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DEPARTMENT OF ARCTIC AND MARINE BIOLOGY

## **Cyclically outbreaking geometrid moths in sub-arctic mountain birch forest: the organization and impacts of their interactions with animal communities**

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*A dissertation for the degree of Philosophiae Doctor – October 2014*



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A dissertation for the degree of Philosophiae Doctor  
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Dedicated to everyone who has helped me along the way

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## Cover photos

Front cover – Larvae of *Epirrita autumnata* feeding on mountain birch during a moth outbreak in northern Norway. Photo: Moritz Klinghardt

Study I – Portrait of *Agrypon flaveolatum*. One of the most important larval parasitoid species in study I. Photo: Ole Petter Laksforsmo Vindstad

Study II – Carcass of an *Operophtera brumata* larva, standing over the cocoon of its killer, the parasitoid group *Protapanteles anchisiades*/*P. immunis*/*Cotesia salebrosa*. Photo: Ole Petter Laksforsmo Vindstad

Study III – Larva of the parasitoid group *Phobocampe* sp./*Sinophorus crassifemur* emerging from *Agriopis aurantiaria* host larva. Photo: Tino Schott

Study IV – An area of healthy mountain birch forest, representative for the undamaged sampling sites in study IV and V. Photo: Jakob Iglhaut

Study V – An area of mountain birch forest that has been heavily damaged by a moth outbreak, representative for the damaged sampling sites in study IV and V. The stems without foliage have all been killed by the outbreak. Photo: Jakob Iglhaut

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## List of original papers

The thesis is based on the following publications and manuscripts, which are referred to by roman numerals in the text:

### I

Vindstad OPL, Hagen SB, Schott T & Ims RA (2010) Spatially patterned guild structure in larval parasitoids of cyclically outbreaking winter moth populations. *Ecological Entomology* **35** (4): 456-463. doi:10.1111/j.1365-2311.2010.01201.x

### II

Vindstad OPL, Hagen SB, Jepsen JU, Kapari L, Schott T & Ims RA (2011) Phenological diversity in the interactions between winter moth (*Operophtera brumata*) larvae and parasitoid wasps in sub-arctic mountain birch forest. *Bulletin of Entomological Research* **101** (6): 705-714. doi: 10.1017/S0007485311000277

### III

Vindstad OPL, Schott T, Hagen SB, Jepsen JU, Kapari L & Ims RA (2013) How rapidly do invasive birch forest geometrids recruit larval parasitoids? Insights from comparison with a sympatric native geometrid. *Biological Invasions* **15** (7): 1573-1589. doi: 10.1007/s10530-012-0393-8

### IV

Vindstad OPL, Schultze S, Jepsen JU, Biuw M, Kapari L, Sverdrup-Thygeson A & Ims RA (2014) Numerical responses of saproxylic beetles to rapid increases in dead wood availability following geometrid moth outbreaks in sub-arctic mountain birch forest. *Plos One* **9** (6). doi:10.1371/journal.pone.0099624

### V

Vindstad OPL, Jepsen JU & Ims RA. Resistance of a sub-arctic bird community to severe forest damage caused by geometrid moth outbreaks. Manuscript

## Preface

In August 2007, during an excursion to field station of the University of Tromsø (UiT) in Skibotn, inner Troms, Professor Arne C. Nilssen (now retired from Tromsø museum) gave a talk on the biology and population dynamics of geometrid moths in northern Scandinavia. His crowd, which happened to include the author of this thesis, was a heterogeneous group of second-year bachelor students about to embark on their very first course in basic ecology. While the talk presented a system that was fascinating in many ways, I was particularly intrigued by the possibility that tiny parasitoid wasps could be key players in the spectacular dynamics of their geometrid hosts. The concept of predator-prey cycles in nature was not new to me, but I had never before encountered parasitoids in the role of the predator (which speaks volumes about my level of ecological education at the time). After the talk, my curiosity got the better of my shyness, and I approached the speaker to ask if any kind of research on moth-parasitoid interactions was being conducted in northern Norway at the time. I was pointed in the right direction, and I soon found my way to the moth ecology (Birchmoth) group at UiT, where I received a very warm welcome (and a topic for a Bc. thesis). As it turned out, I stayed with the Birchmoth group throughout the rest of my education.

7 years after my first encounter with geometrids, I find myself the author of 3 papers on the very same parasitoids that so intrigued me during Arne's talk (Study I – III). Not only that, but I have become involved in research on many other topics related to geometrid dynamics, most notably the ecosystem consequences of their devastating outbreaks. The results of some of that research are also included in this thesis (study IV and V).

The above can be read as a touching story of how small events can have large consequences for a person's life. However, it also begs the question of whether I would still have approached Arne to inquire about parasitoids if I knew what I know today (or if I would just have headed straight for that cup of tea I had been planning, and probably ended up in freshwater ecology instead). My spontaneous answer is "yes". More interestingly, the answer remains the same after recalling endless taxonomic frustrations with parasitoids, noisy data sets, studies with fuzzy conclusions and months of work spent on projects that failed for various reasons. My career as an aspiring scientist has been neither easy nor glamorous, but then again, I had never expected that it would be. I never expected that nature would provide me with clear-cut answers or that I would make ground-breaking discoveries. And I never even dreamt of solving the mystery of the population cycle, that holiest of ecological grails. Not for any extended periods of time anyway. What I *have* always hoped for, is to be able to contribute to the growing pool of knowledge that is giving us a progressively better understanding of the Fennoscandian birch-moth system. Looking back now, I realize that the contributions I have been able to make, in spite of being modest, have far exceeded my initial expectations. I hope the reader will agree with me that the studies in this thesis, in spite of their limitations, have taught us at least some things that we did not know beforehand.

Ole Petter Laksforsmo Vindstad  
Tromsø, October 2014



## Abstract

In sub-arctic mountain birch forest in northern Fennoscandia, the 2 geometrid moth species *Epirrita autumnata* (autumnal moth) and *Operophtera brumata* (winter moth) show high-amplitude population cycles with regular 10-year periodicity. During some population peaks, moth populations attain outbreak densities and cause region-wide defoliation and mortality of mountain birch. The severity and duration of moth outbreaks presently appears to be increasing, owing to climate-driven range-expansions of both native and novel (see below) moth species in the system.

The causal mechanisms of moth population cycles have been widely studied, with research focusing on the role of parasitoids during the last decade. This research has focused on total parasitism rates and has paid little attention to parasitoid community organization and its consequences for the functionality of parasitoid communities. Study I – III of this PhD project addressed this knowledge gap for larval parasitoids, which have received more attention than other parasitoid guilds in the research on parasitism the birch-moth system.

Study I explored the possibility of stochastic extinction-recolonization dynamics – induced by fluctuations in moth host populations – as a driver of the spatial distribution patterns of different larval parasitoid species. The study documented large-scale spatial segregation in the prevalence of different parasitoid species in *O. brumata*, which may have resulted from stochastic extinction-recolonization processes. However, the alternative explanation that the observed patterns were caused by spatial gradients in habitat characteristics could not be rejected. Further, the study found that the magnitude of total larval parasitism rates at a given location was independent of which parasitoid species was locally dominant.

Study II mapped out the phenology of attack of the larval parasitoid species of *O. brumata*. The study showed that the attacks of different parasitoid species followed each other in a successional manner throughout the larval season, so that all larval instars were attacked by at least 1 parasitoid species. The study argued that this phenological diversity within the larval parasitoid guild would reduce the probability of climate-induced phenological mismatches between larvae and many parasitoid species within a single season, hence buffering total larval parasitism rates against stochastic climatic variation.

Study III compared larval parasitoid species richness and prevalence rates among *E. autumnata*, *O. brumata* and *Agriopsis aurantiaria* (scarce umber moth). *E. autumnata* is native species to the mountain birch forest, while *O. brumata* and *A. aurantiaria* invaded this system by range-expansion approximately a century and 15 years ago, respectively. The study found that *E. autumnata* and *O. brumata* hosted similar numbers of larval parasitoid species in the mountain birch system, while the larval parasitoid guild of *A. aurantiaria* was strongly species-impooverished compared to the 2 other moth species. Based on this, the study argued that invasive moth species take at least a century to acquire a larval parasitoid guild with native levels of species richness in the mountain birch forest. Total larval parasitism rates were similar among all 3 moth species, suggesting that invasive geometrid moths do not enjoy release from larval parasitism in the mountain birch forest, despite having species-impooverished larval parasitoid guilds.

Taken together, study I – III pointed towards high levels of functional redundancy among larval parasitoid species in the birch-moth system. This could act to stabilize total larval parasitism rates in space and time. The studies also highlighted that it is necessary to resolve numerous uncertainties surrounding parasitoid taxonomy in order to make further progress in parasitoid community ecology in this system.

While the causes of moth population cycles and outbreaks have been intensively studied, comparatively little attention has been paid to the ecological consequences of moth outbreaks. Some of the most serious knowledge gaps relate to the consequences of outbreak-induced forest

damage for animal communities in the mountain birch ecosystem. Study IV and V addressed this issue by investigating the short-term responses of saproxylic (i.e. associated with dead wood) beetles and passerine birds, respectively, to an outbreak that had caused widespread mortality of birch forest 3 – 5 years before the outset of the studies.

Study IV showed that the proportion of obligate saproxylic species in the beetle community was only about 10 % higher in damaged than undamaged birch forest. The study thereby indicated that saproxylic beetles have limited ability to respond numerically to the enormous amounts of dead wood that are generated by moth outbreaks. Climatic constraints on beetle activity and diversity in my sub-arctic study region, and species-specific preferences for dead wood in certain stages of decay, were suggested as explanations for the weak response of the saproxylic beetle community. The study raised the possibility that saproxylic beetles, owing to weak numerical responses, may play a minor role in wood decomposition in the immediate aftermath of moth outbreaks. This highlighted that there is need to learn more about the role of microbial wood-decomposer communities after outbreaks.

The results of study V mirrored those of study IV, by indicating a weak response of bird communities to outbreak-induced forest damage. In 1 of my 2 main study areas (Kirkenes), the total abundance of birds was roughly 25 % lower in damaged than undamaged forest. Bird species-richness showed an even smaller reduction in damaged forest. Meanwhile, in the other study area (Tana), there were no consistent differences in bird abundance or richness between damaged and undamaged forest. The observed reduction in bird abundance in damaged forest in Kirkenes was mainly driven by the Willow warbler (*Phylloscopus trochilus*); a foliage gleaning species which may have suffered loss of foraging habitat due to outbreak-induced mortality of trees. By documenting a weak response to forest damage in the studied bird community, study V suggested that this community has a high degree of resistance to the habitat disturbance caused by outbreaks. This may be explained by the fact that many of the studied bird species are habitat generalists. It was also suggested that bird populations in the outbreak area might have been maintained by surviving trees and by standing birch trunks, which could serve to maintain the vertical structure of the forest habitat.

Study IV and V were limited in their conclusions by their short-term time perspectives. Thus, both studies highlighted the need for more long-term research on the responses of animal communities to outbreak-induced forest damage in the mountain birch ecosystem.

# 1. Introduction

## 1.1. Introduction to insect outbreaks and population cycles

### 1.1.1. *Insect outbreaks and population cycles as disturbance factors in forest ecosystems*

Forest ecosystems are subject to a range of natural disturbance factors that operate on large spatial scales, including fire (Bond & Keeley 2005), windthrow (Bouget & Duelli 2004) and disease (Weed *et al.* 2013). However, in terms of the size of the area that is affected, insect outbreaks are by far the most important disturbances in many forests. Outbreaks can damage and kill forest vegetation across thousands of square kilometres (Barbosa *et al.* 2012), and are sometimes massive enough to be detected from space by means of satellite images (Jepsen *et al.* 2009a; Rullan-Silva *et al.* 2013). Indeed, few ecological processes operate on larger spatial scales. Outbreaks can inflict great economic loss if they occur in economically valuable forest (Dale *et al.* 2001; Chang *et al.* 2012), and can cause conspicuous changes to forest ecosystems that most people find unappealing (Sheppard & Picard 2006). This includes both short-term changes, like extremely high densities of insects in the forest during outbreak-years (Fig. 1A, B), and long-term changes, like high incidence of dead or damaged trees in the forest (Fig. 1C-E). Thus, outbreaks are often viewed as ecological disasters (Flint 2006), and preventing or rapidly terminating them is generally seen as desirable.

An intriguing characteristic of some outbreaking insect species is that their population densities wax and wane repeatedly with more or less regular time intervals. Such population cycles are particularly common in outbreaking Lepidoptera species. Indeed, some of the most prominent examples of population cycles in the world are found among forest lepidopterans [e.g. Berryman 1996, Ruohomäki *et al.* 2000, Esper *et al.* 2007 and Franklin *et al.* (2014)]. For simplicity, I hereafter refer to insects that display outbreaks and (in some cases) cycles as “outbreaking and cyclic insects” (OCIs).

### 1.1.2. *General trends in the research on insect outbreaks and population cycles*

Given the economic and aesthetic costs of insect outbreaks, and the desire to control them if possible, it is unsurprising that the reason why outbreaks occur in the first place – i.e. their *causes* – has long been a topic of both public interest and scientific research. The question of why populations cycle is very prominent in ecology in general (Kendall *et al.* 1999; Turchin 2003), and it tends to dominate the research agenda for cyclic insects; if there is research on a cyclic insect species, there is a good chance that the cause of the population cycle is the motivating question. When insects display both outbreaks and cycles, research on the causes of outbreaks and cyclicity often become intimately linked, since both are concerned with the determinants of population growth and decline in the focal insect species [see reviews and case studies on insect outbreaks and population cycles in e.g. Berryman (1988), Berryman (2002), Barbosa *et al.* (2012) and Myers & Cory (2013)].

Studies on the causes of outbreaks and cyclicity are most often concerned with interactions between OCIs and environmental factors that are hypothesised to affect OCI population dynamics. The factors that have received the most attention are climate and the food plants and natural enemies of the OCIs. The influence of cyclic extra-terrestrial phenomena, most notably sunspots, has also been studied. Although the effects of extrinsic factors have received the most attention, there has also been much research on factors that are intrinsic to OCI populations, including maternal effects and immunocompetence. Finally, there has been many studies on the specific biology of OCIs, to identify traits that might explain why these species reach outbreak densities. Although definitive answers to why insect populations show cycles and outbreaks have generally remained elusive, this research has made many valuable contributions both to the understanding and management of specific systems and to the development of ecology in general. For instance, the management of gypsy moth and bark beetles – some of the most

## Box 1. Terminology

**Insect outbreak** – An event where an insect population attains sufficiently high density to cause substantial damage to its food plants, usually over a large area.

**Cyclic population** – A population that fluctuates between high and low densities (i.e. population peaks and troughs) with a regular time interval. The peak of an insect population cycle may represent an outbreak, but this is not necessarily the case (i.e. peak population density may not be high enough to substantially damage food plants).

**Population cycle period** – The time interval between successive peaks (or troughs) in a population cycle.

**Population cycle amplitude** – The difference in population density between peaks and troughs in a population cycle.

**Community** – An assemblage of populations of 2 or more species, occupying the same geographical area at a given time.

**Guild** – A group of species that utilize the same resources by means of a similar mechanism.

**Complementarity** – A situation where the species in a community partition resources, so that the overall rate of resource utilization by the community increases with increasing number of species.

**Functional redundancy** – A situation where several species in a community carry out the same function, so that the community will retain its ability to perform that function even if some of the species are lost

**Resistance** – The ability of a community to remain essentially unchanged in the presence of disturbance.

**Metapopulation** – An assemblage of populations (i.e. subpopulations) of a given species which occur in spatially discrete habitat patches, but are linked by dispersal of individuals. Subpopulations are unstable and prone to extinction, but a subpopulation which goes extinct can be re-established by dispersing individuals from other subpopulations.

**Saproxyllic organism** – An organism that is dependent, during some part of its life cycle, upon the dead or dying wood of moribund or dead trees, or upon wood-inhabiting fungi or the presence of other saproxyllics.

**Phenology** – The timing of life cycle events in plants and animals, in relation to environmental factors.

destructive forest pests in north America – has been aided by an understanding of their outbreak dynamics that has been built up through many years of research (Werner *et al.* 2006; Tobin *et al.* 2012). More generally, OCIs have served as model systems for empirical and theoretical research on the causes of population cycles and outbreaks, which also occur in several other taxa (Berryman 2002; Turchin 2003; Esper *et al.* 2007; Barbosa *et al.* 2012). This research has advanced our understanding not only of outbreaks and population cycles in themselves, but also of general ecological topics like density dependence, predator-prey interactions and inducible defences in plants.

The preoccupation with identifying the causes of insect outbreaks and cycles has not been without downsides. Arguably, this somewhat one-sided research agenda has diverted attention from other important ecological questions that relate to OCIs. This has left many gaps in our understanding of the role that OCIs play in the ecosystems, and of the ways in which they interact with other species. Below, I review some of these knowledge gaps and explain the importance of addressing them.

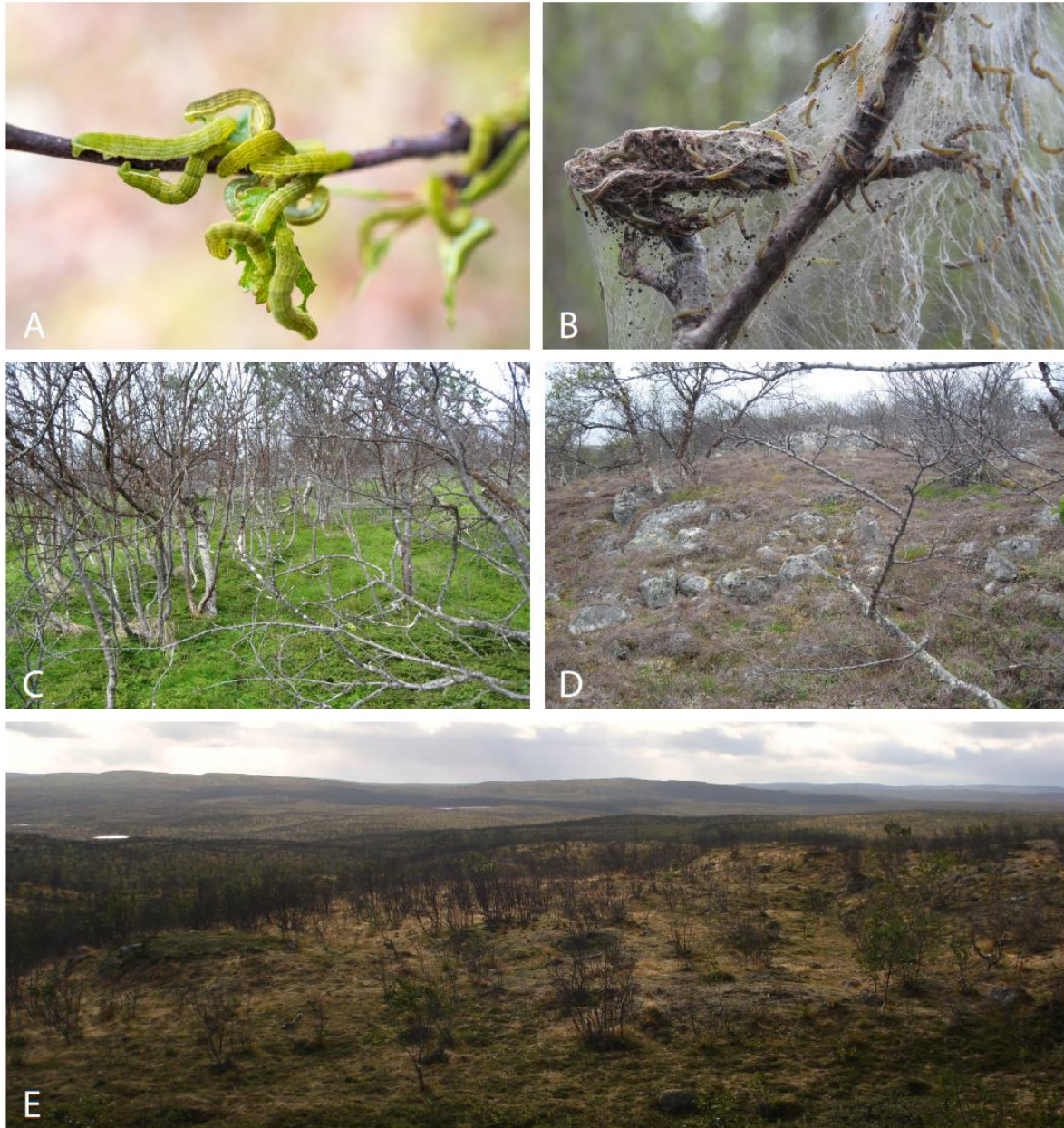
## **1.2. Ecological consequences of insect outbreaks and cycles: extensive but understudied**

### *1.2.1. Potential consequences of insect outbreaks for forest ecosystems*

Probably the most important knowledge gaps that relate to OCIs at the moment concern the ecological *consequences* of their fluctuating population dynamics. When outbreaks occur, even superficial observation makes it clear that they can have extremely pervasive impacts on forest ecosystems. Obvious effects include damage and even state-shifts in vegetation communities (Kenis *et al.* 2009; Gandhi & Herms 2010; Jepsen *et al.* 2013; Karlsen *et al.* 2013). More subtle effects include changes to nutrient cycling regimes (Kaukonen *et al.* 2012; Yang 2012) albedo (Maness *et al.* 2012) and carbon sequestration (Kurz *et al.* 2008; Heliasz *et al.* 2011). The impacts of outbreaks on the productivity and recovery of the treelayer after outbreaks has received much attention, especially in economically valuable forest [see Amoroso *et al.* (2013), Perot *et al.* (2013) and Johnson *et al.* (2014) for recent examples]. Meanwhile, other effects have undergone relatively little research and knowledge about them in many systems is largely based on anecdotal observations or is lacking altogether. This leads to much uncertainty about post-outbreak ecosystem dynamics, including successional trajectories, recovery rates and ecosystem functionality. This, in turn, represents a liability for the management of ecosystems in the aftermath of outbreaks. This is a growing concern. Over the last decade, evidence has been accumulating that on-going climate warming is causing an increase in the severity, duration and spatial extent of insect outbreaks in several systems (Jepsen *et al.* 2008; Weed *et al.* 2013). Thus, the need to fill the many knowledge gaps relating to the ecological consequences of outbreaks is becoming increasingly pressing.

