

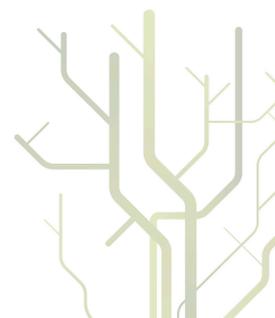
Determinants and effects of moth population dynamics in altitudinal gradients in northern Fennoscandia



TINO SCHOTT

A dissertation for the degree of
Philosophiae Doctor

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Tromsø, April 2013

University of Tromsø, Norway

Faculty of Biosciences, Fisheries and Economics

Department of Arctic and Marine Biology

Dedicated to my wife,
who endured periods of decreased mood
but who is still with me.

Supervisors

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Acknowledgments

Thanks to the Department of Arctic and Marine Biology, University of Tromsø, and the Research Council of Norway for funding my PhD-project. I am grateful for all practical help and theoretical guiding during the time of my PhD education. Apart from my supervisors, special thanks to T, J, L, S, OP, S & J and the fool for accompanying me during field work and qualitative development since the beginning.

Front cover

The picture on the front cover shows a caterpillar of the species autumnal moth (*Epirrita autumnata*) on a branch of mountain birch (*Betula pubescens*) at Reinøya, Troms County, Norway, in July 2012. Large stretches of birch forest at Reinøya had been defoliated suggesting that a new outbreak of autumnal moth was on its way. Photo: Tino Schott.

Preface

When starting my PhD-project in 2008, my aim was to contribute to our understanding of moth population dynamics in northern Fennoscandia. Today, I am certain to have fulfilled this aim. I especially believe, that papers 1 & 3 on parasitoids have produced valuable insights for the so called parasitoid-regulation hypothesis on insect populations. Since the 1930s parasitism by parasitoids has been regarded as the most-likely mechanism to regulate insect (host) populations. Due to the large difficulties connected to studying parasitoids, many parasitoid studies were biased with respect to unnatural surroundings (lab-studies), unnatural ecological settings (introduced hosts and parasitoids in non-native environments), insufficient spatial and temporal replication and/or (perhaps too) simplified theoretical modelling. The result became a *strong and accepted belief* that due to the lack of other explanations for complex insect population dynamics, parasitoids must be the most likely, although invisible cause.

The studies presented here are by no means unbiased with respect to the problematics outlined above but they summarize an extensive observational survey that yields no hints in support of the parasitoid-regulation hypothesis. Paper 3 even digs deeper and presents an explanation of *why* larval parasitoids in the ecological system described here are not capable of regulating their hosts, that is, *something* in direct connection to spatial and temporal variation across altitude and between years has a tight grip on the dynamics of both, the hosts as well as the larval parasitoids in our studies. So what is this *something*?

The most relevant fact I have learned during the recent years is that biologists today (including myself) tend to view nature as too simplistic. We develop sampling methods and statistical tools to allow us to trade quality for quantity. We are absorbed by the *big picture*, which forces us to reject thorough work by the use of spot checks in time and space to be able to cover large distances in shortest possible time with fewest people to gain most data, which subsequently has to be sieved through statistical gold washing. At the end, we try to understand complex interactions in space and time without understanding the individual interactants as there is no time to spend time on their nature and biology. Do we change from biologists to systemologists? And is this the path we are willing to choose? The question is open to everyone who wants to understand nature.

Tromsø, April 2013.

Tino Schott

List of individual papers

Paper 1

Schott T., Hagen S.B., Ims R.A. & Yoccoz N.G. (2010). Are population outbreaks in sub-arctic geometrids terminated by larval parasitoids? *Journal of Animal Ecology*, **79**, 701-708

Paper 2

Schott T., Kapari L., Hagen S.B., Vindstad O.P.L., Jepsen J.U. & Ims R.A. (2013). Predator release from invertebrate generalists does not explain geometrid moth outbreaks at high altitudes. *The Canadian Entomologist*, **145**, 184-192

Paper 3

Schott T., Ims R.A., Hagen S.B. & Yoccoz N.G. (2012). Sources of variation in larval parasitism of two symmetrically outbreaking birch forest defoliators. *Ecological Entomology*, **37**, 471-479

Paper 4

Schott T., Svavarsdottir S., Hagen S.B., Kapari L., Vindstad O.P.L., Biuw M., Jepsen J.U. & Ims R.A. (201X) Coping with variation in prey abundance and phenology: Comparative breeding performance of two passerines at the northern limit of their geographic range. *Manuscript*.

