a warmer climate (Olofsson 1992, Virtanen and Neuvonen 1999, Voigt et al. 2003, Barton et al. 2009). The results from paper II showed a lower survival at higher temperatures, but the mortality seemed to be mainly caused by a bottom-up effect (Fig 6). However, there was a large variation in survival among the larvae exposed to natural enemies which may suggest that the effect of temperature on predators, and thereby the effect on larval survival, depended on spatial and temporal influences. For example is a high temperature during the early developmental stages likely to have a stronger reducing effect on larval survival than if high temperatures occur during the later larval stages.

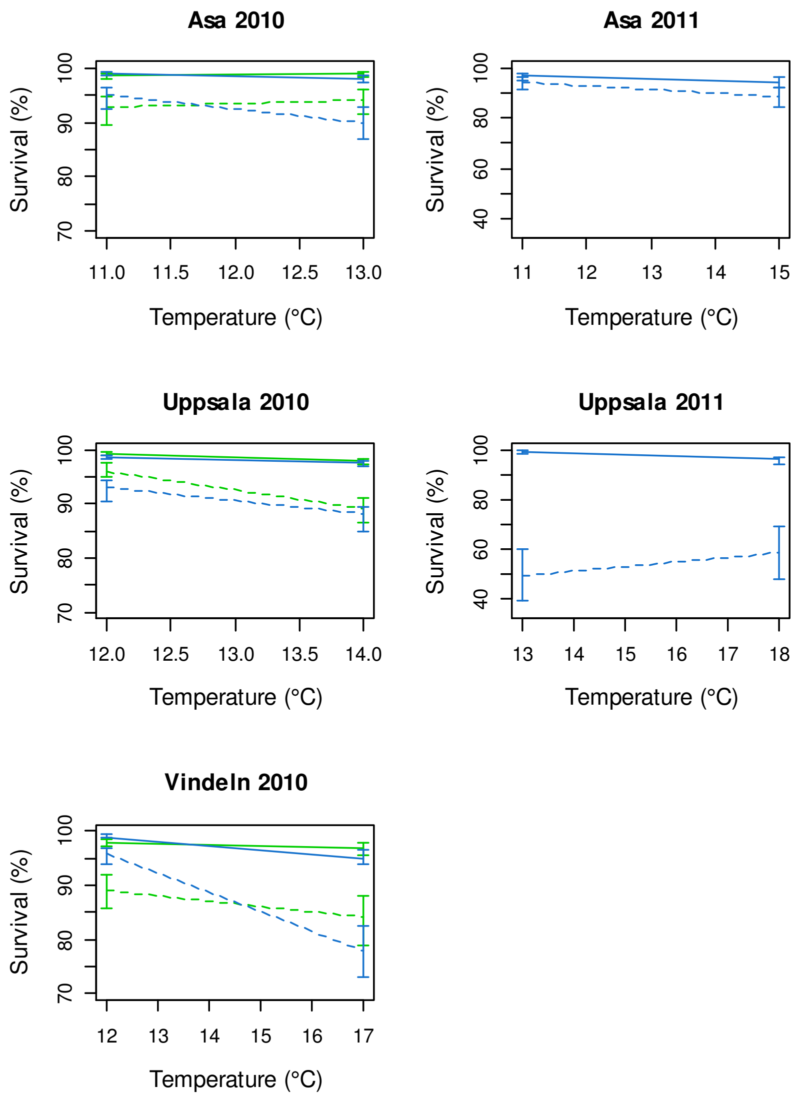

Figure 6. Weekly survival of sawfly (*Neodiprion sertifer*) larvae in 2010 (left column) and 2011 (right column) relative to temperature and needle diterpene content along a latitudinal gradient. All explanatory variables are set to their overall mean values except temperature and needle diterpene content which are set to their first and third quartile for each latitude and year. Note, therefore, that the scales of the x-axes differ. The grey lines represent the survival of larvae feeding on needles with low diterpene content (i.e. first quartile) and the black lines represent the survival of larvae feeding on high diterpene needles (i.e. third quartile). In 2011 diterpene content had no effect on larval survival and therefore there is only one line. Solid and dashed lines represent the survival of caged and exposed larvae respectively.