Some of the key uncertainties that need to be addressed concern the consequences of outbreaks for wildlife communities. Via their dramatic impacts on forest vegetation, outbreaks may affect a wide range of forest-dwelling species. Outbreaks can have negative impacts on herbivores that feed on the same vegetation as the outbreaking insect species (Kenis *et al.* 2009; Yang 2012). Other herbivores may benefit because their food plants are facilitated by outbreaks. For instance, plant species in the understorey may grow more abundant due to improved availability of light if an outbreak reduces canopy cover (Eschtruth *et al.* 2006; Gandhi & Herms 2010). This may benefit herbivores of the understorey vegetation. Outbreak-induced changes to forest vegetation may also alter the physical structure of the habitat for many species. Birds that shelter and nest in tree canopies may suffer habitat loss due to outbreak-induced tree mortality (Rabenold *et al.* 1998; Gale *et al.* 2001; Becker *et al.* 2008). Meanwhile, mortality of trees may benefit species that are associated with disturbed and early successional habitats (Bell & Whitmore 1997; Canterbury & Blockstein 1997). Indeed, the most severe outbreaks can change forest habitats to the extent that few biological taxa can be expected to go unaffected. However,

as is true for the consequences of outbreaks in general, these impacts are often poorly documented and understood. Exceptions to this rule do exist. Most notably, there has been substantial research on the response of bird communities to outbreak-induced forest damage in north-American systems (see references above). Even so, there is a general lack of knowledge about the response of wildlife communities to outbreaks. This is a serious knowledge gap, since the post-outbreak dynamics of an ecosystem will partly depend on how wildlife communities in the system respond to the outbreak.



**Figure 1.** Scenes from an outbreak of geometrid moths in northern Norway. Larvae of both *E. autumnata* (A) and *O. brumata* (B) can reach extremely high densities during outbreak years. Moth outbreaks can have pervasive impacts on the forest vegetation, causing mass mortality of both mountain birch (C) and several plant species in the field layer (D), mainly crowberry and bilberry. E hints at the spatial scale of the destruction wrought on the forest. The blackened trunks of birch trees killed by the outbreak can be seen stretching for miles and miles towards the horizon. Photo: Moritz Klinghardt (A) and Ole Petter Laksforsmo Vindstad (B-E).

An aspect that is fraught with particular uncertainty is the dynamics of saproxylic (i.e. associated with dead wood) decomposer communities in the aftermath of outbreaks. The enormous amounts of dead wood that are left by outbreaks are a potential resource for saproxylic organisms. However, saproxylics must mount a strong numerical response to this superabundant resource if it is to be effectively colonized and exploited. Failing this, exploitation of the dead wood might become very slow, and the degradation process could be retarded. This, in turn, would have implications for the turnover of nutrients and materials that are bound up in the wood. The response of saproxylic insects may be of particular importance in the immediate aftermath of outbreaks, because these insects facilitate both the entry of microbial decomposers into dead wood and the subsequent microbial decomposition process (Muller *et al.* 2002; Stokland *et al.* 2012). Beetles are a key group in this respect, since they are the most diverse and abundant group of saproxylic insects. At present, very few studies have investigated the numerical responses of saproxylic insects to the superabundant dead wood left by insect outbreaks [but see Müller *et al.* (2008), Müller *et al.* (2010) and Lehnert *et al.* (2013)]. Further research on this topic is thus needed to improve understanding of post-outbreak decomposition dynamics.

### *1.2.2. Potential consequences of insect population fluctuations for natural enemy communities*

The fluctuating population dynamics of OCIs affect other species not only via the forest damage caused by outbreaks. By virtue of their abundance, OCIs often constitute an important food resource for a wide range of natural enemies, including insectivorous birds, mammals and invertebrates (Hogstad 2005; Eveleigh *et al.* 2007; Marcello *et al.* 2008; Drever *et al.* 2009; Vandegrift & Hudson 2009). These enemies have to cope with an extremely unstable food supply, experiencing a superabundance of food during OCI population peaks or outbreaks, and a collapse in this food resource when OCI populations decline. The consequences of these resource fluctuations for enemies must be expected to vary depending on enemy functional characteristics. Enemy species with a generalist diet may be relatively little affected by OCI fluctuations because they can exploit alternative prey species when OCI populations collapse. Meanwhile, enemies with high dispersal capability may adopt a nomadic lifestyle, roaming across large areas in search of high-density OCI populations, and settling to breed only where such populations are available (Lindström 1987; Hogstad 2000). However, enemy species that specialize on OCIs and have low dispersal capability lack these options for dealing with OCI population collapses. Accordingly, these enemies must be expected to fluctuate in tandem with their OCI resource populations.

Numerical responses of specialist enemy populations to OCI population fluctuations have been documented in many systems, [e.g. Turchin *et al.* (1999), Venier *et al.* (2009) and Klemola *et al.* (2010)]. These responses of specialist enemies have usually been interpreted in terms of possible enemy impacts on OCI population dynamics (further discussed below). This ties in with the general focus on identifying drivers of OCI population dynamics (section 1.1.2). Meanwhile, few studies have taken the opposite perspective, and asked about the consequences of unstable OCI dynamics for enemies. This is rather surprising, since it is easy to imagine that these consequences could be profound. OCI populations can drop to extremely low densities when they collapse. As a result, specialist enemy populations may be hard pressed to maintain themselves and could even suffer local extinction in some areas. This could conceivably result in a situation akin to metapopulation dynamics (Hanski 1998), where local populations of specialized enemies undergo repeated episodes of extinction and re-colonization. Enemy extinctions, if they occur, are likely to happen in a largely stochastic manner, since small populations can be highly vulnerable to stochastic environmental and demographic variation (Begon *et al.* 2006). As a result, the distribution of different enemy species across a landscape

may also become subject to considerable stochastic variation and show much turnover over time.

It is reasonably well documented that insect predator-prey systems can persist as metapopulations in the field (Lei & Hanski 1998; Weisser 2000; Cronin & Reeve 2014), and it appears to be a general pattern that enemies are more prone to extinctions than their prey in these situations (Cronin & Reeve 2005). However, the possibility of such dynamics in enemies of OCIs have received very little attention, despite the propensity towards extinction-recolonization dynamics that may exist in such systems. This knowledge gap is troubling because the spatiotemporal dynamics of enemy communities may have considerable bearing on OCI-enemy interactions. In particular, if extinction-recolonization dynamics causes the occurrence of different enemy species to vary in space and time, enemy impacts (i.e. predation or parasitism rates) on OCI populations may also become subject to much spatiotemporal variation. This, in turn, may feed back to OCI population dynamics and influence, for example, the probability that an outbreak develops in a given area at a given time.

### **1.3. The role of natural enemies in insect outbreaks and cycles: the need to consider enemy community organization**

#### *1.3.1. General trends in the research on OCI-enemy interactions*

Section 1.2.2 highlights a general tendency in research on OCI-enemy interactions, namely a lack of attention to enemy community organization. An enormous number of studies have explored the role of natural enemies in insect population cycles and outbreaks, but conclusions about enemy impacts have been elusive in most systems. This may, to some extent, be related to the manner in which this research has been conducted. Most studies have quantified predation or parasitism rates on OCI populations and used the results to infer possible roles of enemies in driving OCI population dynamics. Unfortunately, this research has often been conducted without paying much attention to how enemy communities are organized and how this organization may affect the functioning of enemy communities. As a result, aspects of enemy community organization that are important for understanding OCI-enemy interactions may often have gone unappreciated. In the following sections, I review some key topics in the research on enemy community organization, and explain why they deserve more attention in OCI systems.

#### *1.3.2. Diversity-functionality relationships in enemy communities*

At present, one of the most pressing questions about enemy community organization in OCI systems is how the functionality of enemy communities is related to their diversity. Owing to the developing global biodiversity crisis, understanding the relationship between the diversity and functionality of species communities is a key challenge of contemporary ecology (Cardinale *et al.* 2012). However, this topic has received relatively little attention in studies of OCI-enemy interactions.

General theory predicts several possible diversity-functionality relationships that would differ importantly in terms of their consequences for OCI-enemy interactions (Hooper *et al.* 2005): A) If the effects of different enemy species are complementary, or if different enemy species facilitate each other, the magnitude of enemy impacts at a given location will depend strongly on the particular combination of enemy species that are present. Moreover, the overall impact of enemies should be expected to increase with the number of enemy species. B) Enemy-impacts may be driven mainly by a few important enemy species, while the rest of the enemy community has little impact. In this case, the overall magnitude of enemy impacts will still depend heavily on which enemy species are present, but the species-richness of enemy communities will be of lesser importance. C) Most species in the enemy community may perform very similar functions. In this case, the identity of the enemy species that are present



at a given location will be of little consequence for the magnitude of local enemy impacts. Further, if enemy species compete for the OCI resource (which is likely for enemies that are functionally similar), loss of some species from the enemy community may be compensated for by increased impact of the remaining species (i.e. due to competitive release). Thus, no relationship between the diversity and magnitude of impact of the enemy community should be expected. In other words, the species in the enemy community will display a high degree of functional redundancy (Rosenfeld 2002). D) Enemy species may interfere with or prey on each other. In this case, the relationship between the diversity and impact of the enemy community may again become neutral, or even negative. Further, the combination of enemy species that are present may be important, depending on which species have negative impacts on each other. Clearly, the overall magnitude and spatiotemporal stability of enemy impacts on OCI populations may depend strongly on which of the above scenarios apply. Thus, the role of enemies in OCI population dynamics may not become fully appreciated before a better understanding of diversity-functionality relationships in enemy communities has been developed. Studies of diversity-functionality relationships in OCI-enemy interactions would also be valuable to ecology in general. There is a large body of research on diversity-functionality relationships in predator-prey systems, but most of this research has been conducted in agroecosystems or under simplified experimental conditions (Letourneau *et al.* 2009; Griffin *et al.* 2013). Thus, there is a shortage of field studies from natural communities. OCI systems, with their typically species rich and complex enemy communities, could provide useful model systems for studying enemy diversity-functionality relationships in the field.

### *1.3.3. OCI range expansions and enemy diversity-functionality relationships*

Diversity-functionality relationships in enemy communities may be important for understanding not only the current dynamics of OCI systems, but also how these systems will behave under anthropogenic environmental change. Since OCIs and their enemies are usually widespread and abundant, extinctions due to human activities are unlikely to affect the diversity of OCI-related enemy communities in the near future. In contrast, anthropogenically induced range shifts in OCIs can have substantial consequences for the diversity of their enemies. Accidental human introduction of OCIs to new geographical locations is a serious problem across the globe (Kenis *et al.* 2009; Gandhi & Herms 2010). Further, due to anthropogenic climate warming, several OCI species are currently expanding their ranges into areas that have previously been climatically unsuitable (Jepsen *et al.* 2008; Weed *et al.* 2013). Species that invade new areas, due to introduction or range-expansion, typically leave behind some of their enemy species, and hence tend to have impoverished enemy communities in the invaded range compared to the native range (Colautti *et al.* 2004; Torchin & Mitchell 2004). However, the consequences of enemy loss for overall enemy impacts depend on diversity-functionality relationships in enemy communities. If no positive diversity-functionality relationship exists, an invader may not experience reduced enemy impacts in the invaded range, despite losing some of its enemies. Conversely, if there is a positive relationship, enemy loss should cause enemy impacts to be reduced and hence benefit the invader. This could facilitate the establishment and spread of the invader in the invaded range. This has been termed the “enemy release” hypothesis (Roy *et al.* 2011; Heger & Jeschke 2014). It does appear that loss of enemy species during invasion will in many cases also cause enemy impacts on invaders to be reduced (Torchin *et al.* 2003; Liu & Stiling 2006). However, it is still a matter of debate whether this can explain the success that many invaders display in their invaded ranges.

Importantly, enemy release, if it occurs, need not be a permanent condition. In parasitoid-host systems, it is well documented that invasive host species tend to accumulate an increasing number of parasitoid species over time after the invasion (Cornell & Hawkins 1993; Schönrogge *et al.* 2006; Menendez *et al.* 2008; Grabenweger *et al.* 2010). This could be because

native parasitoids adapt to attack the invasive host over time, or because the invasive host gradually encounters more parasitoid species as it spreads throughout different habitat types in the invaded range (Cornell & Hawkins 1993). For hosts that have gradually invaded a new region by range-expansion, the host may also have out-dispersed some of its parasitoid species during the initial stages of expansion. These parasitoids may catch up to the host over time, thus causing parasitoid species-richness to increase in the invaded range over time. Unfortunately, studying the rate of this parasitoid accumulation process is difficult, because it appears to operate on timescales of decades or even centuries (Cornell & Hawkins 1993).

Questions about the occurrence and timescale of enemy release are clearly challenging, but it is nevertheless important to address them. Invasive OCIs can grow abundant enough to cause enormous economic and ecological damage (Lovett *et al.* 2006; Gandhi & Herms 2010), and identifying the mechanisms that allow them to do so is necessary for effective management. If an OCI benefits from enemy release, a possible management option is to introduce enemy species from the OCIs native range into the range that has been invaded (i.e. biological control). Sadly, this strategy can have negative side effects, because introduced enemies may attack not only the OCI but also non-target prey species in the native fauna (Henneman & Memmott 2001; Parry 2009; Elkinton & Boettner 2012). Thus, enemy introductions should be avoided unless it is reasonably certain that the OCI benefits from enemy release, so that beneficial management outcomes from enemy introduction can be expected.

#### *1.3.4. Phenological organization of enemy communities*

Another important aspect of enemy community organization that has received little attention in most OCI systems is the phenological structuring of enemy communities. Owing to the stage-structured nature of insect life cycles, the OCI life cycle stage that a given enemy species exploits may be available only during a limited time period within a season. Thus, the phenology of the enemy and the OCI needs to be closely synchronized. Failing this, the enemy will be unable to exploit the OCI resource and the OCI escapes the impact of the enemy (Godfray *et al.* 1994; Van Nouhuys & Lei 2004; Jeffs & Lewis 2013). This could have severe negative consequences for the enemy population, potentially causing elevated mortality and reproductive failure. This is particularly likely for specialist enemies, which lack alternative prey species. Meanwhile, escape from predation may enhance the population growth rate of the OCI and possibly even precipitate an outbreak. The problem of phenological synchronization between OCIs and enemies is by no means trivial. OCIs are ectothermic, and their phenology therefore tends to be highly sensitive to climate (van Asch & Visser 2007). The same is true for some of their major enemy groups, such as parasitoids (Hance *et al.* 2007; Jeffs & Lewis 2013). Thus, if OCIs and enemies are differentially climate sensitive, stochastic fluctuations in climate may disrupt the phenological synchronization between them.

Few studies have examined phenological synchronization between OCIs and individual enemy species [(but see Cheng (1970) and Weseloh (1976)], and there has been even less attention to the phenology of enemy communities as a whole. This is a substantial shortcoming, since the phenological organization of enemy communities must be expected to affect the probability of severe OCI-enemy mismatch events. If most enemy species aim to attack the same phenological stage of the OCI, there is greater risk that a single freak climatic event will disrupt the synchrony between the OCI and many of its enemies. Such a wholesale mismatch event is less likely if the phenology of the enemies is more varied, with different enemy species exploiting different phenological stages of the OCI. Thus, phenological variation among enemies could buffer the overall impact of the enemy community against climate-induced mismatch events. Of course, the characteristics of individual enemy species are also important in this context. An enemy will be more vulnerable to mismatch if it can only attack an OCI life cycle stage that is short in duration. If the vulnerable OCI stage lasts for a longer time, there is a better chance that the

enemy will encounter it, even if enemy- and OCI phenology become somewhat displaced relative to each other.

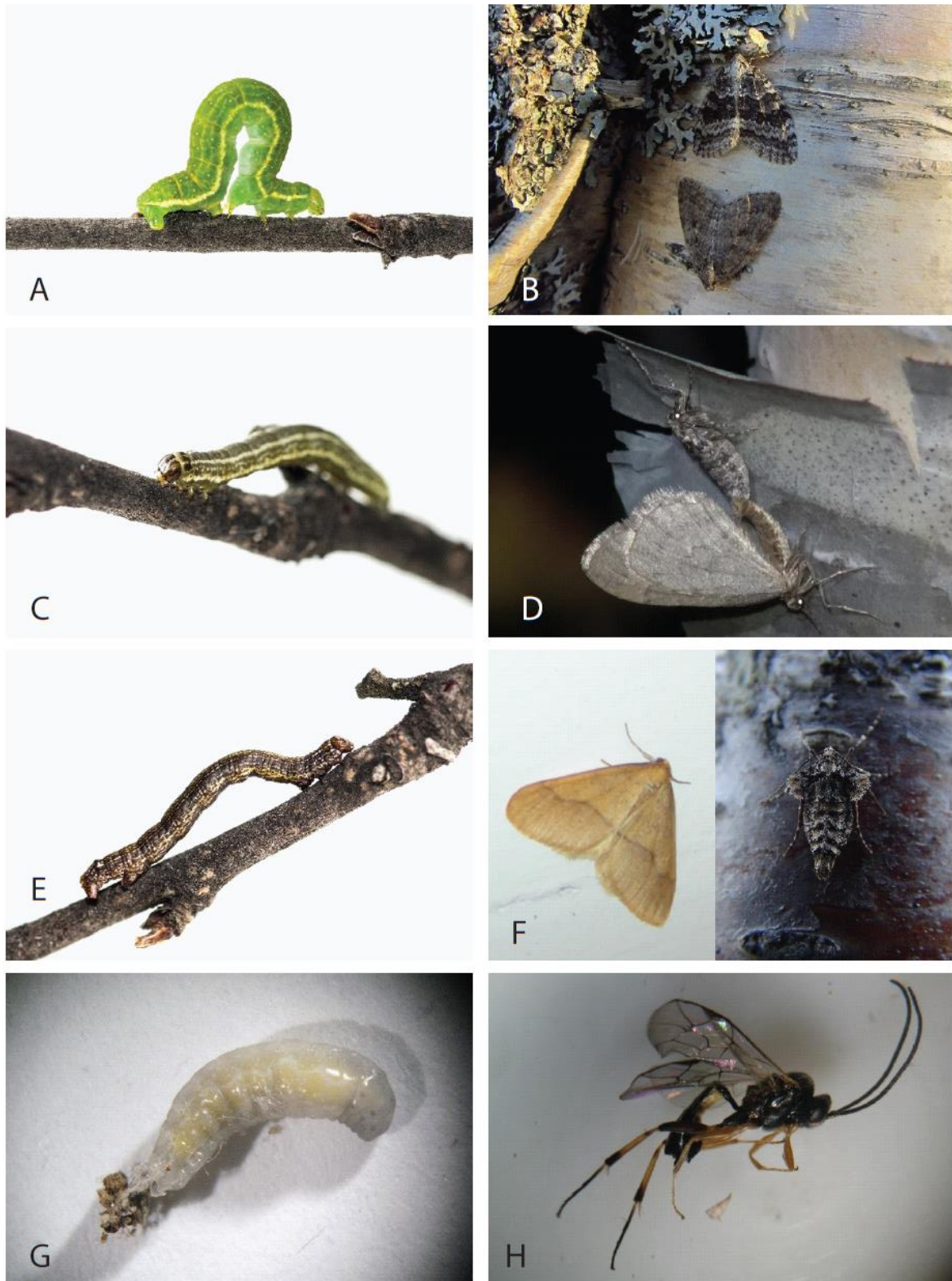
Studying the phenological organization of enemy communities may aid the understanding of OCI population dynamics in several ways. First, OCI outbreaks often develop rapidly and unpredictably. Mapping out the phenology of enemy communities, so that their vulnerability to mismatch events can be assessed, would be a first step in evaluating OCI-enemy mismatches as an explanation for such outbreaks. Second, the phenological synchronization between OCIs and enemies may be disrupted as a result of climate change (Hance *et al.* 2007; Jeffs & Lewis 2013), potentially increasing the likelihood of OCI outbreaks. Again, basic knowledge about the phenological organization of enemy communities is necessary for evaluating the probability of such a scenario.

#### **1.4. The study system: cyclically outbreaking geometrid moths in North-Fennoscandian mountain birch forest**

##### *1.4.1. Introduction to the Fennoscandian birch-moth system*

The aim of the current project has been to address some of the outlined knowledge gaps for one of the most well-studied and highly publicized examples of an OCI system in the world, namely that of geometrid moths feeding on mountain birch (*Betula pubescens* ssp. *Czerepanovii* Orlova) in sub-arctic northern Fennoscandia. The system currently encompasses the 3 moth species *Epirrita autumnata* (Bkh.) (autumnal moth), *Operophtera brumata* (L.) (winter moth) and *Agriopis aurantiaria* (Hübner) (scarce umber moth) (Fig. 2A – F). The former 2 species are long established in the mountain birch ecosystem, with *E. autumnata* being a native species and *O. brumata* invading by range-expansion from the south roughly a century ago (Jepsen *et al.* 2011). Both species show cyclic population dynamics, with population peaks occurring every 9 – 10 years, usually in synchrony areas of hundreds or thousands of square kilometers (Tenow 1972; Bylund 1999; Ruohomäki *et al.* 2000; Jepsen *et al.* 2009b). During some of these decadal peaks, moth populations attain outbreak densities and cause region-wide defoliation and mortality of mountain birch forest (Fig. 1). *A. aurantiaria* is a recently invading southern species, which established itself in the North-Fennoscandian mountain birch system roughly 15 years ago (Jepsen *et al.* 2011). The dynamics of *A. aurantiaria* in this system appear to resemble those of *E. autumnata* and *O. brumata*, and local outbreaks of this invader have already been recorded.