Declaration of contribution

Many assistants contributed to fieldwork and data collection during this PhD-project. The specific contributions of the authors of the papers attached to this thesis are listed below. All authors commented on the paper manuscripts.

Paper 1

I collected and analyzed the data and wrote the manuscript. SBH contributed in the field and during data analyses. The study was originally planned by RAI and NGY who also contributed with writing the manuscript and data analysis, respectively.

Paper 2

I collected and analyzed the data and wrote the manuscript. JUJ contributed with graphics for the paper. The idea for the study was worked out by SBH, JUJ, RAI and me. LK, SBH, OPLV and JUJ assisted in the field. RAI contributed in writing the manuscript.

Paper 3

SBH and me collected the data and contributed to the idea of the study together with RAI. SBH was involved in field- and lab-work. I analyzed the data with contribution by NGY. RAI and me wrote the manuscript.

Paper 4

The data were collected by SS, LK, OPLV, SBH, JUJ and me. Analyzing the data was shared between MB and me. MB produced all final analyses and figures in the paper and contributed to the methods and results section. RAI and me wrote the manuscript, which in part (methods) was based on a master thesis by SS. The idea for the study was worked out by SBH, JUJ, RAI and me.

Summary

The aim of this PhD-project has been to increase our knowledge of trophic interactions along altitudinal gradients in a system of sympatric, cyclically outbreaking geometrid moth species in sub-arctic, coastal birch forest in northern Norway. The project resulted in four scientific publications; two sub-studies focused on the causal effect of natural enemies on the observed complex spatio-temporal dynamics of the moth species (Papers 1 & 2). The other two sub-studies investigated the ecological effects of variable moth larvae densities as a resource for predators in the sub-Arctic ecosystem (Papers 3 & 4). In paper 1, we rejected the hypothesis that larval parasitoids might terminate moth population peaks, one of the most important hypotheses on insect population regulation. We, however, found that larval parasitoids can influence local spatial variation in moth population density. Hence, we concluded that spatial replication of sampling sites is crucial to arrive at non-biased estimates for the temporal effect of larval parasitoids on host populations. The long enduring debate on the regulation potential of parasitoids on insect populations in the scientific literature may be viewed in light of our findings. Similarly, in Paper 2, we tested if the often-observed spatial outbreak patterns of moth populations might be a result of release from invertebrate predators. Along mountain slopes, moth outbreaks in northern Fennoscandia often occur close to the tree line, and we tested if the abundance of ground dwelling invertebrate predators was inversely correlated with altitude, testing the assumption that moth outbreaks may be a result of reduced predation impact at high altitudes. As our analyses could not reveal this predicted pattern, we rejected the hypothesis. Consequently, the first two sub-studies delimited the number of candidate factors that might shape Fennoscandian moth dynamics by reevaluating the role of larval parasitoids and ground-dwelling invertebrate predators. In paper 3, we reanalyzed the data from Paper 1 from the parasitoid's perspective by determining the dependencies of individual parasitoid species to host densities. For comparison, we also estimated the strength of effects hidden in the spatial and temporal attributes of altitude and year on parasitoid prevalence rates. We found that altitude and year, rather than host density, explained by far most of the extra-binomial variation in the parasitoid prevalence data. Hence, we concluded that unknown factors, which co-vary with altitude and year, dominate the prevalence dynamics of the larval parasitoids in our study and, consequently, act to decouple parasitoid dynamics from the dynamics of their hosts. Moth larvae as a resource for predators were also the focal issue in Paper 4, which focused on the importance of prey availability and forest phenology for breeding parameters in the two passerine birds great tit and pied flycatcher. The study was based on the phenological conflict that spring arrives in mountain slopes first at low altitude, while the bird's main food resource during the breeding season (i.e. moth larvae) often dominates forest habitat at higher altitude. Thus, we tested if passerine birds select breeding habitat according to the onset of spring or the availability of moth larvae and if the two bird species differed in this respect. We found that the phenological timing was the main driving force for both species when selecting breeding habitat lowest in the gradients where spring arrived first. However, also the positive correlations with moth larvae density appeared to be significant in our analyses. The main difference between the two species was found in the timing strategy for egg laying and size of clutches, which might make the great tit more prone to mismatch during springs of lower temperature. In addition, while nest box occupancy decreased with altitude in both species, the same relationship with respect to clutch size was only found for pied flycatchers, but not for great tits. Finally, great tits were more prone to fail during their breeding attempt and we concluded that the pied flycatcher, by laying eggs up to two weeks after great tits, appears to be the better adapted species with respect to breeding at sub-arctic conditions. This PhD-thesis strengthens the view that so-called top-down interactions in the ecological moth system in northern Fennoscandia cannot explain complex moth population dynamics, but that moth larvae can be regarded as a valuable resource for species at other trophic levels. The consistent dominance of altitude and year in all our analyses, on the other hand, suggests that explanations for the complex spatio-temporal moth population dynamics ought to be looked for in mechanisms ruled by environmentally governed processes such as phenology.