The reason for lower predation on large larvae is that they are better defended. Moreover, if high temperatures occur at the same time as some especially important developmental phase of the predator, e.g. an increased need for protein, it can also affect the outcome. The types of predators present at the actual site may also influence the survival, some predators are likely to be more sensitive to temperature than others. Ants for example seem to have an increased activity at warmer temperatures (Virtanen and Neuvonen, 1999) while spiders are less affected (Joern et al., 2006).

Mammalian predators on the other hand, are likely to decrease their food intake when temperatures increase because they need less energy to maintain their body temperature (Sibly, 1981). The results from paper IV suggest that predation on pine sawfly cocoons by voles is reduced at increasing temperatures. In the higher temperature, 20°C, the pupal predation was 20% lower than in 15°C.

Regulation of many herbivorous insect populations is attained by both types of predators, arthropods and mammalians. The actual effect of predation on the prey population dynamics at warmer temperatures will then be influenced by how the efficiency of the different types of predators is affected and on the relative importance of the predator types.

5.1.3 Defense

Many plants are chemically protected against herbivores by secondary compounds (Kliebenstein, 2004). The compounds could either work directly on the herbivore or indirectly by affecting herbivore natural enemies (Ode, 2013). In some cases, the herbivore has overcome the defense and uses it in its own anti-predator defense. An interesting question in a climate change perspective, not least in plant protection, is who will benefit the most of having a strong defense, the plant or the herbivore? In the case where the herbivores respond relatively stronger than their natural enemies and thereby increasing their survival, the defense of the plant become of increased importance as a bottom-up control. If predators and parasitoids on the other hand become relatively more active in higher temperatures, herbivore anti-predator defenses, such as sequestered plant secondary metabolites, might become of an increased weight for the survival of the herbivore. Results from paper II suggest that the plants will win the tritrophic battle in a warmer world. Among larvae feeding on low diterpene pine needles, a slightly higher temperature seemed to increase larval resistance against natural enemies, but a further increase seemed to decrease larval survival mainly caused by a bottom-up effect (Fig. 7). Among the larvae feeding on high diterpene needles the survival decreased at higher temperature. For larvae feeding on high diterpene needles the survival seemed to decreased faster among larvae exposed to natural enemies compared to the caged larvae as the temperature increased, suggesting a relatively stronger top-down effect. The increasing predation pressure, mainly on high diterpene needles, may indicate that the anti-predator defense of the sawflies coming from the diterpenes in the host may become less important for the survival of the larvae.

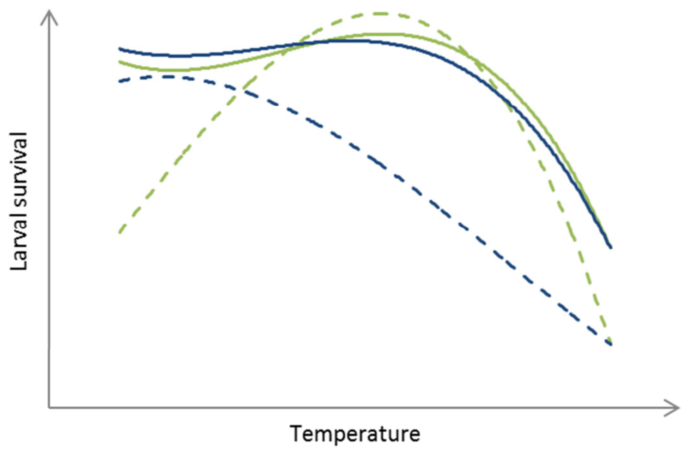

Figure 7. Hypothetical figure over larval survival in response to increasing temperatures compiled from data collected in a latitudinal gradient study of *N. sertifer* in 2010 and 2011. Larval survival is only affected by plant quality in terms of diterpenes (solid lines) or by natural enemies in addition to plant quality (dashed lines). Green and blue lines represent survival of larvae feeding on low and high diterpene pines respectively.