Apart from the occurrence of cycles and outbreaks, the dynamics of moth populations in Fennoscandia show a number of features that have certainly contributed to the long-standing fascination with this system among both scientists and the public. First, the dynamics of *E. autumnata* show a strong latitudinal gradient, with high-amplitude cycles and outbreaks occurring only in northern areas (Klemola *et al.* 2002). *E. autumnata* populations appear to cycle also in southern Fennoscandia, but their fluctuations are much less pronounced there and occur around much lower average densities. Second, moth dynamics show an altitudinal gradient, with moth population densities typically increasing with increasing altitude (Hagen *et al.* 2007). This gradient can be extremely pronounced, with the forest close to the treeline being completely defoliated, and the forest at lower altitudes – often only a few hundred meters away – being almost unaffected by moth herbivory. Thus, both the latitudinal and altitudinal gradient in moth dynamics demonstrate that outbreaks are more likely to occur in harsher and less productive habitats (i.e. higher latitudes and altitudes) (Schott *et al.* 2013). Third, populations of *O. brumata* and *E. autumnata* fluctuate synchronously, but *E. autumnata* usually reaches the peak and collapse phases of the population cycle 1 – 2 years before *O. brumata* (Klemola *et al.* 2009). Thereby, the dynamics of the 2 moth species are phase-locked but also phase-lagged.



**Figure 2.** Study species. A – F: Larvae and adults of *E. autumnata* (A, B), *O. brumata* (C, D) and *A. aurantiaria* (E, F). The wingless adults of the latter 2 species are females. The sexes of the 2 *E. autumnata* adults in panel B are unknown. G and H: Larva (G) and adult (H) of the parasitoid group *Phobocampe* sp./*S. crassifemur*. Photo: Moritz Klinghardt (A, C and E), Malin Ek (B), Jane Uhd Jepsen (male in F) and Ole Petter Laksforsmo Vindstad (D, female in F, G and H).

#### 1.4.2. Key topics and results in the research on moth population cycles and outbreaks

The research conducted in the Fennoscandian moth-birch system is typical for what has been undertaken in many OCI systems. Specifically, most research has been motivated by the question of why moth populations show cycles and/or outbreaks. This has led to extensive inquiries into moth biology and ecology, especially for *E. autumnata*. As a result, numerous studies have been published on topics like moth life history (e.g. growth and fecundity) (Tammaru *et al.* 1995; Tammaru & Yz 1998; Tammaru *et al.* 2001; Tammaru *et al.* 2004), climate-sensitivity (Tenow & Nilssen 1990; Peterson & Nilssen 1998; Ammunet *et al.* 2012) and density-dependence (Klemola *et al.* 2004; 2008). Spatiotemporal patterns in moth population dynamics, and their relationship with climate, have also received much attention (Klemola *et al.* 2006; Hagen *et al.* 2007; Nilssen *et al.* 2007; Hagen *et al.* 2008; Jepsen *et al.* 2009b). Finally, there has been extensive research on the role of trophic interactions in moth dynamics (further discussed in sections 1.4.5 – 1.4.6). While the causes of cycles and outbreaks have not been decisively established, this research has led to many advances in the understanding of moth population dynamics.

A review of the present knowledge of moth dynamics is beyond the scope of this thesis, but some key results should be mentioned to provide context for the following discussion. In particular, it is becoming clear that climate is probably a key driver of both the geographical distribution and amplitude of moth outbreaks. The winter survival of moth eggs and the (temperature-sensitive) phenological matching between moth larvae and birch host plants in spring both appear to be important underlying mechanisms for climate impacts on moth populations (see also section 2.2.1) (Jepsen *et al.* 2011; Ammunet *et al.* 2012). Via these mechanisms, climate seemingly acts to synchronize moth population fluctuations on a regional scale (Klemola *et al.* 2006; Jepsen *et al.* 2009b). As would be expected from their climate sensitive nature, moth dynamics also appear to be responding to climate change. *E. autumnata* and *O. brumata* have been expanding their outbreak ranges into progressively colder areas over the last few decades, probably due to improved egg survival during milder winters (Jepsen *et al.* 2008). *O. brumata* has also shown an altitudinal expansion towards higher and colder altitudes (Hagen *et al.* 2007). Further, there is good evidence that the recent establishment of *A. aurantiaria* in the mountain birch system was facilitated by climate warming, most probably via improved phenological matching between larvae and birch during warmer springs (Jepsen *et al.* 2011).

#### 1.4.3. Ecological consequences of moth outbreaks

While the potential drivers of moth population dynamics have been meticulously scrutinized, research on the ecological consequences of moth outbreaks has lagged far behind. There has been some research on regeneration and productivity in mountain birch following outbreaks (Lehtonen & Heikkinen 1995; Karlsson *et al.* 2004; Tenow *et al.* 2004). A number of largely descriptive studies on the state of vegetation (Kallio & Lehtonen 1973; Lehtonen & Yli-Rekola 1979) and insect (Jussila & Nuorteva 1968; Nuorteva & Jussila. 1969) communities were also published in the aftermath of a severe *E. autumnata* outbreak in northern Finland in the 1960s. Overall, however, there is little knowledge of how different components of the mountain birch ecosystem respond to outbreaks.

Over the last decade, this knowledge gap has become increasingly felt, owing to new developments in moth population dynamics. During the first decade of the 2000s, moth outbreaks of historically unprecedented duration and severity erupted in northern Fennoscandia, damaging an estimated 10 000 square km of mountain birch forest (Jepsen *et al.* 2009a, b). The Varanger region in eastern Finnmark suffered particularly prolonged defoliation owing to consecutive outbreaks by *E. autumnata* (2002 – 2004) and *O. brumata* (2005 – 2009). For *O. brumata*, the Varanger outbreak represented a north-eastern expansion of the species' outbreak

range, probably facilitated by climate warming (Jepsen *et al.* 2008) (section 1.4.2). Owing to the dual outbreaks, the birch forest in Varanger suffered extensive mortality, with close to 100 % of birch stems dying in some areas (Jepsen *et al.* 2013; Biuw *et al.* 2014). Fig. 1C – E and the cover page of study V all show examples of the damage caused to the birch forest in Varanger during the 2000s outbreak.

The devastation caused by the latest outbreak, and the suspicion that climate warming could lead to a higher frequency of similar events in the future, has sparked increased interest in the ecological consequences of moth outbreaks. Thus, over the past 5 years, a number of new research initiatives have been launched to strengthen the knowledge of this topic. This research has already started to reveal the pervasive impacts that outbreaks have on the mountain birch ecosystem. It has been shown that the defoliation caused by outbreaks reduces the capacity for carbon uptake by the mountain birch forest (Heliasz *et al.* 2011). Further, it has been found that outbreaks cause increases in soil nutrient concentrations and change the composition of soil decomposer communities, probably due to deposition of moth frass and cadavers (Kaukonen *et al.* 2013). It has also become clear that outbreaks can have extremely strong impacts not only on the mountain birch but also on the fieldlayer vegetation. In oligotrophic forest, growing on nutrient poor soils, (Fig. 3) the typically dominant dwarf shrubs *Empetrum nigrum* (crowberry) and *Vaccinium myrtillus* (bilberry) often suffer mass mortality during outbreaks (Jepsen *et al.* 2013; Karlsen *et al.* 2013) (Fig. 1D), apparently due to an interaction between moth browsing and infection by fungal pathogens (Olofsson *et al.* 2013). Following this, the Graminoid *Avenella flexuosa* (wavy hair-grass) establishes itself as the dominant plant species in the fieldlayer within just a few years (Fig. 1C). This transition to a grass dominated system seems to benefit graminivorous small rodents, which have been found to be more abundant in forest that has recently been damaged by outbreaks (Jepsen *et al.* 2013). Meanwhile, semi-domestic reindeer, which are the most important large herbivores in northern Fennoscandia, appear to reduce their use of outbreak-affected forest (Jepsen *et al.* 2013). Thus, it is clear that the effects of outbreaks can cascade through several different ecosystem components and affect species that have no direct interaction with the moths themselves.

#### *1.4.4. Knowledge gap: indirect impacts of moth outbreaks on saproxylic beetles and passerine birds*

For the present project, I focused on the indirect impacts of outbreaks on 2 very different communities, namely saproxylic beetles and passerine birds. Saproxylics experience indirect effects of outbreaks in the sense that trees which are killed by moth herbivory constitute a resource that saproxylics can utilize. However, as outlined in section 1.2.1, there is little knowledge about the ability of saproxylics to respond numerically to the massive amounts of dead wood left by insect outbreaks. This question became particularly pressing in the mountain birch system following the extensive mortality of birch caused by the 2000s outbreak. Large tracts of forest suffered mortality of almost all of their birch stems, and the volume of dead wood on the landscape level may have been increased by 2 to 3 orders of magnitude in many areas. Thus, there was reason to believe that the saproxylic beetle community would be unable to mount a numerical response that was proportional to this vast and rapid resource input. However, no empirical data was available to test this prediction. Predictions about the responses of the saproxylic beetle community were also hampered by limited knowledge of which saproxylic beetle species were present in the study region. This provided the motivation for a study aiming to map out the species composition of the saproxylic beetle community in the study region, and assess its capacity for responding numerically to the dead wood left by the outbreak (study IV).

The responses of passerine birds to insect outbreaks are particularly interesting, because many species may experience both direct and indirect effects. Bird species that are insectivorous may

enjoy a superabundance of food during outbreak years. Thus, the direct interaction with the outbreaking insect can provide short-term benefits for birds. However, birds may also experience indirect impacts, via the effects that outbreaks have on the vegetation (section 1.2.1). Species that forage, hide or nest among tree foliage may suffer habitat loss due to the defoliation caused by an outbreak. This effect will be short-term if trees survive the defoliation [e.g. Gale *et al.* (2001)], but it could endure for decades if the outbreak causes mortality of trees. Meanwhile, bird species that prefer open or early-successional habitats may benefit from outbreak-induced tree mortality.

Several studies have investigated how bird communities in the mountain birch forest respond to short-term increases in the availability of food in the form of superabundant moth larvae in outbreak years. This research has shown that several bird species increase reproductive effort during outbreak years (Enemar *et al.* 1984; Enemar *et al.* 2004; Hogstad 2005; Lindström *et al.* 2005). Moreover, the brambling (*Fringilla montifringilla* L.) – one of the most abundant bird species in the mountain birch forest – appears act as a breeding nomad, settling to breed mainly in areas of high moth abundance (Lindström 1987; Hogstad 2000). Thus, it is well known that moth outbreaks can induce short-term changes in bird communities by altering food supply. However, prior to the present project, nothing was known about the responses of bird communities to the massive forest damage inflicted by the most severe moth outbreaks. This knowledge gap became a matter of substantial concern following the 2000s outbreak, since the widespread forest mortality inflicted by this outbreak could be suspected to cause large-scale habitat loss for many bird species. This provided the motivation for a study to investigate how bird communities respond to outbreak-induced forest damage (Study V).

Studying how a community is affected by a disturbance poses methodological challenges, because the state of the community should ideally be documented both before and after the disturbance. This is difficult in the case of forest damage caused by moth outbreaks, since the occurrence of an outbreak that is severe enough to damage the forest cannot be predicted. An alternative approach to studying the effects of disturbance is to compare the state of the target community between disturbed and undisturbed locations. This method is easier to implement for moth outbreaks, because they often leave a landscape-scale mosaic of damaged and undamaged forest. This makes it possible to compare the state of communities between damaged and undamaged locations that are separated by just a few km and which can therefore be assumed to have largely similar environmental conditions. This space-for-time-contrast approach was the methodological basis for my studies of how bird and saproxylic insect communities are affected by outbreak-induced forest damage (see section 2.3.4 – 2.3.5 for details on study design).

#### *1.4.5. Research on the role of trophic interactions in moth population dynamics*

The role of trophic interactions in moth population dynamics has probably been the subject of more research than any other topic related to the Fennoscandian birch-moth system. During the 1980s and 90s, this research focused on inducible chemical defences to moth herbivory in the mountain birch, and their potential for driving moth population cycles. The inducible defence hypothesis was eventually rejected (Haukioja 2005), and the focus shifted to the role of natural enemies in the late 90s and early 2000s. Around the turn of the century, Tanhuanpää and colleagues investigated whether the north-south gradient in the population dynamics of *E. autumnata* could be explained by predation on the egg, larval, pupal and adult stages of the moth (Tanhuanpää *et al.* 1999; Tanhuanpää *et al.* 2001; Tanhuanpää *et al.* 2003). Their results suggested that high impacts of generalist predators on larvae and pupae in southern populations contributed to preventing *E. autumnata* outbreaks in the south. This series of studies heralded a period with highly focused research on the role of natural enemies in moth population dynamics.

The theoretical framework for this research was laid out in a review paper by Klemola and colleagues in 2002. Building on theory of population dynamics developed for cyclic small rodents, the paper suggested that the behaviour of moth populations in Fennoscandia was explained by the dual impacts of generalist and specialist natural enemies. Specialist enemies are expected to show delayed numerical (i.e. reproductive) responses to changes in the density of their preferred prey. The resulting time lag in enemy impacts on prey populations causes the prey to experience delayed negative density dependence, which, according to general theory, can result in population cycles. Meanwhile, generalist enemies, who can exploit many different prey species, are not expected to show strong reproductive responses to changes in the density of any particular prey species. Generalist are, however, expected to show rapid behavioural responses to changes in prey density, switching between prey species to preferentially exploit the ones that are most abundant at the moment. This results in direct (i.e. non-delayed) negative density dependence for prey populations. According to general theory, this has a stabilizing effect on population dynamics (i.e. it counteracts cycles). Klemola and colleagues hypothesised that the relatively stable dynamics of *E. autumnata* in southern Fennoscandia and the high-amplitude cycles in northern Fennoscandia were explained by greater impacts of generalist and specialist enemies in the south and north, respectively. A central tenet of the hypothesis was that enemies in the north were forced into specializing on geometrid moths, due to a paucity of alternative prey species in this species-poor high-latitude community. Meanwhile, the more species-rich prey communities of southern Fennoscandia were hypothesised to allow enemies to adopt a more generalized diet.

#### *1.4.6. Research on parasitoids as drivers of moth population cycles*

Parasitoids were singled out by Klemola and colleagues as the enemies that were most likely to play the key role of specialists in northern regions. This sparked off research initiatives in no less than 3 geographical regions, conducted by 2 independent research groups. One group was the Birchmoth project – which I have worked with during the present PhD project – based in Tromsø, northern Norway. The other was the group of Klemola himself, based in Turku, Finland. The Norwegian group focused on the impacts of larval parasitoids on *E. autumnata* and *O. brumata* in coastal north-west Norway (hereafter coastal Troms). Meanwhile, the Finnish group explored the impacts of larval- and pupal parasitoids in continental northern Finland (hereafter Kevo) and larval- pupal- and egg parasitoids in semi-oceanic north-east Norway (hereafter Hana), in both cases focusing mainly on *E. autumnata*. The approaches of the 2 research groups differed, with the Norwegian group favouring large-scale observational studies with extensive spatial replication, while the Finnish group favoured a combination of observational and experimental studies, conducted on smaller scale and with less spatial replication.

Results and conclusions regarding parasitoid impacts also differed among the research groups, at least initially. Two large-scale observational studies in Troms found no relationship between larval parasitism and population growth rates of *E. autumnata* and *O. brumata*, suggesting that moth population cycles are not driven by larval parasitism in this region (Hagen *et al.* 2010; Schott *et al.* 2010). A small-scale observational study in Kevo found that larval parasitoids show delayed numerical responses to changes in *E. autumnata* density (Klemola *et al.* 2010). Moreover, a small-scale field experiment, where parasitoids were excluded by mesh cages, suggested that larval parasitism causes the collapse of *E. autumnata* populations after the peak of the population cycle (Klemola *et al.* 2010). Both findings were consistent with larval parasitoids being the causal agents of moth population cycles in Kevo. Meanwhile, the prevalence of pupal parasitoids was very low in this region. In contrast, a small-scale field study in Hana found very low prevalence of larval parasitoids in *E. autumnata*. Meanwhile, experimental exposure of *E. autumnata* eggs and pupae revealed that egg- and pupal parasitoids



showed density dependent responses to moth population fluctuations (Klemola *et al.* 2014). These parasitoids were therefore deemed to be likely candidates for driving moth population cycles at Hana.

The interpretation of the North-Fennoscandian parasitism studies has been a matter of some debate, owing to different views about the appropriate methodology for studying parasitoid impacts on moth population dynamics. The Norwegian group has argued that because moth population dynamics are synchronized across enormous areas, parasitoid impacts also need to be studied at large spatial scales (Hagen *et al.* 2010; Schott *et al.* 2010). This calls into question the validity of small-scale studies with little spatial replication. This has created doubts as to whether the contrasting results for larval parasitoids in coastal Troms (large-scale studies – no apparent larval parasitoid impact) and Kevo (Small-scale studies – high apparent larval parasitoid impact) can be attributed to differences in methodology or true differences in parasitoid impact between coastal (Troms) and continental (Kevo) regions. The results of Klemola *et al.* (2014) have helped to resolve this ambiguity, by documenting low impacts of larval parasitoids at the coast-near Hana. This supports the impression that larval parasitoids do in fact play a smaller role in moth population dynamics in coastal than continental regions. Investigating whether egg- and pupal parasitoids are important in coastal Troms (as might be expected from their high importance in Hana) is a topic for future research.

#### *1.4.7. Limitations to the research on parasitoids in the Fennoscandian birch-moth system*

It is clear that much has been learned about the role of parasitoids in moth population dynamics since the publication of Klemola *et al.* (2002). However, the research on parasitism in the Fennoscandian birch-moth system has also suffered from limitations which are typical for studies of enemy impacts on OCI population dynamics (section 1.3.1). In particular, there has been a strong focus on documenting and interpreting total (i.e. across all parasitoid species) parasitism rates for individual parasitoid guilds (i.e. larval-, pupal- and egg parasitoids). The prevalence of individual parasitoid species has often been presented, but apart from this there has been little attention to parasitoid community organization. Treating a parasitoid guild as a single functional unit by lumping its individual species is clearly practical for studying the overall impact of parasitism on moth populations. Unfortunately, this simplified treatment also ignores the fact that the guild is an assemblage of species which i) have their own unique ecological traits and ii) constitute a community with its own internal dynamics. The total parasitism rate is a result of these species traits and the way in which they are expressed in the context of the guild as a whole. As a result, total parasitism rates, and their impacts of moth populations, are unlikely to be fully understood without paying attention to the organization of parasitoid guilds.

As the research on parasitism in the Fennoscandian birch-moth system has progressed, the need to adopt a more community ecological view of parasitoids has become increasingly apparent. This has particularly been the case for larval parasitoids, which have received more attention than the other parasitoid guilds. This motivated me to conduct a series of studies (study I – III) addressing some of the most pressing knowledge gaps relating to the organization of larval parasitoid guilds in this system. Below, I review these knowledge gaps and outline why I considered it to be important to address them.

#### *1.4.8. Knowledge gap: the causes and consequences of spatial variation in larval parasitoid guild structure*

One puzzling feature of larval parasitism in the Fennoscandian birch-moth system is that the relative prevalence of different larval parasitoid species (i.e. larval parasitoid guild structure) can show considerable spatial variation, both within and among studies (Ruohomäki 1994; Kaitaniemi & Ruohomäki 1999; Virtanen & Neuvonen 1999). The causes and consequences of

this variation have received little attention. Spatial variation in species prevalences are usually attributed to deterministic processes, such as species-specific responses to variation in habitat structure or climate. However, as hypothesized in section 1.2.2, the extreme fluctuations in prey density that characterise OCI-enemy systems could also cause local enemy community structure to be heavily influenced by stochasticity in processes of enemy extinction and recolonization. Extinction-recolonization dynamics seem likely for larval parasitoids of birch forest geometrids, since these parasitoids probably have few alternative host species (Klemola *et al.* 2002) and therefore suffer severe declines in host availability when moth populations collapse. Thus, *a priori*, deterministic and stochastic explanations for variation in larval parasitoid guild structure are both plausible. Before the present project, there had been no attempt to differentiate between these explanations, neither had there been any assessment of how variation in larval parasitoid guild structure influenced total larval parasitism rates. As outlined in section 1.3.2, the degree to which variation in enemy community structure affects total enemy impacts will depend on diversity-functionality relationships within the enemy community. Very little was known about such relationships within the larval parasitoid guilds of the focal moth species prior to the present project. These knowledge gaps motivated a study that aimed to evaluate whether spatial variation in larval parasitoid guild structure was most likely to be explained by deterministic or stochastic factors, and whether it was likely to have important consequences for total larval parasitism rates (Study I).

To focus the study, I hypothesized that larval parasitoid guilds of cyclic geometrid moths were structured by a competitive lottery [see Tokeshi (1999) and Munday (2004) for thorough explanations of this model]. Strictly, the lottery model applies to communities where species compete for relatively small patches of space and the resources they contain. The model assumes that all species have similar powers of dispersal and interspecific competition. Further, it is assumed that the species which first establishes itself in an empty patch will retain local dominance until it suffers stochastic extinction, after which the patch becomes available for colonization again. Under these conditions, no species will be particularly advantaged or disadvantaged in the competition for patch occupancy. Hence, the identity of the dominant species in a given patch at a given time will mainly be determined by stochasticity in the processes of extinction and colonization. The lottery model is most likely to apply to guilds of species that utilize similar resources in similar ways. An assemblage of parasitoids utilizing moth larvae would be a potential example of such a guild.