5.1.4 Development

Development was the trait most affected by temperature of the life history traits measured. In the laboratory, the larvae reduced their development times with 39% at the higher temperature (paper I and II). It suggest that larval development could be shortened in a warmer climate and thereby decreasing the risk of predation. Early instars seem sensitive to predation and if especially these will be shortened, then higher temperatures will enable the larvae to escape their predators. Since insect development is closely linked to temperature (Bale et al., 2002) it is commonly suggested that a faster larval development would decrease the predation basically because the time the larvae are exposed to predators and parasitoids is reduced (Benrey and Denno, 1997). This is not obvious from the field experiment however. Although a faster development seemed to increase survival, the effect was not stronger among the exposed larvae. From the study design it is difficult to evaluate how a faster larval development might have influenced larval mortality caused by predation. It may be that an increased survival due to a faster development was leveled out by a decreased survival due to more efficient enemies, which, in turn, may be the reason why there seemed to be no effect of temperature on predation. In 2011 larval survival was lower than in 2010 irrespective of a faster development which suggest that developing fast is not a general recipe to success. A fast development is probably important for decreasing the survival, but not of superior importance.

5.2 Outbreaks

Why outbreaks occur has puzzled ecologists for long time and even though not completely solved, several processes have been highlighted. One of the suggested causes to sawfly outbreaks, and for some other forest defoliating insects, is a release from small mammal predation pressure (Hanski and Parviainen, 1985). Outbreaks of the European pine sawfly are typically associated to warm and dry weather and to forests growing on poor soils (McLeod 1970; Kolomiets et al., 1979). The reason proposed is that small mammal densities are reduced under such circumstances (Hanski and Parviainen, 1985). Small mammals have been shown to have lower reproductive success and, as a consequence, lower population densities during warm and dry summers (Pankakoski, 1985; Lewellen and Vessey, 1998). The results from paper IV suggest that weather and habitat not only affect small mammal densities as proposed, it also affect small mammal behavior. Overall, more cocoons were predated in the sheltered habitat (mimicking a rich forest habitat) compared to the open (mimicking a poor forest habitat), but the effect size was possibly influenced by weather. At sunny, clear days pupal predation was much lower in open habitats as compared to sheltered.

5.2.1 Frequency of outbreaks

In general, our ability to predict future events such as insect outbreaks largely depends on how well we understand mechanistic interactions between different trophic levels and the dynamics of populations and communities, e.g. in response to climate change. Results from paper IV identify weather in combination with habitat potentially having a strong impact on the likelihood for outbreaks. Sheltered habitat is always a relatively good habitat for voles to feed in but weather (i.e. precipitation) influences the propensity of voles to enter open habitats for foraging. In combination with temperature-triggered

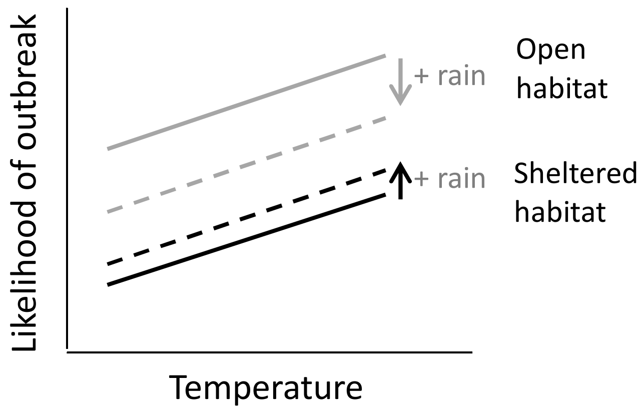

Figure 8. Hypothesized relationship between the likelihood of an outbreak of pine sawfly (Neodiprion sertifer) in relation to temperature in two types of habitat, assuming that small mammals are regulating the sawfly population at endemic levels. Predation rates by small mammals decrease at warmer temperatures as a result of a lower metabolism. The overall predation is higher in sheltered habitats compared to open. Note that rain has a different effect in the two habitats, as a consequence of higher small mammal activity in open habitats when the risk for being eaten by a predators (e.g. bird of prey) is low (e.g. when it is raining). The highest likelihood of sawfly outbreaks is in a future scenario with increasing temperature combined with less precipitation in open, less complex habitats.

physiological responses, such as altered metabolism, changes in behavior related to microhabitat could be a potential contributor to the onset of outbreaks of defoliators which pupate in the ground (Fig. 8). The results highlight the possibility that the contribution of small mammals to the control of forest pest insects at endemic densities may be weaker in a warmer climate.

If a forest stand is prone to outbreaks may be due to the proportion of trees with low and high levels of resin acids. Higher outbreak risks are often connected to stands with mainly trees low in resin acids, which may be due to a better survival among the larvae (Larsson and Tenow, 1984). Stands dominated by high resin acid trees have in general a lower outbreak risk. The results from paper II suggest that pine chemotype may play a less important role for the risk of outbreaks in a warmer climate since the difference in larval survival between trees low and high in diterpene levels decreased with increasing temperature (Fig. 7). The overall high larval mortality at higher temperatures reduced the densities to a level where the small mammals were able to control sawfly populations despite lower predation rates, implying lower risks for outbreaks in a warmer future climate (paper V).

When evaluating the performance and success of larvae in a warming climate it is also important to consider local adaptation (paper III). Larvae origin from eggs collected in Småland increased their weight when the temperature was enhanced in contrast to the larvae origin from Uppland, which suggests that populations adapted to local temperatures and day lenghts respond differently to warmer temperatures. If southern populations respond stronger to increasing temperatures then outbreaks might be more severe in the south compared to the north.

5.2.2 Distribution of outbreaks

Not only the frequency and intensity of outbreaks are interesting from a climate warming perspective, the spatial distribution is also of great concern. To understand population growth, not only survival is important, the number of individuals delivered into the next generation has an effect on population size. From paper V it seemed as female fecundity, i.e. the number of eggs laid of a single female, had a large impact on the number of sawflies. The effect of temperature affected female weight (correlated to fecundity) in paper I, but also photoperiod. A changing climate will of course not affect the day length, but if populations can spread into new areas, e.g. due to warmer winter temperatures, then individuals will be exposed to “new” day lengths. Even though the final female weight was reduced at the higher temperature, a longer photoperiod seemed to modify the response by not reducing the weight as much. Most likely, the explanation is that the larvae were adapted to a day length shorter than the one used in the experiment. This is important when evaluating how climate change can affect the spread of forest pest species. This means that the northward spread of phytophagous invertebrate species can be enhanced if females get larger and more fecund when they get exposed to a longer photoperiod than they are adapted to.

Figure 9. A pine defoliated by the European pine sawfly. The current needles are left which gives the pine the characteristic appearance. (photo: C. Björkman)

5.2.3 Individual performance vs. population performance

Individual-level processes may scale up to population-level responses and cause outbreaks when certain conditions are met. High female fecundity together with high survival may be an important mechanism behind rapid population increase during the very beginning of the epidemic phase in the population dynamics of an outbreak species. Thus, to be able to predict climate-related changes in population densities in insect outbreak species we need to know how outbreak insects respond to enhanced temperatures both as individuals and at a population level. In paper V the relative importance of density independent mortality factors in the larval stage was contrasted against density dependent mortality factors in the pupal stage. At 15°C population growth were faster on low diterpene needles, presumably pointing at the importance of plant genotype for outbreak risks as been suggested before (Larsson and Tenow, 1984). Increasing temperatures strongly affected larval mortality, presumably caused by food quality, but differences in needle diterpene content played a minor role for population growth at 20°C (Fig. 10). The increased larval mortality at the higher temperature prevented sawfly population growth through density-dependent regulation by the small mammals. Even though pupal predation was lower in the warmer temperature, this weaker effect did not increase the risks of outbreak events. The outcome of the model illustrated that even small changes in insect performance during their larval stage play a role in insect population dynamics.