The main testable prediction of the lottery model is that the dominant species at given sites should change randomly over time. Testing this prediction is demanding, because the presence of different species at given locations needs to be monitored over time so that extinction and colonization events can be observed. When a sufficiently long time series has been collected, it becomes possible to assess whether the dominant species at the different sites changes randomly over time. This approach is unfeasible in the birch-moth system, since the moth population collapses proposed to drive parasitoid extinctions only occur once a decade. However, the lottery model also predicts that different species should be randomly distributed across a landscape. This will follow if species dominance in individual patches is randomly determined. Moreover, the distribution of species should be expected to be random even across a homogeneous landscape, where species distributions are not influenced by spatial variation in habitat characteristics (i.e. deterministic factors). Testing this prediction is more manageable, because it can be done by sampling over a homogeneous landscape over a short time period. Unfortunately, it is also less satisfying, because it is difficult to eliminate habitat variation from a spatial sampling design. Thus, it will also be difficult to eliminate the alternative explanation that spatial variation in species prevalences is simply due to variation in habitat characteristics. Nevertheless, quantifying species prevalences across an area with minimal habitat variation can

give a useful indication of whether lottery processes are likely to be operating. This was the underlying reasoning for the design of study I (see section 2.3.1 for details on study design).



**Figure. 3.** Typical growth form of mountain birch on nutrient poor soils: individual trees have numerous small stems. Photo: Ole Petter Laksforsmo Vindstad.



**Figure. 4.** Typical growth form of mountain birch on nutrient rich soils: individual trees have few and large stems. Photo: Ole Petter Laksforsmo Vindstad.

#### 1.4.9 Knowledge gap: the phenological organization of larval parasitoid guilds

Another aspect of larval parasitoid community ecology that has been subject to knowledge gaps is the phenological organization of parasitoid guilds. (Kaitaniemi & Ruohomäki 1999) studied the phenology of larval parasitoids of *E. autumnata* in northern Finland, but prior to the present project there had been no research on the phenology of larval parasitoids associated with *O. brumata* in the mountain birch system. Thus, the distribution of parasitoid attacks across the larval stage of this moth was unknown. Following the reasoning of section 1.3.4, the probability of phenological mismatch events between parasitoids and *O. brumata* larvae should be influenced by the capacity of parasitoids for attacking different larval instars (i.e. instar-specificity) and the sequence of attack of different parasitoid species.

Lack of knowledge about these phenological parameters represented a liability in several respects. First, it was impossible to assess the role of larvae-parasitoid mismatches as a contributor to *O. brumata* population dynamics. Larval parasitism rates of *O. brumata* are frequently in the range of 30 – 60 % (Hagen *et al.* 2010; Schott *et al.* 2010; 2012) and may hence be a limiting factor for moth population growth (even if parasitism is not necessarily causing moth cycles). Thus, a severe mismatch between *O. brumata* and most of its larval parasitoid guild could contribute to the development of a moth outbreak. This would help explain why the amplitude of the *O. brumata* population cycle shows pronounced temporal variation, with moth densities at some cycle peaks being too low to cause visible defoliation and other peaks taking the form of outbreaks that cause region-wide defoliation and mortality of mountain birch (Tenow 1972; Jepsen *et al.* 2009b). A scenario where larvae-parasitoid mismatches contribute to outbreak-development seemed particularly likely for the climatically unstable coastal region of North-west Norway. This area is subject to extensive inter-annual variation in temperature during spring and early summer, with the onset of the growing season varying by more than 3 weeks between years (Karlsen *et al.* 2007). Moreover, weather conditions tend to change rapidly and unpredictably within years. Thus, the risk of phenological asynchrony between parasitoids and larvae could be high in this system. However, a proper evaluation of this hypothesis was impossible without knowing the phenology of the larval parasitoid guild of *O. brumata*. Lack of knowledge about parasitoid phenology was also a liability for the interpretation of larval parasitism rates that had earlier been documented for *O. brumata*. Depending on the phenology of parasitoid attacks, estimates of parasitism rates can be sensitive to the timing of host sampling (van Driesche 1983; Jervis 2005). Prior to the present project, lack of knowledge about parasitoid phenology made it impossible to assess whether biases related to the timing of sampling could be an important influence on estimates of larval parasitism of *O. brumata*. These issues motivated a study to map out the phenology of the larval parasitoid guild of *O. brumata* (Study II).

Additional motivation for a study of parasitoid phenology was provided by the altitudinal gradient in moth density, where moth outbreaks tend to occur most frequently close to the altitudinal treeline (section 1.4.1). One possible explanation for this phenomenon is that larval parasitoids suffer a progressively poorer phenological match with host larvae towards higher altitudes. Such a situation could arise if parasitoids were more sensitive than host larvae to the climatic variation experienced along an altitudinal gradient. Poor phenological synchronization between larvae and parasitoids at high altitudes would cause parasitism rates there to be reduced, and could hence facilitate the development of moth outbreaks. This hypothesis had not been tested prior to the present project. Thus, my study of parasitoid phenology was conducted within an altitudinal gradient design, so as to examine the temporal patterning of parasitoid attacks at different altitudes (see section 2.3.2 for details on study design).

#### 1.4.10. Knowledge gap: larval parasitism of invasive geometrid species

The on-going range-expansions of *E. autumnata*, *O. brumata* and *A. aurantiaria* in the mountain birch system (section 1.4.2) have also highlighted important knowledge gaps about the organization and functionality of larval parasitoid guilds. Specifically, experience with species invasions in other systems (see section 1.3.3 for explanation and references) raise several community ecological questions regarding larval parasitoids and their role in geometrid range-expansions: A) Do geometrids lose some of their larval parasitoid species when they invade new regions? This should be expected from the pattern of enemy loss that has been documented in many other invasive species. B) Does loss of parasitoid species (if it occurs) lead to reduction in total larval parasitism rates? If this is the case, the establishment and spread of geometrids in new regions could be facilitated by enemy release. However, the answer to this question is strongly dependent on diversity-functionality relationships within the larval parasitoid guild (section 1.3.2). If there is no positive relationship between larval parasitoid species-richness and total larval parasitism rates, loss of parasitoid species in invasive geometrids should not cause release from parasitism. C) How long can loss of parasitoid species and/or parasitism rates in invasive geometrids be expected to last? It has repeatedly been documented that invasive species tend to accumulate an increasing number of enemy species over time, so parasitoid loss and/or release in invasive geometrids should be expected to be temporary. None of these questions had been addressed prior to the present project.

The ecological situation in the study region of the Birchmoth project in coastal Troms provided me with an opportunity to improve the understanding of larval parasitism in invasive Geometrids. This region is (so far) the only place in the mountain birch system where high-density populations of *E. autumnata*, *O. brumata* and *A. aurantiaria* occur in sympatry. Moreover, the history of all 3 species in the region is well known. *E. autumnata* is a native species, while the occurrence of *O. brumata* was first documented roughly a century ago (first record near Tromsø in 1892). Meanwhile, *A. aurantiaria* has been present for roughly 15 years [see Jepsen *et al.* (2011) for details on Geometrid invasions in the system]. Further, the 3 species are relatively closely related and have a very similar ecology (section 2.2.1). Thus the structure and functionality of their larval parasitoid guilds can reasonably be assumed to be inherently similar, i.e. all 3 geometrid species should be expected to have a similar number of parasitoid species and similar total parasitism rates under native conditions. Thereby, I had a situation where it was possible to compare parasitism between a recent (*A. aurantiaria*) and long-established (*O. brumata*) invader and a native “reference species” (*E. autumnata*). This comparison would indicate if invasive geometrids have species-impooverished larval parasitoid guilds and reduced larval parasitism rates. Importantly, the contrasting residence times of the 3 geometrids would also allow me to assess how rapidly invasive geometrids accumulate larval parasitoid species in the mountain birch system. An additional advantage was that larval parasitism of all 3 geometrids had previously been documented in Western Europe, where all 3 species are native. This made it possible to test the assumption that their larval parasitoid guilds should be comparable under native conditions. It would also allow parasitism rates of *A. aurantiaria* and *O. brumata* to be compared between their native and invaded ranges, thus allowing more robust inference about release from parasitism in these invaders than simply comparing their parasitism rates with the native *E. autumnata* within the mountain birch system. This favourable situation motivated me to map out the species-richness and prevalence of larval parasitoids in *E. autumnata*, *O. brumata* and *A. aurantiaria*, in coastal Troms and Western Europe, and address the outlined questions by means of the comparative approaches described above (Study III) (see section 2.3.3 for details on study design).

## 1.5. Specific questions addressed by the PhD project

Each of my studies focused on addressing a number of core questions. These are summarized below for the convenience of the reader.

### Study I

- I a. Is spatial variation in larval parasitoid guild structure most likely to be explained by deterministic factors or stochastic lottery processes?
- I b. Does spatial variation in larval parasitoid guild structure cause total larval parasitism rates to vary in space?

### Study II

- II a. What is the phenology of attack of the individual larval parasitoid species of *O. brumata*?
- II b. Are individual larval parasitoid species, and the larval parasitoid guild as a whole, likely to be vulnerable to phenological mismatches with *O. brumata*?
- II c. Are outbreaks of *O. brumata* close to the treeline explained by poor phenological matching between the moth and its larval parasitoids at high altitudes?

### Study III

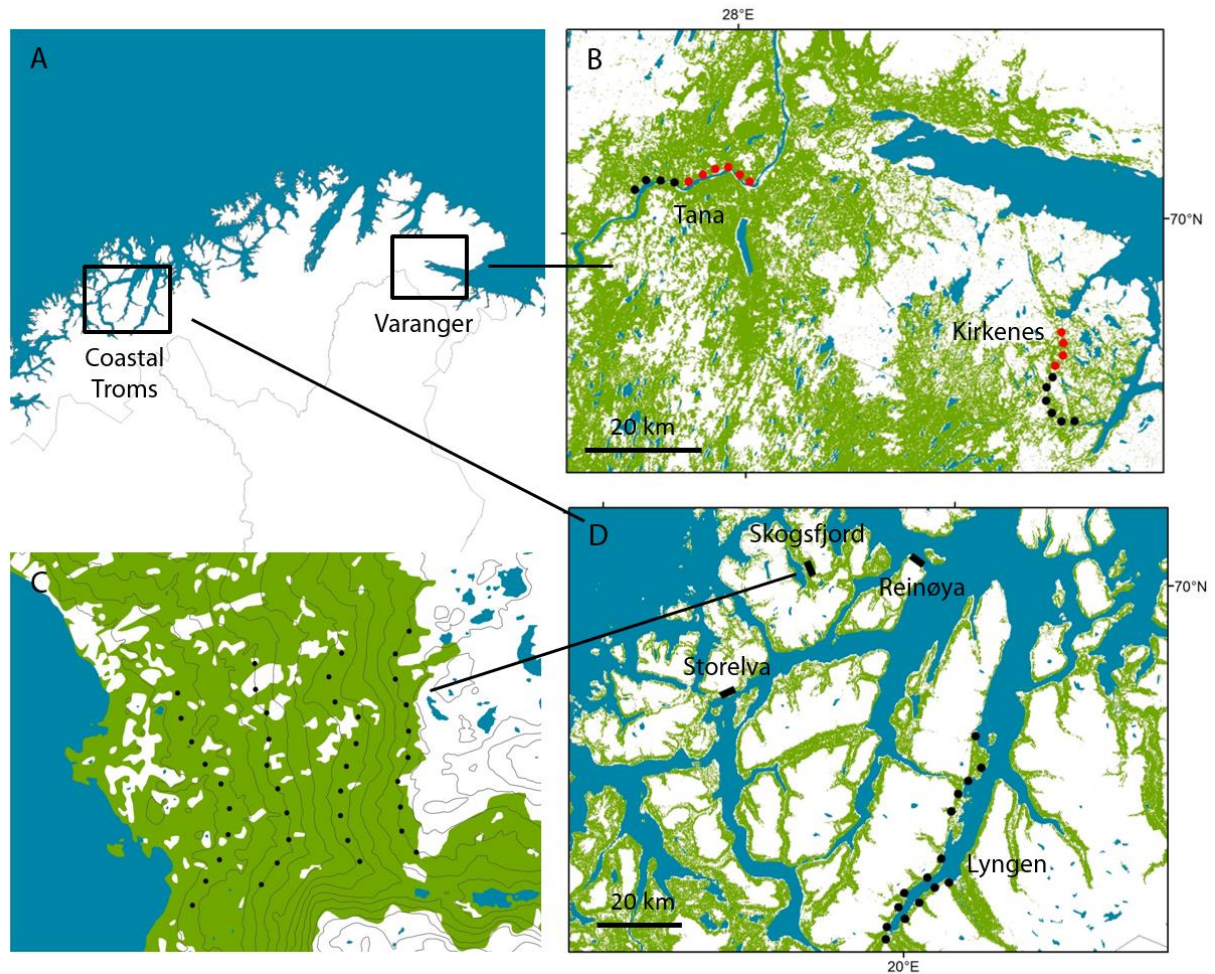
- III a. How does larval parasitoid species-richness and total larval parasitism rates in the mountain birch forest vary among the native geometrid *E. autumnata*, the long established invader *O. brumata* and the recent invader *A. aurantiaria*?
- III b. How rapidly are the larval parasitoid guilds of the 2 invasive geometrids approaching native levels of species-richness and prevalence (as represented by *E. autumnata*)?
- III c. Is release from larval parasitism likely to influence the climate-induced establishment and spread of invasive geometrids in the mountain birch forest?

### Study IV

- IV a. What is the magnitude of short-term numerical responses of saproxylic beetles to dead wood generated by moth outbreaks?
- IV b. Are the numerical responses of saproxylic beetles weak compared to the magnitude of dead wood resource input, suggesting important constraints on beetle responses?
- IV c. Have numerical responses occurred only in saproxylic beetle species that are associated with dead wood in a particular stage of decay?
- IV d. Has the outbreak caused changes in saproxylic beetle community structure, as would be expected if only a subset of the species in the community have responded numerically to the outbreak (cf. question 3)?

### Study V

- V a. How is the abundance and species-richness of bird communities in the mountain birch forest affected by forest damage caused by moth outbreaks?
- V b. Does the response of individual bird species depend on their foraging ecology?



**Figure 5.** Overview maps of study regions and sampling stations. A: Map of northern Norway, indicating the locations of the 2 main study regions – coastal Troms and Varanger. B: Map of the Varanger study region, showing the sampling stations of the 2 transects Tana and Kirkenes. Red and black dots represent damaged and undamaged stations, respectively (see section 2.3.4 for explanation). D: Map of the study region in coastal Troms, showing the sampling stations of the Lyngen transect (black dots) and the 3 altitudinal gradients, Skogsfjord, Storelva and Reinøya (black rectangles). Note that each dot in Lyngen represents a pair of sampling stations, one at 30 and one at 100 m.a.s.l. C: Map of the detailed layout of sampling stations (black dots) in the Skogsfjord altitudinal gradient (see section 2.3.2 for details). The gradients at Storelva and Reinøya have a similar design.

**Table 1.** Overview of the sampling locations used for the studies in this thesis. See Fig. 5 for a map over the locations.

Study	Sampling locations
I	Lyngen
II	Skogsfjord
III	Lyngen, Skogsfjord, Storelva and Reinøya
IV	Kirkenes and Tana
V	Kirkenes and Tana

## 2. Materials and methods

### 2.1. Study regions

All of the field work for the present project was conducted in mountain birch forest in northern Fennoscandia. Mountain birch is by far the most common deciduous tree species in this region, and it forms large tracts of forest (see the cover page of study IV for an example) in the transition zone between the boreal coniferous forest to the south and the tundra to the north. These birch forests are found in both coastal and inland climates and show remarkable variation in stature and growth form. Mountain birch forest growing on nutrient poor soils is dominated by small polycormic (i.e. multi-stemmed) trees, where individual trunks are usually well below 15 cm in diameter and rarely exceed heights of 5 – 6 meters (Fig. 3). In contrast, forests on richer soils are dominated by trees with fewer and more massive trunks, or even monocormic (i.e. single-stemmed) trees (Fig. 4). These 2 extremes are part of a continuum, and a wide variation of intermediate forms is found throughout the range of the mountain birch.

My sampling locations were divided between 2 geographical areas, namely the coastal region of Troms County, North-west Norway (hereafter coastal Troms), and the Varanger region in Finnmark County, North-east Norway (hereafter Varanger) (Fig. 5A). Study I – III, focusing on larval parasitoids were conducted in coastal Troms, for the most part in healthy mountain birch forest. Meanwhile, Study IV and V, focusing on the impacts of moth outbreaks on saproxylic beetles and birds, were conducted in Varanger, where much of the birch forest was severely damaged by moth outbreaks during the first decade of the 2000s (section 1.4.3) (Fig 1C – E. Cover page of study V). The climate in coastal Troms is oceanic, with mild winters, cool summers and much precipitation. Tromsø has a mean temperature of -3.8°C and 11.8°C in January and July, respectively, and precipitation of about 1000 mm per year (meteorological station at Tromsø Airport. 69°38' N, 18°57' E). Varanger has a slightly more continental climate, with less precipitation and more pronounced differences in temperature between seasons. Mean temperatures are -12.2°C for January and 12.3°C for July, while precipitation is about 450 mm per year (Rustefjelbma meteorological station. 70°23' N, 28°11' E).

### 2.2. Study species

#### 2.2.1. Geometrid moths

*E. autumnata*, *O. brumata* and *A. aurantiaria* (Fig. 2A – F) are all members of the insect order Lepidoptera and the family Geometridae. *E. autumnata* and *O. brumata* belong to the subfamily Larentiinae, while *A. aurantiaria* belongs to the Ennominae. All 3 species have holometabolous life cycles which invariably have a single generation per year. Adult moths are active during night in the autumn. The adult flight period in northern Fennoscandia typically occurs from mid-August and mid-September for *E. autumnata* and roughly 1 month later for *O. brumata*. The flight period of *A. aurantiaria* in this region has not been subject to systematic observation, but it appears to be somewhat intermediate between the other 2 moth species (OPLV pers obs). Both sexes are winged in *E. autumnata*, although the females are poor fliers. In *O. brumata* and *A. aurantiaria*, the females have strongly reduced wings and are flightless. Female moths have high potential fecundity and have been recorded to lay a maximum of approximately 250 eggs in *E. autumnata* and *O. brumata* (Heisswolf *et al.* 2009; Klemola *et al.* 2009). However, realised egg production depends strongly on resource acquisition during the larval stage, since adult moths do not feed. Females lay their eggs singly on the trunks and branches of trees, usually somewhat hidden under lichens or crevasses in the bark. The eggs are the overwintering stage and are hence extremely resistant to cold, tolerating temperatures down to approximately -36°C for *E. autumnata* and *O. brumata* and -31°C for *A. aurantiaria* (Ammunet *et al.* 2012).

The eggs hatch to produce tiny larvae around the time of birch budburst in spring. This usually occurs during the second half of May in northern Fennoscandia. As is the case in many species



of forest Lepidoptera (van Asch & Visser 2007), the hatching of the larvae needs to be well synchronized with the budburst of the host plant. Larvae that hatch too long before budburst will starve due to lack of birch foliage. Meanwhile, larvae that hatch too long after budburst suffer reduced food quality, because birch leaves undergo mechanical toughening and accumulate defensive chemicals as they grow older. The larvae feed on birch leaves throughout spring and early summer and pass through a total of 5 instars. Larvae of *E. autumnata* and *A. aurantiaria* feed openly on the leaves, while *O. brumata* larvae prefer to feed between leaves that are loosely spun together by silk, especially in the earlier instars. The development rate of the larvae is strongly dependent on temperature, so the time required to complete the larval stage may vary between roughly 3 and 6 weeks. However, larval development is typically complete at some point between mid-June and mid-July in northern Fennoscandia. The larvae then descend to the ground and pupate 1 – 2 cm beneath the soil surface.

### 2.2.2. Larval parasitoids

Approximately 10 larval parasitoid species are associated with *E. autumnata*, *O. brumata* and *A. aurantiaria* in coastal Troms. Fig. 2G and H show the larval and adult morphology of 1 commonly encountered species. The exact number of parasitoid species in the region is difficult to establish due to taxonomic uncertainties (Box 3). Because of these taxonomic issues, the term parasitoid “group” has been used as a substitute for parasitoid “species” throughout study I – III (Box 3). This practice will also be followed throughout the rest of this thesis. All of the studied parasitoids are wasps (order Hymenoptera) and most of them belong to the 2 families Ichneumonidae and Braconidae. In addition, there is a single parasitoid group from the family Eulophidae. All groups lay their eggs in or on moth larvae during spring and early summer. When the parasitoid larvae emerge from the eggs, they start to feed on the still living moth larvae. All parasitoid groups are so-called koinobionts (Askew & Shaw 1986), implying that the moth larvae continue to feed and function normally after they have been parasitized. All of the Ichneumonid and Braconid groups are endoparasitoids, whose larvae develop inside the body of the moth host larvae. The Eulophid is an ectoparasitoid, whose larvae develop on the external surface of the host.

Host larvae are normally not killed until the development of the parasitoid larvae is complete. The developmental stage of the host where this happens varies among parasitoid groups. For the present project, I made a distinction between early- and late eclosing groups. Early eclosing groups kill the host during the larval stage. For most groups, this happens because the parasitoid larvae emerge through the host body wall before spinning their cocoons and pupating. *Aleiodes gastritor* is an exception in that it mummifies the host larvae and subsequently pupates inside it. Late eclosing parasitoid groups kill the host after it has pupated. These groups do not leave the host, so their cocoons are found inside the remains of dead moth pupae. All of the parasitoid groups overwinter in cocoons spun by the parasitoid larvae. Exceptions are *A. gastritor*, who overwinters inside mummified host larvae and *Agrypon flaveolatum*, who overwinters as an adult wasp inside dead moth pupae. Apart from these basic facts, little is known about the biology of most of the larval parasitoids of the 3 focal moths.

## 2.3. Study design

### 2.3.1. Study I

As outlined in section 1.4.8, study I focused on the prediction that a larval parasitoid guild organized by a competitive lottery should exhibit a variable species composition even across a homogeneous landscape. Because nothing was known about the sensitivity of the studied larval parasitoids to environmental factors, and because the resources available for this largely exploratory study were limited, I did not approach this prediction by establishing a design that aimed to minimize variation in specific environmental factors. Rather, I tested the prediction

## Box 2. Sampling and rearing of larvae for estimation of parasitism rates

Sampling of moth larvae in the field, and subsequent rearing in the lab, was the methodology used to obtain estimates of larval parasitism rates in study I, II and III. Larvae are sampled by shaking birch branches over a large plastic box. This dislodges the larvae into the box, so that they can be easily collected, but rarely causes physical harm to the larvae. The method is equally effective for sampling all 3 geometrid species, since their larvae occur in the exact same habitat (section 2.2.1). Note that station-specific estimates of larval density are obtained in a similar way, by counting the number of larvae that are dislodged by shaking 10 haphazardly sampled birch branches of roughly 1 m length thoroughly over the box [see Ims *et al.* (2004) for details on this method, which played a relatively minor role in data collection for the present project].

Larvae are usually sampled during instar 4 or 5. It is assumed that the majority of parasitoid attacks have occurred at this time, so that a reasonable estimate of the total mortality due to larval parasitism (i.e. total larval parasitism rate) can be obtained. Study II was an exception, in that larvae were collected throughout most of the larval stage to study the phenology of parasitoid attacks (section 2.3.2). To ensure robust estimates of parasitism rates, at least 20 larvae are gathered per sampling station whenever possible. These larvae are collected within a radius of 20 – 30 m of the station. Larvae that are collected are transferred to a soft mesh bag, containing some birch leaves, for transport back to the lab.

In the lab, the larvae are transferred to 1-liter plastic boxes for rearing. The boxes contain a thin layer (1 – 2 cm) of moist soil where the larvae can pupate and a small amount of *Sphagnum* moss to help retain moisture in the boxes. A maximum of 20 larvae are kept in each box. Larvae are fed with freshly clipped birch leaves every third day. When rearing larvae of the first 3 instars, care is taken to provide leaves that are soft and not too far developed. This is less of a consideration for larvae of the last 2 instars, which would normally feed on older and tougher leaves. During feeding, the larvae are counted and mortality due to emergence of early eclosing parasitoids and other factors is recorded. A parasitism event is only recorded when a parasitoid cocoon is found in the box. Parasitism rates may thus be slightly underestimated, because larvae that perish from the stress of containing a parasitoid before the parasitoid has emerged are recorded as unexplained mortality. This is unlikely to be a major bias though, since unexplained mortality rarely exceeds 1 – 2 larvae per box, while total parasitism rates are frequently in the range of 30 – 60 %.

The boxes are usually kept in the laboratory while the larvae are being reared. This is for practical reasons, since the larvae develop more rapidly at room temperature than under ambient conditions (the air temperature in the study region rarely approaches 20°C during the larval season). Experience suggests that the survival and performance of the larvae is similar for boxes that are stored outdoors and in the lab. Thus, I have no reason to believe that parasitism rates should be importantly affected keeping the boxes indoors either.

When the larvae have pupated, the boxes are stored outdoors, under ambient temperature conditions, until all adult moths have emerged. Subsequently, the soil and moss is carefully examined to detect the remains of moth pupae that have hatched to produce adults and pupae that have died before hatching. Dead pupae are opened to check whether they contain late eclosing parasitoid species. When this activity has been completed, the rearing project concludes and the logs can be summarized. The final dataset will only contain individuals whose fates have been recorded, i.e. individuals that emerged as adults, were killed by parasitoids or died from other causes.

on a dataset that was already available when I joined the Birchmoth project. The dataset originated from a large-scale transect that had been established around the inner part of the Lyngen fjord (69°20' N, 20°00' E) in coastal Troms in 2005 (Fig. 5D). The transect was 70 km long and had 15 more or less equally spaced sampling stations at each of the altitudes 30 and 100 m.a.s.l. Estimates of larval parasitism and larval density (Box 2) of *E. autumnata* and *O. brumata* were available for each station, but only *O. brumata* had been sampled in sufficient quantities to provide robust estimates of parasitism rates at the station-level. Thus, the analysis focused on this moth species (section 2.4.2). The transect ran through an almost continuous belt of mountain birch forest, which was expected to be largely homogeneous in terms of forest age and structure. Moreover, data from 3 climate stations located close to station 1, 5 and 12 suggested that there were minimal differences in long-term average air temperatures along the transect (Appendix 1 of Study I). Thereby, this dataset was suitable for conducting a simple test of the lottery model by exploring variation in larval parasitoid guild structure across a landscape with little environmental variation.

### 2.3.2. Study II

The data for study II was collected using an altitudinal gradient design that has been at the core of the activities of the Birchmoth project in coastal Troms since 2001. As of 2014, the project has a total of 3 gradients (Fig. 5D), located at Skogsfjord (69°55' N, 19°18' E – Established in 2008), Storelva (69°38' N, 18°57' E – Established in 2006) and Reinøya (70°00' N, 19°49'E – Established in 2001). These gradients are established by selecting a roughly 2 km long section of slope which is covered by mountain birch forest from its base and up to the treeline ( $\approx$  250 m.a.s.l.). A roughly linear transect with 10 sampling stations, separated by about 200 m, is laid out at each of the altitudes 30, 100, 170 and 240 m.a.s.l. (50 m at Skogsfjord due to topographical reasons). Thus, a gradient has 40 sampling stations in total. Fig. 5C shows the layout of stations in the Skogsfjord gradient, which is representative also for Storelva and Reinøya. The replication within each altitude allows for robust inference about altitudinal variation in the variables being studied. Because temperature drops with increasing altitude, the altitudinal gradients also represent a gradient in phenology for ectothermic organisms. It has been shown that this gradient amounts to a roughly 1-week delay in the phenology of moth larvae between 30 and 240 m at Reinøya (Mjaaseth *et al.* 2005). This corresponds to approximately 1 larval instar.

The sampling for study II was conducted in the Skogsfjord gradient. At the time of sampling – in the summer of 2008 – this location harboured a severe but local outbreak of *O. brumata* close to the treeline. There was a distinct altitudinal gradient in larval density, with defoliation of the birch forest gradually increasing from close to zero at 50 m to almost 100 % at 240 m (Fig. 6). The outbreak had been ongoing since 2006 (Jepsen *et al.* 2009a), so the prevalence of parasitoids was expected to be high throughout the area. Thus, Skogsfjord was a suitable location for testing the hypothesis that altitudinal gradients in *O. brumata* density resulted from progressively poorer phenological matching between larvae and parasitoids with increasing altitude. Owing to the high logistic demands of gathering and rearing the multiple larval samples needed for the study (see below), only 5 sampling stations were used within each altitude.

To study the phenology of parasitoid attacks, 3 consecutive larval samples (Box 2) were taken at each altitude. The samples were separated by roughly a week, and all 4 altitudes were sampled within the span of 2 days for each of the 3 samples. Thus, within each altitude, the 3 samples would represent a temporal gradient in phenology. Meanwhile, within each sample, the 4 altitudes would represent a spatial gradient in phenology. For a parasitoid group flying early in the larval season, parasitism rates would be expected to be similar for larvae gathered at all 3 sampling dates (i.e. most attacks should have happened already before the first date).

Meanwhile, a later flying parasitoid group should increase in prevalence towards the later sampling dates. Further, within dates, a decline in parasitism with increasing altitude would be expected, due to the altitudinal phenology gradient (at least for parasitoid groups that were still flying at the date in question).

To assess whether individual differences in phenology between larvae affected the risk of parasitism, larvae were separated according to instar within a few hours of sampling. Larvae of different instars were subsequently reared separately, to produce instar-specific estimates of parasitism. The larval body grows continuously throughout each instar, but larval head capsules are sclerotized and do not grow within instars. Thus, when a larval sample contains different instars, they can be easily distinguished by the characteristic size of their head capsules.

### 2.3.3. Study III

To study the identity and species-richness of the larval parasitoids attacking *E. autumnata*, *O. brumata* and *A. aurantiaria* in coastal Troms, I drew together all of the parasitism data (Box 2) that the Birchmoth project had gathered in this region between 2001 and 2011. Parasitism data had been collected at the 4 locations described in section 2.3.1 and 2.3.2, namely the large-scale transect in Lyngen and the 3 altitudinal gradients at Skogsfjord, Storelva and Reinøya (Fig. 5D). For each of these 4 locations, I compiled a list of the larval parasitoid groups that had been reared from each geometrid species throughout the sampling period.

Larvae of the different geometrid species had been collected from populations of highly variable densities and cycle phases. Thus, because parasitism rates are expected to vary according to both moth density and cycle phase, it was not meaningful to calculate a single overall parasitism rate across the entire larval sample of each geometrid. For comparing total parasitism rates among geometrids, I rather selected locations where different geometrid species had been sampled while showing comparable densities. Such data was available for *O. brumata* and *A. aurantiaria* at Storelva for the period 2006 – 2008, and for *O. brumata* and *E. autumnata* at Reinøya for the period 2001 – 2005. A comparison of total larval parasitism rates between *O. brumata* and *E. autumnata* at Reinøya was published in Schott *et al.* (2012). Meanwhile, a comparison of parasitism rates between *O. brumata* and *A. aurantiaria* at Storelva became a component of my study III.

I studied the larval parasitoid guilds of the 3 geometrids in Western Europe – where all 3 species are native – by reviewing the published literature on parasitism of these species. For each geometrid, I compiled a list of the larval parasitoid species that had reared in each country where parasitism studies had been conducted. The number of larvae that had been reared and the number of sites that had been sampled in each country were recorded as measures of sample size.

### 2.3.4. Study IV

As outlined in section 1.4.4, I used a spatial contrast between damaged and undamaged birch forest to study the numerical response of saproxylic beetles to dead wood left by moth outbreaks. This contrast was studied in 2 areas in Varanger, namely Tana (70°03′ N, 27°45′ E) and Kirkenes (69°46′ N, 29°20′ E) (Fig. 5B), which had been affected by outbreaks in 2006 – 2007 and 2007 – 2009, respectively. In both of these areas, I used a roughly linear transect that crossed a sharp transition between forest that had been severely damaged by outbreaks and forest that was still healthy. Both transects were about 20 km long and consisted of 10 more or less equally spaced sampling stations (Fig. 5B). The transects were established in 2011. At this time, the outbreaks had collapsed in both areas, so that the density of moth larvae was extremely low throughout the transects. A visual scoring of the condition of birch trees around the stations (methodology described in study IV and V) showed that the great majority of stems were dead at stations 1- 4 in Kirkenes and stations 1 – 6 in Tana. Meanwhile, most of the stems at the

remaining sampling stations were either undamaged or showed light loss of foliage compared to a healthy stem (this is typical for normal, healthy mountain birch forest). These station-specific damage scores were representative not only for the state of the forest in the immediate vicinity of the stations, but also at the landscape level. Thus, in practice, my stations represented spatial replicates within 2 different forest types, namely forest that had been severely damaged by the moth outbreak and forest that was undamaged. I therefore made a simple dichotomous grouping where stations were designated as being either “damaged” or “undamaged” (the terms “dead” and “living” were used in study IV, while “damaged” or “undamaged” were used in study V. For simplicity, I use only the latter terms in this thesis).

In 2011 and 2012, beetles were sampled along the transects by means of window traps (Fig. 7). These traps consist of a pair of plexiglass plates that intercept insects in flight and a funnel that causes the insects to fall down into a bottle of preserving liquid (in this case glycol thinned down by water). Three traps were installed at each station, resulting in a total of 30 traps per transect. The traps were operative from mid-June to mid-August, thereby covering the peak of insect flight activity in the study region. Insect samples from the traps were processed in the lab to extract all beetle individuals. The beetles were thereafter sent to a taxonomic expert for identification. Thus, for each trap, I obtained a list of the number of individuals that had been captured of each beetle species. The species lists were subsequently pooled across the 3 traps within each station, so as to produce a single list for each station in each year.

Beetle species were classified into 3 groups based on their degree of association with dead wood, namely obligate saproxylic, facultative saproxylic and non-saproxylic. These groups are hereafter referred to as dead wood association (DWA) groups.

#### *2.3.5. Study V*

The sampling for study V was conducted in the same transects that were described for study IV (section 2.3.4) (Fig. 5B). The bird community at each station was sampled by means of a census technique, where an observer recorded all birds (species and number of individuals) that could be seen or heard from the centre point of the station during a period of 15 minutes. This census was repeated 3 times per station in each of the years 2011, 2012 and 2013. In each year, the 3 visits were conducted within the span of 3 days across all stations in both transects. The census period fell between 25 June and 1 July in all 3 years, and thus represented the early part of the breeding season for most bird species in the study region. The purpose of repeatedly sampling the bird community within each year was to obtain a dataset that could be analysed by means of a hierarchical model. The advantages of such models are outlined in section 2.4.6.

## **2.4. Statistical analyses**

### *2.4.1. Analytical philosophy and general considerations*

Throughout the studies of this project, I endeavoured to let the data speak for themselves as much as possible, while using statistics mainly as a tool to aid interpretation. Thus, whenever possible, I presented plots of raw data, often overlain with predictions from statistical models. I considered this to be more transparent and informative to the reader than only presenting model outputs.

As outlined in section 2.3, all of my studies involved spatial replication, with sampling being repeated at a number of well-separated sampling stations. The individual sampling stations were treated as independent replicates in most of the statistical analyses conducted throughout this project. The only exception was study III, where there was some aggregation of data across stations prior to analysis (section 2.4.4).

Owing to their flexibility and reliability, generalized linear models (GLMs) were the main tools of analysis in most of the studies. My data predominantly consisted of counts of individuals and proportions (typically the proportion of larvae parasitized), and these were analysed with log

and logit link functions, and Poisson and Binomial error distributions – i.e. log-linear and logistic models – respectively. This also applied for the generalized additive models (GAMs) used in study I (section 2.4.2).

The fit of statistical models was always assessed using appropriate diagnostic tools, as described in the individual studies. No major difficulties with model fit were encountered for any of the studies, but a varying degrees of overdispersion was often an issue when fitting GLMs. This was adjusted for by implementing quasi-likelihood corrections. When models with alternative sets of predictor variables were considered, model selection was performed using appropriate techniques for the model type in question. Approaches to model selection are described in detail in the individual studies.

All analyses and plotting were conducted with the statistical software R (R Development Core Team 2012), using the extension packages (specified in the studies) that were needed for the analytical tasks at hand. In the following sections, I summarize the reasoning and methods underlying the analyses for the different studies.

#### 2.4.2. Study I

For study I, I needed to assess how total parasitism rates and the prevalence of individual parasitoid groups in *O. brumata* varied along the transect in Lyngen. I had no *a priori* expectations of how parasitism rates should be patterned along the transect. Thus, I needed a statistical tool that would allow me to identify the spatial patterns that might be present, regardless of their shape. GAM was suitable for this purpose, because it draws the best-fitting curve through a cloud of datapoints, without having to make prior assumptions about the shape of the curve (Wood 2006). Moreover, GAM provides a statistical test of whether there are significant non-linear patterns in the data. Thus, I fitted separate GAM models with the prevalence of the 3 most common larval parasitoid groups and total parasitism rates as response variables, and the over-land distance from the first station in the transect as predictor. Similar models were fitted for the density of *O. brumata* and *E. autumnata* larvae, to assess whether there were spatial patterns in host density that coincided with observed patterns in parasitism. For all response variables, I fitted a single GAM curve through the datapoints from the sampling stations at 30 and 100 m altitudes. This made little difference for the conclusions about spatial patterns, but allowed more robust model fits (see study I for details). The relationship between larval density and parasitism was also assessed by regressing the parasitism rates of the 3 most common parasitoid groups on *O. brumata* density by means of logistic regression models.

#### 2.4.3. Study II

The aim of the analysis for study II was to quantify the effects of sampling date and altitude on larval parasitism rates, so as to assess temporal and spatial patterns in parasitoid phenology, both for individual parasitoid groups and the larval parasitoid guild as a whole. Thus, I fitted logistic models using total and species-specific parasitism rates as response variables, and date (1, 2 or 3), altitude (50, 100, 170 or 240 m) and their interaction as predictors. Date and altitude were taken as categorical predictors, since their effects appeared to be non-linear for some parasitoid groups. These models aimed to estimate the effects of date and altitude on parasitism across the entire larval population. After these effects had been estimated, I added larval instar (2, 3, 4 or 5) at the time of sampling as an additional predictor to the models. This was done to estimate how variation in larval phenology, within dates and altitudes, affected the risk of parasitism. Instar appeared to have linear effects and was therefore taken as a continuous variable.

Model selection did not support interactions between predictor variables in any of the models that were fitted. The main effects of the predictors were never considered for removal, since the

analysis aimed to estimate their effects. Thus, all models used for study II included only the main effects of the predictors.

#### 2.4.4. Study III

Although study III was based on an extensive dataset, its use of statistics was modest. I judged that the larval sample sizes obtained for the 3 geometrids between 2001 and 2011 were large enough to detect any larval parasitoid groups of ecological importance in the study region. It was therefore unnecessary to apply statistical techniques (such as rarefaction) to adjust parasitoid species-richness for the different geometrids according to the number of larvae sampled. The studies that I surveyed for information on larval parasitism of the geometrids in Western Europe varied widely in the methods that they had used and the amount of information they provided about their methodology. Thus, the information I obtained from these studies was poorly suited for statistical analyses. I therefore judged that simple descriptive summaries was the most appropriate way of presenting the results from the literature survey.

For the reasons above, statistics were only used to analyse parasitism patterns of *O. brumata* and *A. aurantiaria* at Storelva during 2006 – 2008. Total parasitism rates of the 2 geometrids were compared with a logistic model that regressed parasitism of *A. aurantiaria* on logit transformed parasitism of *O. brumata*. Logistic models were also used to regress the total parasitism rates of both geometrids on their respective, log transformed, current-year, larval densities. Because the *O. brumata* and *A. aurantiaria* shared a parasitoid group, their total parasitism rates were also modelled against the pooled larval density of both species. Since the station-specific larval samples were often rather small, I pooled the data across all sampling stations within each altitude in each year. This provided a dataset of 12 year- and altitude-specific parasitism rates. Larval densities were averaged within altitudes to provide corresponding year- and altitude-specific datapoints. This handling of the data provided robust estimates of parasitism and density within altitudes but also resulted in a small number of datapoints. Thus, it was not possible to regress parasitism rates on larval densities from previous years (which were only available back to 2006).

#### 2.4.5. Study IV

The analysis for study IV aimed to assess the short-term numerical responses of saproxylic beetles to the dead wood left by the outbreak by comparing beetle abundance and community structure between damaged and undamaged forest. Thus, all analyses focused on the categorical predictor variable forest damage, with the 2 levels damaged (greatly elevated availability of dead wood) and undamaged (normal availability of dead wood). In addition, the categorical predictors year (2011 and 2012) and location (Kirkenes and Tana) were used to account for variation in the beetle community between the 2 years and transects of the study.

I used log-linear models to assess how the response variable beetle abundance (counts of individuals) was affected by the predictors forest damage, location, year and their two-way interactions. This was done for the summed counts of all species in each of the 3 DWA groups (section 2.3.4). This analysis was also performed separately for the counts of the 9 most abundant beetle species in the dataset (all with counts > 80 individuals), which collectively accounted for almost 70 % of the sampled individuals. The raw counts of the DWA groups showed conspicuous large-scale spatial gradients along the transects, which did not appear to be consistently related to forest damage. Thus, to help clarify if saproxylic beetles had responded numerically to the outbreak, I also modelled the proportion that each DWA group constituted, out of the total beetle count (all species in the dataset summed). Proportional counts were taken as response variables in logistic regression models, using the same predictors as for the log-linear models described above. Model selection was used to identify the appropriate mixture of predictors and interactions for each different model. The main effect of forest

damage was never considered for removal, since the aim of the analysis was to estimate the effects of this predictor.

Differences in beetle community structure between damaged and undamaged forest were investigated using redundancy analysis (RDA). Hellinger transformed (Legendre & Gallagher 2001) beetle counts were taken as response variables, while forest damage, year and location were used as predictors. Further, I used variance partitioning to estimate how much of the variance in beetle community structure was explained by forest damage, year and location. RDA and variance partitioning was performed separately for each DWA group. These analyses were also conducted for the beetle community as a whole, to assess the overall community response to the outbreak.

#### 2.4.6. Study V

The aim of the analysis for study V was similar to that of study IV, i.e. to compare the bird community between damaged and undamaged forest to assess short-term community responses to the outbreak. The analysis was based on a hierarchical community model (Iknayan *et al.* 2014). Because such models are still not established as standard methodology in ecological studies, it is appropriate to outline their advantages. In brief, hierarchical models assume that a dataset on species abundances reflects i) the true underlying abundances of the species – which cannot be observed directly – and ii) the sampling process – where there is always a certain probability that organisms go undetected even if they are present. By modelling detection and true abundance as separate processes, hierarchical models allow abundance to be estimated after accounting for imperfect detection. Detection probabilities can be estimated when sampling sites have been visited multiple times, so that repeated attempts of detecting organisms have been made. Hence the multiple visits to the sampling sites in study V in each year (section 2.3.5).