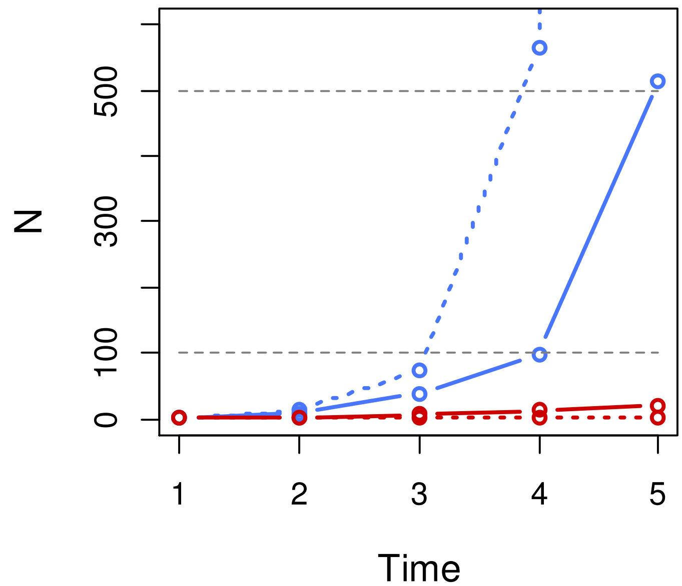

Figure 10. Population growth of *N. sertifer* in different temperatures and on different food qualities as predicted by a population model. Population density (N, number of pupae) is plotted against time. All populations start from endemic densities (approximately 1 pupa per m^2). When N exceeds 100, outbreaks densities are reached. When N exceeds 500, heavy defoliation takes place. The blue and red lines represent population growth at 15 °C and 20 °C respectively. The scenario from paper V in which needle diterpenes affect the survival at both 15 °C and 20 °C is presented. Dashed lines=low diterpenes and solid lines=high diterpenes.

5.3 Conclusions

The aim of this thesis was to study how temperature affects trophic interactions and to consider the effect of outbreak risks (Fig. 9). An often asked question is if there will be more outbreaks in a warmer future climate. It is a highly complex question. Based on the results from this thesis, outbreaks of the sawfly will occur less frequently. Both interactions with its host plant and natural enemies are affected by temperatures, and their relative importance for the survival of the herbivore probably depends on its temporal and spatial context. Irrespectively of the reason, larval mortality seems to increase with increasing temperatures. Pupal mortality is mostly due to predation by small mammals and pupal predation seems to decrease with temperature. It is difficult from the results presented here to assess the importance of the effect of temperature as compared with other factors affecting small mammal predation rates, e.g. is the local habitat important to consider. Nevertheless the decreased mortality in the larval stage seems to have a stronger impact on sawfly population regulation. Due to the low numbers of pupae, the small mammals sustain controlling the populations leading to fewer outbreaks.

The relevance of generalizing the results presented here into also other systems may be questioned. In general, it may be difficult since trophic interactions are both species specific and stage specific. Factors that are important in one system may not be of relevance in another. For example, the mortal effect on the sawfly larvae presumably caused by the host plant seemed to have a strong impact on the population dynamics, but may be irrelevant for other species. Nevertheless, the study elucidates the importance of investigating temperature effects on trophic interactions over entire life cycles and at different spatial and temporal scales. Furthermore it emphasizes the importance of using several different approaches and study designs.

6 Future Research and Challenges

Herbivores are exposed to both direct and indirect impacts of climate change. Currently, temperature is the best-explored direct influence of climate change on insect herbivores. Temperature influences phenology, life cycle, growth, developmental rates and distribution patterns, but the indirect effects of herbivores from responses by plants and natural enemies can also be as important. We have seen from previous research that different climate factors affect traits of plants, herbivores and natural enemies in different ways. Increased temperatures might have a positive effect on a specific trait, while elevated CO_2 levels may have a negative effect. It is impossible to predict what the outcome might be in general terms with respect to herbivory effects on plants, without evaluating the interactions of all these factors. As each species is regulated by many factors, and because these regulatory factors may differ among species, making general predictions about herbivory rates very difficult.

Latitudinal studies are often used as a proxy for temperature gradients for the purpose of estimating performances of various species in relation to climate warming. Some of the complexities involved with assessing climate change effects on tri-trophic interactions with this method are reflected in paper II, for example that interactions with temperature can change between sites and years. Latitudinal studies give us valuable information that can be difficult to achieve from other methods, but to be able to legitimately generalize from the results it is highly important to account for spatial and interannual variations in temperature by accurate replication over several years. From the studies behind this thesis it is obvious that location and time have a strong impact on trophic interactions. More studies, ideally running over large spatial and temporal scales, are needed before we can start formulating any more general conclusions about how changes in temperature will affect the relative impact of bottom-up and top-down processes for herbivore dynamics and outbreak risks.

The question this thesis has not being able to answer is if predators and parasitoids will become more effective in warmer temperatures. There are reasons to dig deeper into the results from paper II to understand the mechanisms behind the patterns described. The solution might be to do a combination of controlled experiments in the lab and in the field to understand if natural enemies become more efficient as predators and how defenses and developmental times affect the survival of the prey.

Several of the results point in the direction that survival is not always the most important trait to increase population size. How many eggs a female deliver in the next generation may have a large or even larger effect. Fecundity is known to be affected by several factors, among these being temperature and food quality. How the combined effect of temperature and food quality affect female fecundity would therefore be of great importance and interest to study.

Few studies have been done on small mammal predation in these aspects, especially under field conditions. Another important, but difficult task, is to establish the numerical and functional responses of small mammals in different forest types. One should study pupal predation in natural forest stands with varying density of small mammals to study the numerical response, and with varying density of sawfly cocoons to study the functional response. A successful experiment would give us valuable insights into the mysterious world of population regulation.

The focus of this thesis has been on the onset of outbreaks, i.e. what causes population densities to go from endemic to epidemic densities. However, looking into the other end, i.e. how temperature affect the factors suppressing high densities, would also gain knowledge of the intensity of outbreaks in relation to climate change and perhaps how to prevent them. Virus is a major cause to end outbreaks. It takes a few years for the virus population to build up but after that virus has radical effects on sawfly numbers. Paper I gave hints on that needle chemistry may affect virus susceptibility of sawflies, at least under lab conditions. It would be interesting to investigate how these results translate into natural population. And in warmer temperatures.

An immense challenge is how we can extrapolate insights from "snap-shot" experiments over the longer time scales of which climate change occur. Climate change will affect forest composition, pines distribution, pine growth, nutrients, and resins. Species can either adapt, through rapid evolution or high plasticity, or disperse. Species will also be involved in new interactions, and old interactions will change. All these aspects have to be considered when assessing the impact of climate change on life on Earth.

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Svensk populärvetenskaplig sammanfattning

Skadedjur benämns sådana djur som konkurrerar med mänskliga intressen. Ett exempel är växtätande insekter. Ofta behöver de vara många för att göra stor skada och fånga vår uppmärksamhet. Tänk på Egyptens gräshoppor, där hela himlen färgas svart och allt i deras väg blir uppätet. Men det behöver inte vara så bibliskt teatraliskt. Vem har inte äcklats av att hitta en halv larv efter att ha bitit en tugga i det där äpplet?

Klimatet har stor betydelse för djur och natur och påverkar bland annat arters överlevad och utbredning. Då klimatet på jorden blir allt varmare finns det anledning att undersöka hur insekter reagerar på detta. Insekter är särskilt påverkade av temperatur. Det beror på att insekter inte kan reglera sin kroppstemperatur utan den bestäms av den omgivande temperaturen. I Sverige förväntas temperaturen att öka mellan 2 till 5°C inom de närmaste 100 åren. Den högsta temperaturökningen kommer att vara under vintern. Hur detta påverkar insekter som lever i skogmiljö och klassas som skadeinsekter är alltså intressant även ur ett ekonomiskt perspektiv på grund av risk för produktionsförluster.

Den röda tallstekeln (*Neodiprion sertifer*) är en skadeinsekt i tallskogar. Larverna äter på tallbarren och kan ibland orsaka stor skada. Vissa år sker det en massförökning och på grund av larvernas stora aptit äts stora delar av barren upp vilket leder till en minskad tillväxt hos tallen. Anledningen till att det kan bli en massförökning är kopplad till de reglerande mekanismer som vanligtvis håller tallstekelpopulationerna i schack. Exakt hur regleringen går till är inte helt klarlagt, men smådäggdjur som äter pupporna, och på så sätt håller nere populationsstorlekarna verkar vara betydelsefulla. Smådäggdjur kan dock inte äta hur mycket som helst så om tätheten av puppor blir alltför hög undkommer många stekelpuppor smådäggdjuren och tallstekelpopulationen kan snabbt växa till sig. Antalet puppor bestäms också till stor del av larvöverlevnaden som bestäms dels på födokvalitén och dels på rovinsekter.