The hierarchical model I fitted is described in detail in study V. In short, I modelled the true abundance (i.e. number of individuals) of each bird species as a Poisson variable, influenced by the predictors forest damage (damaged and undamaged) and location (Kirkenes and Tana). Detection of individuals was modelled as a binomial variable, also influenced by damage and location. Year was not modelled as a predictor variable, since I had no explicit interest in estimating an effect of this variable. However, the model allowed detection probabilities and true abundances to vary between years, to account for temporal variation in the bird community. The inferences for study V were based exclusively on predictions and parameter estimates from the hierarchical model. In that sense, the study departed from my philosophy of presenting raw data together with model outputs (section 2.4.1). The reasoning of hierarchical modelling is that raw data are biased by imperfect detection of organisms and that the models correct for this bias. Within this framework, it makes little sense to present model predictions and raw data together, unless the goal is to investigate how the modelling affects the inferences derived from a dataset.

### 3. Results and discussion

#### 3.1 Study I

##### 3.1.1. Spatiotemporal dynamics of larval parasitoid guilds

My analysis of the dataset from the Lyngen transect revealed spatial patterns in larval parasitoid guild structure that were consistent with expectations from the lottery model. Specifically, there was a conspicuous tendency for spatial segregation in the occurrence of the 3 most common parasitoid groups, namely *Phobocampe* sp./*Sinophorus crassifemur*, *Cryptus titubator* and *A. flaveolatum*. The first 5 stations were dominated by *Phobocampe* sp./*S. crassifemur*, while the last 4 were dominated by *A. flaveolatum*. Meanwhile, *C. titubator* dominated most of the



stations around the middle of the transect. These patterns were emphasised by the GAM models, who showed that there were statistically significant non-linear patterns in the parasitism rates of all 3 groups along the transect. Thus, larval parasitoid guild structure showed pronounced spatial variation, despite the fact that there appeared to be little environmental variation along the transect. Moreover, the analysis gave no indication of consistent relationships between larval densities and parasitism patterns in any of the parasitoid groups. This result was encouraging, by providing some support for the idea of stochastic extinction-recolonization dynamics in the studied larval parasitoid guild.

This being said, it is important to be aware of the limitations of study I. The most obvious issue is that the degree of environmental variation along the transect was not quantified, but simply assumed to be minimal. Moreover, owing to the poor biological knowledge of the parasitoids, it was impossible to assess their sensitivity to any environmental variation that might have been present. Thus, the alternative deterministic explanation that the observed spatial patterns were simply caused by species-specific responses to changes in environmental conditions along the transect could not be rejected with any degree of confidence. A reviewer noted that the stochastic explanation for the patterns was certainly interesting, but that the study, as it stood, was entirely unable to distinguish it from a deterministic explanation based on parasitoid responses to environmental variation. I fully agree to this view.

Another limitation of study I is that it lacked temporal replication. Additional years of data would greatly have benefited the study, because it would have allowed assessment of the stability of the observed patterns over time. The lottery model predicts that the same parasitoid group should retain dominance at a site for as long as moth density is high enough to sustain the parasitoid population. Change in local dominance should only be possible when the reigning parasitoid group goes extinct due to a moth population collapse. Temporal replication would have allowed a test of this important prediction. Later studies of the same parasitoid guild in different locations in coastal Troms have included multiple years of data, and have found that the relative prevalence of different parasitoid groups at a given location can change strongly from one year to the next (Schott *et al.* 2012; Study III). This speaks against lottery competition as the main structuring mechanism of the larval parasitoid guild.

There are at least 2 other reasons why the lottery model is probably unsuitable for studied larval parasitoid guild. For one, the model asserts that species compete for vacant space and that the first species to colonize an empty patch will come to dominate it. It is easy to imagine that a species can monopolize a patch of space, but it is harder to see how the studied parasitoids could monopolize the larvae in a given area. Admittedly, if 2 parasitoid species attack the same larval instar, and the species which first deposits its eggs has a competitive advantage within the host, the species which is first present in an area may well be able to dominate it. However, as was demonstrated by study II, the larval parasitoid groups of *O. brumata* attack a range of different larval instars. If an early-flying parasitoid group oviposits in a larva, and the same larva is parasitized again (say, a few weeks later) by a late-flying group, the early group will either kill the newcomer or the opposite will happen, depending on which group is the stronger within-host competitor. It is difficult to see how the competitive balance between the early and late flying group should be shifted based on which group was first present in an area (although note that the competitive balance could easily change according to environmental conditions). This critique hits home heavily for study I, since *Phobocampe* sp./*S. crassifemur* attacks larvae during instar 1 – 2, while *A. flaveolatum* and *C. titubator* attack instar 4 – 5.

A second issue with the lottery model is that it assumes equal capacity for dispersal among competing species. The larval parasitoids of *O. brumata* vary considerably in size, with the largest group having a wingspan that is at least twice as long as that of the smallest group. Thus, there is little reason to expect that the capacity for colonizing vacant areas should be equal across all groups in this parasitoid guild. In defence of study I, the 3 parasitoid groups that

showed segregating distribution patterns are rather similar in size. Therefore, the assumption of similar dispersal capacity may hold for these 3 groups, if not for the guild as a whole.

If lottery competition is improbable, what is a more realistic model for the spatiotemporal dynamics of the larval parasitoid guild of *O. brumata*? I should stress that I regard the basic idea of local parasitoid extinctions after moth population collapses to be realistic. Moth populations can collapse to levels that are virtually undetectable, and subsequently remain in this state for several years. It therefore seems plausible that local parasitoid populations can be reduced to levels where they are prone to extinction due to stochastic variation in demographic and environmental factors. However, the frequency and spatial scale of such extinctions is difficult to judge. This must be expected to depend on how low moth populations drop, and how favourable climatic conditions are for the parasitoids in the critical years of low moth density. The dynamics of parasitoid recolonization after extinctions also reside in the realm of the speculative. Study I proposed that populations of different parasitoid species might be present only in widely dispersed patches after a trough in the moth population cycle. Such populations could serve as centres for parasitoid expansion when moth populations again increased. Gradual spatial expansion of parasitoids from epicentre populations could produce segregating distribution patterns on relatively large spatial scale, exactly as documented in study I. This still seems like a plausible scenario.

Notably, similar scenarios could arise even without local parasitoid extinctions. If the densities of different parasitoid groups differ at the outset of the increase phase of the moth cycle, these groups could show very different population trajectories over the following years. This is particularly likely if groups differ in maximal population growth rates or exhibit non-linear dynamics. Thus, stochastic variation in the size of low-density parasitoid populations during the through of the moth cycle could influence dominance relations within the larval parasitoid guild during the subsequent moth population peak. While this hypothesis seems plausible, it is difficult to reconcile it with the observation that the dominant parasitoid group at a location can change abruptly from year to year even at high moth densities (see above). The degree to which such dynamics would be stochastic is another matter, seeing as how given parasitoid groups could be favoured by given habitat characteristics. If this is the case, the population- density and survival of different groups during the through of the moth cycle would not vary randomly across a landscape. The probability of colonization and the rate of population growth for different parasitoids would also vary consistently between locations. Thus, there would be a strong deterministic component to the spatial distribution of parasitoid groups.

It is clear from the above that study I, with its single-year snapshot of a spatial pattern, had little hope of discerning the spatiotemporal dynamics of the larval parasitoid guild of *O. brumata*. These dynamics may be shaped by a complex array of both stochastic and deterministic processes, which we know very little about at present. Nevertheless, I think that the study made a valuable contribution by exploring the idea of stochastic extinction-recolonization dynamics in parasitoids of geometrid moths [the possibility that parasitoids can suffer local extinction following moth population collapses was introduced already by Ruohomäki (1994)]. The study also presented intriguing large-scale spatial patterns in parasitoid guild structure, which had not previously been documented for the study system, and which are in need of explanation. I am happy that the reviewers recognized these positive aspects of the study (as well as its limitations) and provided constructive criticisms that helped it to become published. As for the proposed lottery model however, it should probably have been left with the fishes (Munday 2004).

### *3.1.2 Relationships between larval parasitoid guild structure and total larval parasitism rates*

Study I provided an important clue to the functionality of the studied larval parasitoid guild. In spite of the conspicuous changes in larval parasitoid guild structure along the transect, there

were no consistent spatial patterns in the total parasitism rate. Total parasitism rates at the individual stations varied between 0.1 and 0.7, but the GAM curve for total parasitism was largely flat and indicated no significant spatial structuring along the transect. This finding indicates that the 3 parasitoid groups which dominated different sections of the transect have similar capacities for inflicting mortality on host populations. This, in turn, points towards a high degree of functional redundancy among larval parasitoid species of birch forest geometrids. This topic is addressed in more detail in section 3.4.2.



**Figure. 6.** Severe defoliation of mountain birch close to the treeline at Skogsfjord (the sampling location for study II) in 2008. Brown belts of defoliated forest can be seen stretching across the landscape. Photo: Ole Petter Laksforsmo Vindstad.

### 3.2. Study II

#### 3.2.1. Phenological organization of the larval parasitoid guild of *O. brumata*

Study II revealed a remarkable degree of phenological structuring in the attack patterns of the larval parasitoid groups of *O. brumata*. In particular, the patterning of group-specific parasitism rates among sampling dates showed that the attacks of different parasitoid groups followed each other in a successional manner throughout the larval season. Table 2 provides an overview of the larval instars inferred to be attacked by the different parasitoids. Owing to the succession of attacks by different parasitoid groups, the total larval parasitism rate progressively increased throughout the 3 sampling dates. Further, it appeared that all larval instars were attacked by at least 1 parasitoid group.

Following the logic from sections 1.3.4 and, the phenological patterns revealed by study II have important implications for the probability of phenological mismatches between larvae and parasitoids. First, the study suggested that individual parasitoid groups target just 1 or 2 larval instars. If this is the case, it means that the parasitoids can successfully attack the larvae only during a rather short period of time (under typical temperature conditions, moth larvae take approximately 1 week to complete an instar in the study region). The impression of a limited

time window for larvae-parasitoid interactions was strengthened by the analysis of the effects of larval instar on parasitism. For all parasitoid groups where instar effects could be modelled, the analysis showed that parasitism rates decreased with increasing larval instar within dates and altitudes. This suggested that parasitoids prefer and/or have higher success with the less developed individuals within a population of larvae. This further stressed the importance of timing for the larvae-parasitoid interaction. It should be noted that the capacity of parasitoids for attacking different larval instars can only be decisively established by experiments. However, the weight of evidence from study II suggested that the larval parasitoids of *O. brumata* show a rather narrow instar-specificity.

A limited time window for successful interaction with larvae implies that parasitoids may be vulnerable to phenological mismatches with their hosts. One reason for this is that even small shifts in the relative timing of larvae- and parasitoid emergence could cause parasitoids to lose synchrony with susceptible larval instars. Another reason is that adverse weather conditions may prevent parasitoids from flying while larvae are vulnerable to attack. Adverse impacts on parasitoid activity by low temperatures, precipitation and high wind speeds have been documented in other systems (Nyrop & Simmons 1986; Gu & Dorn 2001; Menon *et al.* 2002; Zamani *et al.* 2006), and probably occur also for the presently studied parasitoids. The shorter the duration of the susceptible larval stages, the greater the risk that parasitoids will miss the chance for parasitism due to adverse conditions. It is particularly easy to envisage the occurrence of mismatches in climatically unstable coastal regions, where temperature and precipitation can fluctuate strongly both within and between years.

While study II indicated that individual parasitoid groups may be vulnerable to host asynchrony, it also suggested that total larval parasitism rates are more robust to such events. The main argument for this is extremely simple: because the attacks of different parasitoid groups are distributed across the entire larval season, rather than aggregated to a short time interval, there is less risk that a freak climatic event will cause many groups to become asynchronous with larvae. In other words there is a spreading-of-risk effect which should increase the probability that at least some parasitoid groups will maintain host synchrony.

It might also be speculated that the segregated flying times of different parasitoids increase the opportunity for compensatory dynamics with respect to total parasitism rates. Asynchrony of some parasitoid groups may benefit species that fly at other times, by reducing interspecific competition for larvae. For instance, an early flying group will not find itself displaced from larvae by a competitively superior later flying group if the latter group suffers a severe mismatch. Meanwhile, if an early flying group becomes mismatched, larvae that went unparasitized by that group may later be attacked by late flying group. In both cases, the mismatch of one group will be compensated for by the action of another, thus stabilizing the total parasitism rate. The idea of such compensatory dynamics in larval parasitoid guilds of geometrids is supported by observations from study I and III. Study I suggested that total larval parasitism rates are independent of which parasitoid group dominates the guild. Study III indicated that total parasitism is also independent of the number of attacking parasitoid species. Both observations suggest that a mismatch in some larval parasitoid groups can be compensated for by the action of other guild members (see also section 3.4.2.).

An important aspect that was inadequately stressed by study II is that compensation requires larvae which go unparasitized by a mismatched parasitoid group to be exploited by other groups. Hence, it assumes that parasitoid groups compete for the same larvae. Multiparasitism of *E. autumnata* larvae has been documented (Klemola *et al.* 2009), but nothing is known about the extent of interspecific competition among the studied parasitoids. The assumption of interspecific competition therefore cannot be substantiated at present. Note, however, that

### Box 3. Parasitoid identification

Parasitoid wasps are an extremely species-rich group, but the morphology of parasitoid species is often non-distinct to human eyes. Identifying parasitoid species can thus be difficult even for experienced experts. This is a challenge for ecological studies, where there is often need to rear and identify many parasitoid individuals. To obtain a manageable identification protocol for the present project, I used a system where parasitoids with similar cocoon morphology were treated as single taxonomic units. This resulted in 9 different units (Table B3) which were easy to distinguish visually. An additional advantage was that parasitoids could be identified without being reared to adulthood. The drawback of the system was that different parasitoid species with similar cocoon morphology risked being lumped into the same taxonomic unit. To acknowledge this uncertainty, I adopted the term parasitoid “species group” instead of parasitoid “species” for the cocoon-based taxonomic units in papers I – III. The identities of adult specimens of the parasitoid groups had been assessed by experts before the start of my project. The original species names established in this way were presented in papers I – III. However, new information that came to light during the project period prompts re-evaluation of the identity of some of these names, as discussed below (summarized in table B3).

*Agrypon flaveolatum* (Grav.). Although this species attacks both *E. autumnata* and *O. brumata* in my study area, it only parasitizes in *E. autumnata* in continental Finland (Klemola *et al.* 2010). *A. flaveolatum* may thus encompass cryptic species that are specific to just 1 of the 2 geometrid species.

*Cryptus titubator* (Thunb.). During a recent rearing project of *O. brumata* (OPLV unpublished data), I obtained 2 morphologically distinct types of adult parasitoids (1 orange and 1 red and black) from cocoons assigned to the *C. titubator* group. Based on a photograph, Dr. Gavin Broad at the British Museum of Natural History identified the orange specimens to the genus *Netelia*, most likely the species *N. latungula* (Thoms.). This seems probable, since *N. latungula* is a common parasitoid of *O. brumata* further south in Europe (see study III). Arrangements were being made to send the red and black specimens to Professor Klaus Horstmann (retired from Würzburg University, Germany), but, sadly, Horstman died before the specimens reached him. No further progress has been made towards identifying these specimens. The specimens that were originally identified as *C. titubator* have been lost. It is therefore difficult to judge if the name *C. titubator* represents a misidentification of *N. latungula*, or the true identity of the unidentified red and black specimens. The name *C. titubator* thus requires further validation.

*Ichneumonidae* *indet.* This parasitoid is found as a small white larva inside dead *O. brumata* pupae. Identification has been problematic because I have never managed to rear these larvae to adult parasitoids. Ten larval specimens were subjected to DNA barcoding in 2010, but their sequences gave no matches in public barcode databases at that time. However, these databases expand rapidly, and re-submission of the *Ichneumonidae* *indet.* sequences to the Barcode of Life (BOLD) database in 2014 produced close matches (> 98% for all specimens and 100% for some) to another of my parasitoid groups, namely *A. flaveolatum*. The parasitoid originally designated as *A. flaveolatum* is found as a fully developed adult wasp inside dead moth pupae, and overwinters in this state. Thus, the finding that the unidentified larvae are probably *A. flaveolatum* suggests that these larvae died before completing their development (larvae show no signs of life when they are found) or that *A. flaveolatum* can overwinter as both larva and adult.

### Box 3. Parasitoid identification (continued)

*Protapanteles anchisiades* (Nix.)/*P. immunis* (Hal.)/*Cotesia salebrosa* (Marsh.). Specimens assigned to this parasitoid group have never been unambiguously identified, but suggested by experts to represent one of the 3 listed candidate species. Ruohomäki *et al.* (2013) recently confirmed that all 3 species attack *E. autumnata* in northern Scandinavia, so all of them are likely to occur also in my study area. Thus, this group probably contains all 3 of the listed candidate species.

**Braconidae indet.** (“Yellow Cluster” in study I): Ten adult specimens of this parasitoid were subjected to DNA barcoding in 2010, but, as for Ichneumonidae indet., the results were uninformative at the time. Re-submission of the Braconidae indet. sequences to the BOLD database in 2014 yielded a 100% match with the species *C. eulipis* (Nix.) for all specimens.

At present, I have no reason to believe that the identities assigned to *Aleiodes gastritor* (Thunb.), *Zelex deceptor* (Wesm.) or *Eulophus larvarum* (L.) are ambiguous. There has been no progress towards resolving the identity of *Phobocampe* sp./*Sinophorus crassifemur* (Thoms.) during the project.

**Table B3.** Overview of the parasitoid species groups presented in study I – III, with host species affinity and comments on taxonomic status (see main text of box 3 for details). EA = *E. autumnata*. OB = *O. brumata*. AA = *A. aurantiaria*.

Parasitoid species group presented in study I – III	Host species	Comments
<b>Family Ichneumonidae</b>		
<i>Agrypon flaveolatum</i>	EA, OB	The group may contain cryptic species specific to EA or OB
<i>Cryptus titubator</i>	EA, OB	The group probably contains <i>Netelia latungula</i> . Validity of <i>C. titubator</i> is uncertain
<i>Phobocampe</i> sp./ <i>Sinophorus crassifemur</i>	EA, OB, AA	-
Ichneumonidae indet.	OB	True identity is probably <i>A. flaveolatum</i>
<b>Family Braconidae</b>		
<i>Aleiodes gastritor</i>	EA	-
<i>Protapanteles anchisiades</i> / <i>P. immunis</i> / <i>Cotesia salebrosa</i>	EA, OB	The group probably contains all 3 of the listed candidate species
<i>Zelex deceptor</i>	EA	-
Braconidae indet. (“Yellow cluster” in paper I)	OB	True identity is probably <i>C. eulipis</i>
<b>Family Eulophidae</b>		
<i>Eulophus larvarum</i>	EA, OB	-

competition should not be deemed unlikely because parasitism rates are usually far below 100%. This is because only a fraction of the larvae in a population may be susceptible to parasitism, depending on factors like body condition and immune status. Thus, parasitoids may in practice be competing for a subset of the larval population, causing parasitism to be less than 100% even in the presence of intense parasitoid competition.

The finding that the phenological organization of the larval parasitoid guild of *O. brumata* probably reduces the risk of severe larvae-parasitoid mismatch events, argues against such mismatches as an important influence on *O. brumata* population dynamics. Thus, study II did not support the hypothesis that the pronounced variation in amplitude of the *O. brumata* population cycle might be explained by stochastic climate-induced variation in larvae-parasitoid phenology matching. This conclusion could be generalized to *E. autumnata*, since Kaitaniemi & Ruohomäki (1999) showed that this geometrid is also attacked by a succession of different parasitoid species throughout its larval stage, much in the same way as was documented for *O. brumata* in study II. Thus, according to present knowledge, variation in phenological matching between larvae and birch host plants is probably of greater importance for geometrid dynamics than larvae-parasitoid matching.

### 3.2.2. Phenological mismatch between larvae and parasitoids at high altitudes?

While study II shed light on the phenological organization of the larval parasitoid guild of *O. brumata*, it allowed few conclusions about the possible role of larvae-parasitoid mismatches in explaining altitudinal variation in moth density. Almost all of the studied parasitoid groups (and hence also the total parasitism rate) showed decreasing prevalence with increasing altitude. However, study II did not allow these altitudinal clines in parasitism to be attributed to any particular mechanism. The clines could, of course, result from progressively poorer phenological matching between larvae and parasitoids with increasing altitude. However, they could equally well have been caused by reduced parasitoid activity in the lower temperatures at high altitudes, more intense predation on parasitoids at high altitudes, or a host of other abiotic and biotic factors varying along the altitudinal gradient. Further, parasitoids may simply have been unable to respond functionally and/or numerically to the extremely high densities of larvae at the highest altitudes in the gradient. In other words, the altitudinal variation in moth density may have been the cause, rather than the consequence, of altitudinal clines in parasitism. Study II did not allow discrimination among these alternative explanations. It should be noted though, that the study provided no indication of a greater delay in parasitoid phenology along the altitudinal gradient than the roughly 1 week phenological delay that has been documented between larval populations at 30 and 240 m altitudes. Thus, there was no indication that larvae-parasitoid mismatch effects were more likely to explain the altitudinal clines in parasitism than any other candidate mechanism.

### 3.2.3. Methodological implications for studies of larval parasitism

An aspect that was overlooked in the original discussion of study II is the implications of the observed temporal parasitism patterns for the timing of sampling in studies of larval parasitism of birch forest geometrids. The study revealed that the total larval parasitism rate of *O. brumata* nearly doubled during the 8 days that separated sampling date 2 and 3. This implies that serious downward biases in estimates of total parasitism can result if larvae are sampled just a few days too early. This represents a practical challenge. It is logistically unfeasible to monitor the phenology of larval populations on a day-to-day basis, in order to select the optimal time of sampling for parasitism studies. In practice, sampling can only be timed in a rough manner, depending on past experience with phenology at different sites and the availability of time and personnel. As a result, the phenology of larval populations at the time of sampling can vary considerably from year to year. Judging from the results of study II, this may well produce substantial between-year variation in estimates of total larval parasitism. It is unlikely that this can negate consistent temporal patterns in parasitism and hence explain why larval parasitoids are seemingly unable to regulate geometrid populations. It should also be noted that several parasitoid groups of *O. brumata* and *E. autumnata* have been shown to exhibit temporal trends in prevalence that cannot easily be explained by random year-to-year sampling bias (Schott *et*

al. 2012). Nevertheless, it seems likely that some of the unexplained between-year variation in larval parasitism which is often observed in studies of birch forest geometrids [e.g. Schott *et al.* (2010) and study III] is attributable to variation in the timing of larval sampling. Surprisingly, this possibility has rarely been discussed. In general, the timing of host sampling represents one of the greatest methodological challenges in research on host-parasitoid interactions (Vandriesche 1983; Jervis 2005). Study II demonstrates that the present study system is no exception from this rule.