I den här avhandlingen undersöktes om den röda tallstekeln gynnas av varmare temperaturer och om vi därför kan förvänta oss mer skadeverkningar av denna i ett framtida klimat. Temperaturens betydelse för larvernas överlevnad och tillväxt undersöktes i lab- och fältförsök där särskilt samspel med födokvalité och naturliga fiender studerades. I klimatrum studerades om smådäggdjurs predation på puppor påverkades av temperatur. Vi använde två olika temperaturer, 15°C och 20°C, för att representera klimatet i nuläget och framtiden. Resultaten pekar på att temperatur är en viktig faktor som påverkar tallstekelns samspel mellan födokvalité och naturliga fiender på både larver och puppor. Dock kan det ibland finnas omständigheter som påverkar effekten. I regel var överlevnaden hos larverna lägre i de högre temperaturerna. Det kan bero på att när det blev varmare ökade larverna sitt intag av föda, och därmed även giftiga växtämnen från barren. Gruppstorlek och larvutvecklingsstadie påverkade även överlevnaden. Larvernas försvarsförmåga mot fiender ökar med ökad ålder och med ökad gruppstorlek, vilket kan vara en del av förklaringen. Om en ökad temperatur sammanfaller med de särskilt känsliga tidiga larvstadierna kan dödligheten bli stor. För puppöverlevnaden verkar det lokala habitatet ha stor betydelse. Även om puppredationen minskade i varmare temperaturer så kanske det bara har betydelse på öppna lokaler med få gömställen.

Om vi är intresserade av effekterna av förhöjda temperaturer på populationstillväxt hos skadeinsekter måste man veta vilka faktorer som är viktiga för överlevnaden men också hur dessa faktorer reagerar på temperatur och samspelar med varandra. Vad blir effekten på den totala populationstillväxten mellan år om dödligheten i larvstadiet ökar, men minskar i puppstadiet, för att bara nämna exempel på processer som inträffar under året. Resultaten från den här avhandlingen pekar på att den minskade larvöverlevnaden har störst betydelse för utbrottsrisken i ett varmare klimat. På grund av att antalet puppor hålls låg genom hög larvdödlighet kan smådäggdjuren bibehålla sin reglerande förmåga genom att äta tallstekelpuppor, och därmed minskar risken för utbrott.

Om man utifrån dessa resultat kan dra paralleller till andra växtätande insekter är svårt att säga. Ofta säger vi att man måste veta vilka reglerande processer som är viktiga i ett system innan man kan ge sig på och förutspå en framtida populationsutveckling. Det är dock möjligt att processer som har identifierats som viktiga under rådande förhållanden inte är viktiga i ett framtida klimat. Eller än värre, att vi inte bryr oss om att studera processer som vi inte tror är viktiga i dagens klimat. Dessa processer kan visa sig bli avgörande i framtiden. Att vissa processer kan ha olika betydelse i olika temperaturer blev vi varse från dessa resultat. Larvdödlighet anses inte vara särskilt viktigt för tallsteklars populationsdynamik, men verkar ha en överordnad betydelse i varmare temperaturer.

Att förstå hur effekter av ökande temperaturer kommer att påverka livet på jorden är en stor och viktig utmaning. Det vanligaste, och kanske enklaste, är att studera hur en ökad temperatur påverkar individer av en enskild art. Lägger man sedan till att studera en ytterligare faktor, kan den komma att påverka den första faktorn. Lägger man till fler faktorer är det möjligt att dessa påverkar samspelet mellan de två första. Den här avhandlingen fokuserar på den röda tallstekeln, men temperatureffekterna har främst studerats på samspelen i det system där tallstekeln ingår. Varmare temperaturer påverkar larvöverlevanden, men till exempel födokvalité kan påverka hur väl en organism klarar temperaturförändringar. Robusta förutsägelser om framtiden kräver studier som inbegriper hela system, eftersom naturen är en tämligen komplex plats där i stort sett allt samverkar. I den här avhandlingen har flera olika aspekter av temperaturpåverkan på tallstekelns väl och ve undersökts samtidigt, något som så vitt jag vet bara gjorts i ett fåtal studier av andra organismer.

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