**Table 2.** Overview of the larval instars attacked by different parasitoid species groups of *O. brumata*, as inferred from study II. Instars in parenthesis seem likely to have been attacked, although this could not be established with certainty based on the data. The probable species identities of Ichneumonidae- and Braconidae indet. are indicated in parenthesis (See box 3 for explanation).

Parasitoid species group	Instar attacked
<i>Phobocampe</i> sp./ <i>Sinophorus crassifemur</i>	1, 2
<i>Protapanteles anchisiades</i> /P. <i>immunis</i> / <i>Cotesia salebrosa</i>	(2), 3, 4
Braconidae indet. ( <i>C. eulipis</i> )	3, 4
<i>Eulophus larvarum</i>	4, 5
<i>Cryptus titubator</i>	4, 5
<i>Agrypon flaveolatum</i>	(4), 5
Ichneumonidae indet. ( <i>A. flaveolatum</i> )	(4), 5

### 3.3. Study III

#### 3.3.1. Accumulation of larval parasitoid species on invasive birch forest geometrids

A total of 7823 *E. autumnata* larvae, 18 239 *O. brumata* larvae and 3756 *A. aurantiaria* larvae had been reared by the Birchmoth project during 2001 – 2011. These larvae had been attacked by 7 different parasitoid groups in the case of both *E. autumnata* and *O. brumata* but only a single parasitoid group in the case of *A. aurantiaria* (see table B3 for an overview of the detected parasitoid groups and their host associations). This figure should probably be revised to 6 groups for *O. brumata*, since *A. flaveolatum* and Ichneumonidae indet. probably represent the same group (Box 3). Throughout the rest of this discussion, I treat these 2 groups as 1. The parasitoid *Phobocampe* sp./*S. crassifemur* was shared by all 3 geometrids. In addition to this, *E. autumnata* and *O. brumata* shared 4 other parasitoid groups. Finally, 2 parasitoid groups were exclusively hosted by *E. autumnata*, while 1 was hosted exclusively by *O. brumata*. For each geometrid species, all of the parasitoid groups that it hosted had been found at all locations where larvae of that geometrid had been sampled (the sole exception was *E. autumnata* at Skogsfjord, where only 3 parasitoid groups were found in this geometrid, probably due to a small sample size). This suggested that the sampling had been adequate to detect all important larval parasitoids attacking the geometrids in coastal Troms.

Assuming that *E. autumnata* is an appropriate point of reference for how the larval parasitoid guilds of *O. brumata* and *A. aurantiaria* should look under native conditions, study III clearly suggests that *A. aurantiaria* has barely begun to accumulate larval parasitoids in the mountain birch forest. Meanwhile, the accumulation of parasitoids on *O. brumata* would appear to be complete, or close to complete. Putting this into a temporal perspective, it suggests that the accumulation of larval parasitoids on invasive geometrids is still in its initial stages 15 years (approximate residence time of *A. aurantiaria*) after establishment, but is reaching completion a century (approximate residence time of *O. brumata*) after establishment. The discussion of study III originally proposed that the accumulation process should take at least a few decades



to reach completion, while the upper time limit would be around a century. However, this was based on treating *A. flaveolatum* and Ichneumonidae indet as separate parasitoid groups, so that 7 groups were found in both *O. brumata* and *E. autumnata*. Assuming that these 2 groups represent the same parasitoid, *O. brumata* hosts 1 parasitoid less than *E. autumnata*, and it may be appropriate to adjust the inferred time frame for parasitoid accumulation upward compared to the suggestion from study III.

The literature survey supported the assumption that *E. autumnata* and *A. aurantiaria* should have comparable larval parasitoid guilds under native conditions. Kenis *et al.* (2005) had documented that the larval parasitoid guilds of these 2 geometrids in Switzerland (where both are native) were very similar both in terms of species-richness (9 and 10 species for *E. autumnata* and *A. aurantiaria*, respectively) and taxonomic composition. It was harder to verify the assumption of inherently similar larval parasitoid guilds in *O. brumata* and *E. autumnata*. The reason for this was that the sampling effort for *O. brumata* in Western Europe vastly exceeded that of *E. autumnata*, both in terms of the number of larvae and locations sampled. This was not surprising. *O. brumata* is a serious pest of broadleaved trees in both Europe (Cross *et al.* 1999) and North America [where the species has been introduced (Roland & Embree 1995)], and much effort has been expended in identifying parasitoids that might make suitable biocontrol agents for this geometrid. In total, 18 different larval parasitoid species had been reported from *O. brumata* across Western Europe. However, many of these species had been encountered only rarely, and may have represented uncommon species or incidental attacks, recorded only due to the extensive sampling effort. Another complication was that Tachinids (i.e. parasitic Diptera of the family Tachinidae) were much more common in *O. brumata* in Western Europe than they were in *E. autumnata*. Tachinids are currently absent from the larval parasitoid guilds of the 3 focal geometrids in northern Norway, but given the importance of these parasitic flies in Western Europe, it seems possible that North-Norwegian *O. brumata* populations will eventually start to accumulate them. For these reasons, my comparison of the larval parasitoid guilds of *O. brumata* and *E. autumnata* in the mountain birch forest (and the inferred time frame for parasitoid accumulation) should be treated with caution.

Study III allowed no certain conclusions about the origins of the larval parasitoids attacking *O. brumata* and *A. aurantiaria* in the study region. Several of these parasitoids had also been recorded in Western Europe, and may therefore have followed the invasive geometrids during their northwards range-expansion. However, all of these parasitoid groups also occurred in *E. autumnata*. Thus, the invasive geometrids could equally well have recruited them from *E. autumnata* after arriving in the mountain birch forest.

Regardless of details in the timeframe for parasitoid accumulation on invasive geometrids, and the origin of their parasitoids, my results in study III matched findings from other systems. It has repeatedly been found that the accumulation of parasitoid species on invasive hosts is well under way, although seemingly still incomplete, a few decades after the invasion (Cornell & Hawkins 1993; Vercher *et al.* 2005; Gröbler & Lewis 2008; Grabenweger *et al.* 2010; Folcher *et al.* 2011). This is reasonably consistent with my finding of very low and almost native levels of parasitoid species-richness in geometrids which invaded the mountain birch system roughly 15 and 100 years ago, respectively.

### 3.3.2. Parasitism rates and prospects for enemy release in invasive birch forest geometrids

While parasitoid species-richness in *O. brumata* and *A. aurantiaria* in the mountain birch forest matched expectations from research in other systems, study III yielded more surprising conclusions with respect to the parasitism rates of these invaders. Specifically, I found that the total larval parasitism rates of *A. aurantiaria* and *O. brumata* at Storelva were very similar across both altitudes and years, despite the contrasts in residence time and larval parasitoid species-richness between the 2 geometrids. Further, Schott *et al.* (2012) found similar total

parasitism rates of *E. autumnata* and *O. brumata* at Reinøya during a 5 year period. Taken together, these results suggest that the 3 focal geometrid species suffer similar levels of larval parasitism in the study region. This contrasts with findings from other systems, where total parasitism rates of invasive hosts have often been found to increase with increasing residence time in the invaded area (Schönrogge *et al.* 1998; Gröbler & Lewis 2008; Menendez *et al.* 2008).

The finding of seemingly native levels of larval parasitism in *A. aurantiaria* as little as 15 years after establishment suggests that release from larval parasitism is unlikely to have facilitated the establishment and spread of invasive geometrids in the mountain birch system. The literature survey supported this conclusion, because it indicated that *A. aurantiaria* and *O. brumata* do not suffer less from larval parasitism in the mountain birch forest than in their native ranges in Western Europe. Study III thereby provided absolutely no support for larval parasitoid release as an important mechanism in geometrid invasions in the study system. Jepsen *et al.* (2011) presented evidence suggesting that the invasion of *A. aurantiaria* has been facilitated by improved phenological matching between larvae and birch budburst under climate warming, and study III gives no reason to question this as the most plausible mechanism behind the invasion.

In addition to rejecting larval parasitoid release as an important mechanism in geometrid invasions, the comparison of parasitism rates among geometrids shed further light on diversity-functionality relationships in the studied parasitoids. Specifically, the fact that total larval parasitism rates were similar in geometrid species that hosted contrasting numbers of parasitoid groups indicates that there is no relationship between larval parasitoid species-richness and the magnitude of total larval parasitism rates in birch forest geometrids. This topic is discussed further in section 3.4.2. Finally, there was no evidence for significant relationships between total parasitism rates and current-year larval density (both species-specific and pooled) in either geometrid species.

### **3.4. Study I – III: general discussion**

Although my 3 studies of larval parasitoids addressed largely independent questions, some topics surfaced throughout all of these studies and therefore deserve more general discussion.

#### *3.4.1. Parasitoid taxonomy*

As outlined in Box 3, the species identities of many of the parasitoid groups used throughout this project are uncertain. Taxonomic uncertainty is a relatively minor concern for research on the impact of total parasitism rates on host populations, but it represents a serious obstacle for studies of parasitoid community ecology. This became increasingly clear to me throughout the work with study I – III.

The main taxonomic limitation of the present project was the use of poorly resolved parasitoid species groups as a substitute for parasitoid species. One issue with species groups is that they obscure inferences about parasitoid sharing between host species. Five of the parasitoid groups in this project were taken to be shared between *E. autumnata* and *O. brumata*, and 1 was shared between all 3 geometrid species. However, it is far from certain that these groups represent the same parasitoid species in all 3 geometrids. This hampered inferences about the degree to which invasive geometrids had recruited parasitoids from the native *E. autumnata* in study III. Another problem with obscure species groups is that they can bias estimates of parasitoid species-richness in different species of host. Three of the groups that were taken to be shared between *E. autumnata* and *O. brumata* in this project potentially break down into 2 or 3 parasitoid species, but the degree to which they do so in the 2 geometrids is not known. It follows that these 3 groups could represent a different number of species in *E. autumnata* and *O. brumata*.

This could have substantial consequences for study III, which inferred parasitoid accumulation rates by comparing the richness of parasitoid groups between geometrid species.

The true number of species per parasitoid group is also an issue in studies that focus on a single species of host. Study I documented similar total parasitism rates among locations that were dominated by 3 different parasitoid groups. Based on this, the study concluded that many parasitoid species of *O. brumata* may be functionally equivalent. This conclusion does not hold if some of the groups in reality represent several different species. As can be seen from table B3, this possibility cannot be ruled out for 2 of the groups in question. Meanwhile, lumping of several parasitoid species into a single group could have distorted some of the phenological patterns inferred from study II.

It is uncomfortably clear from the above that important inferences from study I – III depend, to some extent, on untested assumptions about parasitoid taxonomy. This worry is not trivial. Several recent studies utilizing molecular methods have shown that parasitoid communities often contain high levels of cryptic diversity which is overlooked when parasitoids are identified based on morphological characteristics (Kaartinen *et al.* 2010; Hrcek *et al.* 2011; Smith *et al.* 2011). It is therefore clear that the parasitoids which were grouped together for this project, based on similar cocoon morphology, cannot be safely assumed to represent single species, neither within, nor between geometrid host species. My results need to be interpreted with a healthy respect for this fact.

Another issue with taxonomic confusion is that it diminishes the value of one's publications to other researchers. Study I – III have included several enigmatic parasitoids, including the nameless Ichneumonidae indet, and *C. titubator*, which has not been listed as a larval parasitoid of *O. brumata* or *E. autumnata* in any other publication that I am aware of. Only after the publication of study III have I learned that Ichneumonidae indet is probably equivalent to *A. flaveolatum*, while the *C. titubator* group probably includes *Netelia latungula* (Box 3). Both *A. flaveolatum* and *N. latungula* are common parasitoids of *O. brumata* throughout much of its range. However, because of misidentifications presented in my studies other researchers could at worst interpret them as unique parasitoids of *O. brumata* in my study system. This kind of confusion hampers research on parasitoid host ranges and geographical variation in parasitoid assemblages. Confusion also carries through to basic biological traits of parasitoids (such as phenology, i.e. study II), because given traits may be attributed to the wrong parasitoid species. The literature on parasitoids is rife with misunderstandings of this kind, and every new study with misidentified parasitoids contributes to the confusion.

In light of the issues above, why were not greater pains taken to resolve parasitoid taxonomy during this project? As outlined in box 3, several attempts at resolving parasitoid identity were made, but met with ill fortune. However, the main problem was that the time and resources to resolve the taxonomic confusions were never available. Publication of data could not be put on hold indefinitely while waiting for these matters to improve, and parasitoid taxonomy therefore had to be dealt with in the best way that was possible, based on the available information. This led to the use of the species group system for study I – III.

Based on my experiences in this project, I would argue that the taxonomic confusion surrounding larval parasitoids in the study system has presently reached a critical level, and that further studies of parasitoid community ecology should *not* be attempted before there has been substantial progress towards resolving this issue. I should hasten to add that I think this challenge is now entirely surmountable, even with modest levels of funding, due to recent methodological advances. The main tool that would be helpful in this respect is DNA barcoding. The cost of barcoding has rapidly decreased over the last few years, while the number of species in publically available reference databases has expanded massively. This means that it is much more feasible to identify parasitoids based on barcoding today than it was at the outset of the present project. Importantly, barcoding provides substantial advantages even if DNA is

obtained from parasitoid species that are not present in a reference database. Using bioinformatic methods, DNA sequences with a high degree of similarity can be grouped into so-called molecular operational taxonomic units (MOTUs), which have a high probability of representing species (Coissac *et al.* 2012). Breaking down the larval parasitoid guilds of *E. autumnata*, *O. brumata* and *A. aurantiaria* into MOTUs would be helpful for establishing the true parasitoid species-richness in each geometrid species and the true degree to which the 3 geometrids share parasitoid species. Of course, parasitoid specimens grouped into unidentified MOTUs should subsequently be subjected to morphological identification to help resolve species identity. (Ruohomäki *et al.* 2013) recently employed a combination of barcoding and morphological identification to resolve the taxonomy of *Protapanteles* and *Cotesia* species attacking *E. autumnata*. It is my hope for the future that similar progress can soon also be made for other geometrid parasitoids with confused taxonomy.

### 3.4.2. Diversity-functionality relationships in larval parasitoids of geometrid moths

Study I – III all provided clues to diversity-functionality relationships in the larval parasitoid guilds of the 3 focal geometrids. Study I and III showed that the magnitude of total larval parasitism rates of the geometrids can be largely independent of both the identity of the locally dominant larval parasitoid species (section 3.1.2) and the number of attacking parasitoid species (section 3.3.2). This indicates that different parasitoid species perform very similar functions and that some species can, therefore, be lost from the guild without reducing its overall impact. In other words, there appears to be a high level of functional redundancy (Rosenfeld 2002) among the studied parasitoid species, resulting in a lack of positive relationships between larval parasitoid species-richness and the magnitude of total larval parasitism.

The results above are not entirely surprising. A positive relationship between species-richness and the magnitude (or rate) of resource exploitation is expected if species are complementary in their resource utilization modes. If this is the case, resource exploitation by different consumer species will be additive, so that overall exploitation will increase with increasing number of species (Letourneau *et al.* 2009). Complementarity requires that there is resource partitioning among species, i.e. that species utilize resources in different ways so that interspecific competition is decreased (Hooper *et al.* 2005). The studied larval parasitoids belong to a single guild, where all species utilize the same resource (i.e. moth larvae) according to the same mechanism. Thus, there may be limited opportunities for resource partitioning among these parasitoids, so that the impacts of different species are non-complementary. If this is the case, adding extra species will only serve to increase interspecific competition for the larval resource, rather than increasing total exploitation (i.e. total larval parasitism).

My finding of a seemingly neutral relationship between larval parasitoid species-richness and total larval parasitism of geometrid hosts is in line with empirical results from other host-parasitoid systems. Rodriguez & Hawkins (2000) compared larval parasitism among 16 species of grass-feeding wasps in the genus *Tetramesa*, and found that the total larval parasitism rates of different host species were unrelated to the species-richness of their larval parasitoid guilds. Lack of complementarity in the resource utilization of the studied larval parasitoids was suggested to explain this result. Meanwhile, Tylianakis *et al.* (2006) studied parasitism of cavity nesting bees and wasps, and found a positive relationship between total parasitism rates and parasitoid species-richness. This study included a more diverse array of host- and parasitoid life history strategies than Rodriguez & Hawkins (2000) and the authors suggested that there was therefore greater scope for resource partitioning and, hence, complementarity within their study system. My present results add to the impression that positive relationships between parasitism rates and parasitoid species-richness will not be found in systems where there is little potential for complementarity among parasitoid species.

While my results indicate no connection between parasitoid species-richness and the magnitude of total parasitism, they do suggest that the studied parasitoid guild has functional characteristics which increase the *stability* of total parasitism rates. Following to the so called insurance hypothesis (Naeem & Li 1997; Naeem 1998), a high level of functional redundancy among parasitoid species should decrease spatiotemporal variation in total parasitism rates. This is because loss of redundant species from the guild should not detract from its overall functionality. Further, loss of redundant parasitoid species should reduce interspecific competition for the larval resource, so that the impact of remaining species increases. These mechanisms could buffer total larval parasitism rates against variation in larval parasitoid species-richness in both space and time. As outlined in section 3.2.1, study II also suggested that the diverse phenological trajectories of the studied parasitoids could stabilize total larval parasitism rates by reducing the risk of phenological mismatches between larvae and many parasitoid species within a given year. Thus, the studied parasitoid guild may harbour a positive diversity-functionality relationship with respect to the stability, if not the magnitude, of total parasitism.

The suggestion that total larval parasitism rates of geometrid moths are subject to several stabilizing mechanisms may seem to contradict the observation that parasitism of these moths can fluctuate between years and locations [e.g. Schott *et al.* (2010) and Schott *et al.* (2012)], Study III). However, the arguments above only consider the stability of total parasitism against variation in the number of attacking larval parasitoid species. Total parasitism could still be affected by climate effects that influence all species in the guild. For instance, total parasitism might decrease in years when temperatures are low or precipitation is high throughout the larval season, so that most or all parasitoid species experience negative effects. Further, total parasitism may be affected by variation in geometrid density. Although relationships between larval parasitism rates and host density appear to be weak at least in coastal regions, these relationships are not absent (Schott *et al.* 2012). Moreover, both study II and my personal observations suggest that parasitoids tend to be swamped when larval densities become very high, so that parasitism rates decrease in these cases. Finally, as outlined in section 3.2.3, temporal variation in larval parasitism rates in my study system may be increased by phenological biases related to the timing of sampling. Thus, although study I – III suggest that total larval parasitism rates of birch forest geometrids are subject to stabilizing mechanisms, there is still large potential for total parasitism to vary in this system.

### **3.5. Study IV**

#### *3.5.1. Numerical responses of saproxylic beetles to dead wood left by moth outbreaks*

Study IV suggested that the saproxylic beetle community in Varanger had shown a detectable short-term numerical response to the dead wood left by the moth outbreak. The log-linear models indicated that the abundance of all 3 DWA groups was higher in damaged than in undamaged forest in Kirkenes, but this pattern was strongest for obligate saproxylic beetles, who showed roughly 3.5 times higher predicted abundances in damaged than undamaged forest in Kirkenes. Meanwhile, the predicted abundances of facultative- and non-saproxylic beetles were roughly 1.5 and 2 times higher, respectively, in damaged forest in Kirkenes. This pattern was reversed in Tana, with predicted abundances of facultative- and non-saproxylic beetles being roughly one third and one half as high in damaged as in undamaged forest. For obligate saproxylics, the predicted abundances in Tana were very similar between forest types. These patterns were consistent between the 2 years of the study. Thus, when the 3 DWA groups were compared, it would appear that obligate saproxylic beetles were favoured by damaged forest. This impression was supported by the logistic modelling, which showed that the proportion of obligate saproxylic individuals in the beetle community was higher in damaged than in undamaged forest in both Tana and Kirkenes. However, this increase in the proportion of

obligate saproxylics in damaged forest amounted to no more than about 10%. Thus, study IV suggested that the numerical response of the saproxylic beetle community to the outbreak had been remarkably weak, even considering initial expectations that the response might not be proportional to the magnitude of dead wood input (section 1.5.5).

There are several possible explanations for the apparently weak numerical response of the saproxylic beetle community. First, because saproxylic beetle species usually prefer dead wood in particular stages of decay (Ehnström *et al.* 2002; Langor *et al.* 2004; Stokland *et al.* 2012), only a subset of the beetle community may be able to respond to an outbreak at any given time. Log-linear modelling of individual beetle species showed that the positive response of obligate saproxylics to the outbreak was mainly driven by the 2 species *Elateroides dermestoides* (L.) and *Rabocerus foveolatus* (Ljungh). Both of these species prefer recently dead and dying trees, and they should therefore have enjoyed increased resource availability during the 3 – 5 years separating the conclusion of the outbreak and the onset of study IV. Meanwhile, the last birch-associated obligate saproxylic species that was modelled, namely *Podistra schoenherri* (Dejean), showed no clear response to the outbreak. This species prefers dead wood in more advanced stages of decay. Thus, study IV provided some support for the hypothesis that species-specific decay-stage-preferences will allow only some species in the saproxylic community to respond to an outbreak at any given time.

The cold climate of my high-latitude study region may also act to constrain beetle numerical responses. The low temperatures of this region may prolong the development time of beetle larvae in the dead wood. For instance, beetle species that complete their development within a single year in warmer climates may require several years of development in high-latitude regions. This would lower reproductive rates and hence also limit numerical responses. There may also be climatic constraints on beetle diversity in my study region. I recorded a total of 52 obligate- and 47 facultative saproxylic beetle species. This is considerably less than what studies with comparable sampling efforts have recorded in more southern systems (Martikainen & Kaila 2004; Menke 2006; Sverdrup-Thygeson & Birkemoe 2009). Several taxonomic groups that form important parts of the saproxylic community in many southern regions were also rare in my dataset. For instance, the families Cerambycidae and Buprestidae, and the subfamily Scolytinae, were collectively represented with less than 30 individuals. These 3 groups have been shown to mount strong and rapid numerical responses to dead wood generated by windthrow in continental Europe (Wermelinger *et al.* 2002). Thus, the beetle community I studied probably lacks many species that would have been able to respond to an outbreak in more a more southern system. It should also be taken into account that my study region represents the northern distributional limit for many of the beetle species in the dataset (Ehnström *et al.* 2002). These species may hence exist close to their tolerance limits for abiotic conditions, like temperature, and could therefore be very sensitive to stochastic year-to-year variation in environmental conditions (Brown *et al.* 1995).

A weak numerical response of saproxylic beetles could have important implications for the decomposition of the dead wood left by moth outbreaks. Saproxylic beetles contribute directly to the decay of dead wood by consumption and physical degradation, and also facilitate the entry and activity of wood-decomposing fungi and bacteria (Zhong & Schowalter 1989; Schowalter *et al.* 1992; Stokland *et al.* 2012; Ulyshen 2013; Ulyshen & Wagner 2013). Accordingly, a weak numerical response of saproxylic beetles to the dead wood left by an outbreak could retard the decomposition of this wood, with possible implications for the turnover of nutrients and materials. Given the enormous quantities of dead wood that outbreaks generate, this could affect the post-outbreak dynamics of the entire ecosystem. On the other hand, the relative importance of microbial decomposer communities may increase in the absence of strong numerical responses from saproxylic beetles, so that decomposition rates will remain largely similar. These important questions raised by study IV highlight directions for

future research. I would suggest that the actual utilization of dead wood by beetles and microbial decomposers is quantified and compared between forest that has been affected by outbreaks and not. This would shed light on both the taxonomic composition of decomposer communities and the relative rates of wood decay in the 2 forest types, and hence reveal whether decomposition dynamics differ importantly between outbreak-affected and healthy mountain birch forest.



**Figure. 7.** A window trap used for sampling saproxylic beetles, mounted in undamaged mountain birch forest. Photo: Ole Petter Laksforsmo Vindstad.

### *3.5.2. Moth outbreaks and beetle community structure*

The RDA produced some separation of damaged and undamaged sampling stations for obligate saproxylic beetles, thus suggesting that the community structure of saproxylic beetles differed between the 2 forest types. This was in line with the finding that only some of the obligate saproxylic species in my data showed evidence for a numerical response to the outbreak. However, the separation of damaged and undamaged sites was not very clear, thus emphasising that the responses had been rather weak. This was underscored by the variance partitioning, showing that the contrast between damaged and undamaged forest explained only about 11 % of the total variation in saproxylic beetle community structure.

Interestingly, the RDA for non-saproxylic beetles produced a clearer separation of damaged and undamaged sites than for obligate saproxylic species. Thus, the outbreak would appear to have affected also beetle species that should not benefit from the dead wood left by the outbreak. This is not entirely surprising, since the forest damage wrought by outbreaks could alter habitat characteristics for beetles in many ways. Indeed, given the dramatic disturbance caused by the outbreak, it is more surprising that I did not find stronger responses in the beetle community. Most of the individually analysed beetle species (both saproxylic and non-saproxylic) showed no consistent differences in abundance between damaged and undamaged forest. To the contrary, the abundance patterns of most species showed a reversal with respect to forest damage between Tana and Kirkenes, with abundances being highest in damaged forest in Kirkenes and highest in undamaged forest in Tana. This suggests that outbreak-induced forest damage is less important than other habitat characteristics for many beetle species. The birch-

associated herbivore *Polydrusus fulvicornis* was an interesting exception, in that it was quite abundant in undamaged forest but virtually absent from damaged forest in both transects. This suggests that moth outbreaks can negatively affect herbivorous beetle species by killing host plants.

### 3.6. Study V

#### 3.6.1. Bird community responses to outbreak-induced forest damage

The results of study V mirrored those of study IV, in the sense that the bird community appeared to respond weakly to the forest damage caused by the moth outbreak. The hierarchical model indicated that the total abundance of birds was about 25% lower in damaged than undamaged forest in Kirkenes. Bird species-richness was also slightly lower in damaged forest, but this effect was even weaker than for abundance. For Tana, the hierarchical model indicated no consistent differences in bird abundance or species-richness between damaged and undamaged forest. Thus, study V gave the impression that the studied bird community has considerable resistance [i.e. ability to remain essentially unchanged in the presence of disturbance (Grimm & Wissel 1997)] to the forest damage inflicted by moth outbreaks. As was the case for study IV, this result was quite surprising, given the severe impacts of outbreaks on the birch forest habitat.

There are several possible explanations for the apparent resistance of the bird community to outbreak-induced forest damage. First, scattered surviving trees always occur throughout an outbreak area. These trees could help maintain bird populations if birds do not require many living trees within their home ranges. The dead trees left by an outbreak may also be significant. At the conclusion of study V, almost all of the trunks that were killed by the outbreak were still standing. Thus, much of the vertical structure of the forest habitat was still present. Structural variables, like vegetation height and density, have been found to be strong predictors of bird species-richness and abundance in other systems (Müller *et al.* 2009; Flaspohler *et al.* 2010; Tattoni *et al.* 2012). Moreover, Ims & Henden (2012) and Henden *et al.* (2013) showed that the species-richness of bird communities in Norwegian low-arctic tundra (including many of the species from study V) declines dramatically when thicket-forming *Salix* shrubs disappear from the landscape. Thus, there is reason to believe that vegetation structure is important for birds also in mountain birch forest. A point that must be stressed here though, is that vegetation structure will only influence birds if it correlates with ecologically relevant habitat characteristics, like nesting- or hiding places (Zellweger *et al.* 2013). It is presently an open question whether dead birch trunks can serve these functions. Thus, studying if and how birds utilize the dead trunks in outbreak areas would be helpful for understanding their responses to outbreaks. Finally, it should be noted that several of the most abundant bird species in study V are known to be habitat generalists, which are not restricted to forest habitats (Virkkala 1988, 1991). This may also help explain why the studied bird community appears to be resistant to outbreak-induced forest damage.

Another finding from study V that is in need of explanation is that bird abundance and species-richness seemed to be affected by forest damage only in Kirkenes. Further, even damaged forest in Kirkenes showed considerably higher bird abundance and species-richness than any of the forest types in Tana. It might be speculated that these differences between locations are linked to differences in habitat productivity and structure. The number of stems per tree was generally higher, and the diameter of stems lower, in Tana than in Kirkenes (Appendix 1 of study V). This indicates that Tana is a habitat of lower productivity than Kirkenes (since the growth form of the mountain birch correlates with habitat productivity. Section 2.1). This might explain why the overall abundance and richness of birds was lower in Tana. It is less clear how differences in productivity could account for the different response of the bird community to forest damage



in Kirkenes and Tana. However, an interaction between habitat productivity, forest damage and bird territory size could be suspected (see study V for a more detailed discussion).

A total of 22 bird species were recorded in study V, but the 4 most common species, namely the Brambling, Common redpoll (*Carduelis flammea* L.), Willow warbler (*Phylloscopus trochilus* L.) and Redwing (*Turdus iliacus* L.) collectively accounted for more than 80 % of the total individual count in the dataset. Thus, there was little basis for generalizing about relationships between bird foraging habits and responses to the outbreak. However, it was noteworthy that only the Willow warbler showed a clear negative response to the outbreak (being roughly half as abundant in damaged as undamaged forest). The Willow warbler forages mainly among leaves in the canopy, and its negative response to the outbreak may thus have been due to loss of preferred foraging habitat. The other 3 common species do more of their foraging on the ground, and this may explain their weaker responses.

Another interesting observation from study V is that no bird species showed increased abundance in damaged forest. This was somewhat surprising, since studies in other systems have often found some bird species to respond positively to outbreak-induced forest damage, typically species that are associated with open or disturbed habitats. However, it does appear that these positive responses often coincide with increased density and height of the tall shrub layer in the understorey vegetation (Bell & Whitmore 1997; Canterbury & Blockstein 1997; Rabenold *et al.* 1998; Gale *et al.* 2001; Becker *et al.* 2008). There has been a shift in dominance from dwarf shrubs to grass in the understorey at our outbreak-affected study sites (section 1.4.3), but this has so far not led to changes in the density or height of the understorey vegetation. This may explain why no bird species appear to have been favoured by the damage caused by the outbreak.

### **3.7. Study IV and V: general discussion**

Two short-term studies allow few generalizations about community responses to forest damage caused by moth outbreaks. Nevertheless, there are some interesting parallels in the observations made by study IV and V. Further, both studies have methodological issues that would benefit from a general discussion. These topics are discussed below.

#### *3.7.1. Methodological limitations*

Study IV and V were conducted within the same sampling design and hence share some methodological limitations. The most important of these – as reviewers repeatedly pointed out – is the use of a spatial contrast between damaged and undamaged forest to infer community responses to outbreak-induced forest damage. Strictly, this approach is only valid if damaged and undamaged sampling stations have no consistent differences in environmental conditions, except for the damage inflicted by the outbreak. This assumption is difficult to verify. Moreover, the simple fact that some stations were affected by the outbreak while others were not points towards some consistent environmental differences between them.

This is far from saying that I believe the spatial contrast of study IV and V to be uninformative with respect to community responses to outbreaks. Within transects, most of the inter-station distances between damaged and undamaged stations were well below 20 km (the total lengths of the transects). Thus, damaged and undamaged stations within transects should have the same regional species pool, and the potential for consistent climatic differences between them should be limited. The quantitative environmental data that is available at the station level also suggests that damaged and undamaged stations are comparable. First, neither Kirkenes nor Tana showed consistent differences in the number or diameter of birch stems between damaged and undamaged stations (Appendix 1 in study V). This suggests that the inherent productivity of damaged and undamaged stations is comparable. Second, there were no consistent differences in topographical variables, namely elevation, slope and aspect, between damaged and

undamaged stations within transects (Appendix 1 in study V). Thus, in summary, it is difficult to see how the spatial damaged-undamaged contrast could be so confounded with other environmental variables that it can say nothing about community responses to outbreaks.

I should also stress that designs of the type used in study IV and V – although easy to criticise – will often be the only practical way of studying community responses to outbreaks. A community at a given site can rarely be monitored indefinitely, in the hope that an outbreak will eventually occur. Usually, resources only permit more targeted studies of community responses *after* an outbreak (indeed, questions about the effects the outbreak will often not be raised before this time). In this case, the state of the community at an unaffected site is the only available baseline for comparison. While such studies must be interpreted cautiously, I would argue that they are greatly preferable to knowing nothing about the outbreak responses of the target community.

Another methodological issue of study IV and V is the question of spatial scale. My quantification of forest damage at the individual sampling stations was highly local (50 m to each side of the station midpoint). However, study IV and V did not ask how birds and beetles responded to forest damage at this very local scale. Within transects, the damaged stations were embedded within large continuous areas of heavily damaged forest. The aim was to infer the state of the target communities for these damaged areas as a whole, and compare this with the state in the undamaged areas. Thus, the individual sampling stations within damaged and undamaged forest served to provide replicate observations of community state within the 2 forest types. Arguably, the exact scale at which organisms respond to outbreak-induced forest damage was not a major concern, since the forest in the outbreak area showed a uniformly high degree of damage from the very local scale around the stations and up to the landscape level. Thus, responses on both large and small spatial scale should have been detected by study IV and V.

The station-specific damage scores were only provided for illustrative purposes, to show the typical state of the forest within damaged and undamaged areas. However, in retrospect, it is easy to see that these very local scores could have created confusion as to the spatial scale that was considered by study IV and V. A researcher working in the birch-moth system knows from experience that outbreaks can leave large continuous tracts of heavily damaged forest, but this is not necessarily obvious to a person who is unfamiliar with the system. Clearly, it would have been preferable to quantify forest damage also at larger spatial scales, to show that damaged stations did not simply represent small patches of damaged forest. Unfortunately, ground measurements at larger scale were not logistically feasible when the studies were conducted. Further, aerial images from the time after the outbreak are not available for the study region. Satellite-derived maps of defoliation (drop in NDVI) during the outbreak do exist (Jepsen *et al.* 2009a, b), but these do not appear to have a simple relationship with the levels of outbreak-induced forest mortality observed on the ground (Jepsen and Vindstad unpublished data). Thus, there were no good alternatives to the small-scale quantification of forest damage presented in study IV and V.

A final concern regarding study IV and V is that both were conducted only 3 – 5 years after the collapse of the moth outbreak. Hence, they address only short-term responses of the studied communities to the outbreak. It should be stressed that these responses are not necessarily representative for the long-term effects of the outbreak. This reservation is very important for the present study system, because decomposition and successional processes in this cold high-latitude system are likely to be slower than what is generally the case. Thus, study IV and V present snapshots of beetle and bird communities only in the immediate aftermath of the disturbance wrought by the moth outbreak. Research on the long-term responses of these communities will be necessary if their reactions to the outbreak are to become fully understood.

### *3.7.2. General observations on community responses to moth outbreaks*

Study IV and V yielded surprising results, by suggesting weak short-term responses of bird and beetle communities to the massive habitat disturbance wrought by the moth outbreak. In both cases, the direction of the response of the outbreak was predictable, but the magnitude of the response was unexpected. This illustrates that we still have much to learn about the effects of outbreaks on wildlife communities, and that empirical studies are needed to make progress in this respect.

Interestingly, study IV and V suggested that the short-term effects of moth outbreaks on the target communities was less important than effects of other environmental variables. In study IV, the spatial abundance patterns of most beetle species and the DWA groups (section 2.3.4) showed large-scale spatial gradients along the sampling transects. In most cases, however, these gradients lacked consistent relationships with outbreak-induced forest damage, thus indicating that they were driven by beetle responses to other habitat variables. In study V, the contrast between the 2 study locations (i.e. Kirkenes and Tana) appeared to have larger effects on the bird community than the contrast between damaged and undamaged forest within locations. Again, this suggests that most species in the community were more affected by other habitat characteristics than forest damage.

I will not speculate on what habitat variables are decisive for the spatial abundance patterns of the studied bird and beetle communities. However, the surprising absence of clear responses to the outbreak may suggest that some degree of pre-adaptation to such disturbance exists within these communities. Study IV argued that this was unlikely for saproxylic beetles, owing to their seeming inability to effectively respond to the dead wood left by outbreaks, and the fact that outbreaks which cause severe forest damage occur rarely (perhaps only once every 50 – 60 years). However, the fact that responses were weak in species that would be expected to suffer severe habitat loss due to the outbreak (e.g. birds associated with the tree canopy) argue in favour of evolved adaptations to outbreak-induced forest damage in these species.

Another noteworthy observation from both study IV and V, is that community-level changes in abundance in response to the outbreak (to the degree that such changes occurred) were mainly driven a few very common species. Such dominance of a small number of species is typical for high-latitude communities and was therefore not unexpected. An interesting avenue for future research would be to conduct more detailed studies of the mechanisms by which these dominant species respond to outbreaks. For saproxylic beetles, it would be useful to study fecundity and developmental rates, so as to understand the capacity for responding numerically to outbreaks. Studying interactions between common beetle species and saproxylic fungi could also give valuable insights into post-outbreak decomposition dynamics. For birds, it would be useful to know how common species utilize the birch trunks killed by outbreaks and whether territory size, and hence breeding density, changes in outbreak areas. Studying mechanisms of habitat selection would also be of interest, so as to understand why these species apparently do not shy away from settling to breed in heavily damaged forest. Clearly, other habitat variables than forest damage must be important in habitat selection. Because a few dominant species appear to drive community responses to outbreaks, such studies would, in effect, give insight into mechanisms that may be important to the entire birch forest ecosystem.

### **3.8. Overall perspectives and future directions**

After more than 40 years of research, substantial progress has been made towards understanding the dynamics of the birch-moth system in northern Fennoscandia. Perhaps most importantly, the role of natural enemies in driving moth population cycles is becoming understood (section 1.4.5 – 1.4.6) and the dramatic impacts of climate change on moth outbreak dynamics is becoming clear (1.4.2 – 1.4.3). Yet, as has repeatedly become apparent throughout this thesis, much still remains to be learned, also with respect to these 2 topics.

From a perspective of management and adaptation to climate change, I would argue that the most important priority for future research in the birch-moth system is to gain a better understanding of the ecosystem impacts of moth outbreaks. Present evidence suggests that climate warming is driving the system towards a state characterized by outbreaks of greater severity and duration (Jepsen *et al.* 2008; 2009a, b; 2011; 2013). Anticipating the ecosystem trajectories that will result from this requires a better understanding of the ecological consequences of outbreaks than what we have at present. Study IV and V of this thesis illustrate that it can be difficult to predict how given ecosystem components will respond to an outbreak, and that initial expectations about outbreak-responses are not necessarily met. This underscores that the impacts of outbreaks will only be understood by obtaining hard, solid data from the field. The 2 studies also highlight that short-term research allows limited understanding of how ecosystem components respond to outbreaks. It is therefore important that research on outbreak-impacts is extended into the long-term. Indeed, given the climate-driven changes that the birch-moth system is presently experiencing, and our limited ability to predict the consequences of these changes, hypothesis-driven long-term monitoring of key ecosystem components is one of the most valuable research activities that can be undertaken in this system over the coming decades (Ims *et al.* 2013). This, in combination with studies that elucidate the underlying mechanisms of outbreak-responses (e.g. in important species, section 3.7.2), should be of great help for understanding the dynamics of the North-Fennoscandia mountain birch ecosystem under changing moth outbreak regimes.

While I would argue that questions about the ecological consequences of moth outbreaks should be high up on the research agenda for the Fennoscandian birch-moth system in the future, the more traditional questions about drivers of moth population dynamics should not be forgotten. As outlined in section 1.4.6, recent contributions have gone a long way towards resolving the role of parasitoids in moth population cycles (Schott *et al.* 2010; 2012; Klemola *et al.* 2010; 2014). Still, a solid consensus about the role of parasitoids cannot be reached before the results of Klemola *et al.* (2014) – which suggest egg- and pupal parasitoids as drivers of moth cycles in oceanic regions – have been repeated in coastal Troms. If this can be achieved, we can have more confidence in the conclusion that different parasitoid guilds are key drivers of moth cycles in different environmental contexts, with larval parasitoids dominating in inland areas, and egg- and pupal parasitoids dominating on the coast.

The next important question would be *why* the impacts of different parasitoid guilds appear to be context-dependent. This would need to be addressed by research that expands on the present project, by studying the organization and functionality of parasitoid guilds. Throughout this thesis, I have highlighted several topics that would benefit from further research. First, I have repeatedly speculated on the sensitivity of parasitoids to climate and weather [as have others before me (Schott *et al.* 2012)]. A first step towards filling this knowledge gap would be to study the flight activity of adult parasitoids and its relationship with variables like temperature, precipitation and wind speed. This could be done with insect traps and equipment for local meteorological observations, all of which are readily available. The main challenge for such studies would be identifying adult parasitoids, but this could hopefully be accomplished in cooperation with taxonomic experts. The need to get a better grip on parasitoid taxonomy in the birch-moth system was discussed in section 3.4.1, and I stress again that this should be a high priority for future research.

Another topic that has been highlighted by this thesis is the seemingly high degree of functional redundancy (with respect to total larval parasitism rates) among larval parasitoid species in the birch-moth system. Studying the underlying mechanisms for this phenomenon would give a deeper understanding of the functionality of the larval parasitoid guild. Establishing the degree to which parasitoid species compete for larvae would be the most important research topic in this context (section 3.2.1). I will not speculate widely on the best methods for studying

parasitoid competition. However, metabarcoding (Pompanon *et al.* 2012) of moth larvae, to look for DNA from multiple parasitoid species within single larval individuals, may be a good starting point.

Finally, it is important that future research considers egg-, larval- and pupal parasitoids in context with each other, rather than treating parasitoid guilds in isolation. With respect to climate-sensitivity, comparative studies of the 3 parasitoid guilds will help us to understand the apparent context-dependency in their impacts on moth population dynamics. As for functional redundancy, this should be studied not only within, but also *among* parasitoid guilds. The fact that different guilds can seemingly act as drivers of moth cycles in different contexts suggests that functional redundancy exists also on a between-guild level in this system. Future research should explore this possibility. By adopting a multi-guild perspective, we will move towards and understanding of the impact and functionality of the entire parasitoid complex of the focal geometrid moths.

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**Study I:**  
Spatially patterned guild structure in larval parasitoids of cyclically  
outbreaking winter moth populations



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## Study II:

Phenological diversity in the interactions between winter moth (*Operophtera brumata*) larvae and parasitoid wasps in sub-arctic mountain birch forest



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### **Study III:**

How rapidly do invasive birch forest geometrids recruit larval parasitoids? Insights from comparison with a sympatric native geometrid



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## Study IV:

Numerical responses of saproxylic beetles to rapid increases in dead wood availability following geometrid moth outbreaks in sub-arctic mountain birch forest



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## **Study V:**

Resistance of a sub-arctic bird community to severe forest damage  
caused by geometrid moth outbreaks



Manuscript

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