Background and aim

Larvae of the two geometrid species autumnal moth (*Epirrita autumnata*, Brkh.) and winter moth (*Operophtera brumata*, L.) regularly defoliate large areas of mountain birch forest (*Betula pubescens* ssp. *czerepanovii* Orlova) in Fennoscandia. The occurrence of outbreaks and tree defoliation is very relevant for people living in the region, as the moth outbreaks are very conspicuous and often cause tree mortality. This probably has strong impact locally on recreational land use, such as hunting, and the general perception of the natural surrounding. The effects of moth outbreaks can be severe and can have outstanding impact on the terrestrial ecosystem. During the 1960s, outbreaks of the autumnal moth resulted in the disappearance (die-back) of forests over very large areas in the Utsjoki-region in northern Finland, which turned open birch forest habitat into tundra habitat (Ruohomäki et al. 2000). Similarly, in the beginning of the 21st century, outbreaks and large-scale defoliation of trees reoccurred in northern Fennoscandia and eliminated forest habitat over an area of several thousand square kilometers (Jepsen et al. 2009).

In 1972, Olle Tenow published an extensive survey on the population dynamics of the two moths in Fennoscandia (Tenow 1972). The survey covered fluctuations of moth densities over a period of 100 years and revealed that the high-density outbreak dynamics of the two species were cyclic by intervals of 9-11 years (Tenow 1972). Besides the temporal re-occurrence of the outbreaks, the survey also revealed a particular spatial structure in the outbreak formations, both at the regional and local scale. On the regional scale, outbreaks of the autumnal moth were more frequent in the interior of Fennoscandia compared to winter moth outbreaks, which happened more frequently along the coasts. Apart from this, outbreak amplitudes (i.e. density of larvae during outbreaks) appeared to decrease gradually from North to South in Fennoscandia. At the local scale, outbreaks of both moth species were restricted to a particular zone within altitudinal slopes and occurred at or close to the altitudinal tree line in the mountainous districts of Fennoscandia. As the tree line increases in altitude from northern to southern Fennoscandia, outbreaks generally happened at higher altitude in the South compared to the North.

Ecological research on the two moth species after 1972 mainly aimed to reveal causal relationships in nature, which might lead to the observed cyclic dynamics and outbreaks. Within the subsequent 30 years after Tenow's outstanding contribution, many hypotheses were tested which suggested different potential regulators on moth densities. Such hypotheses included the importance of chemical or physical defenses by the moth's host plant mountain birch (Haukioja 1991), Moran effects mediated through sun spot activity (Myers 1998), parasitoids (Ruohomäki et al. 1994, Bylund 1995) and the effect of predators (Neuvonen 1988, Tanhuanpää et al. 1999). Despite the great effort put into this research, most hypotheses had been dismissed by the time a last thorough review paper was published by Ruohomäki and colleagues in 2000. Although it never could be shown that parasitoids were able to regulate natural moth populations, the magnitude of their impact through mortality of parasitized larvae during some years of moth outbreaks was astonishing (e.g. up to 100%, Bylund, 1995). Hence, the idea that parasitoids were causing the observed moth outbreak patterns was prevailing at the turn of the century. Surprisingly, this conviction seemed rather to be based on the lack of evidence from other alternatives recently explored (see above), than empirical results on the effect of parasitoids. Consequently, the field demanded empirical data shedding light on the capability of parasitoids in regulating insect populations.

After 1972, a few studies also explored the pronounced spatial structure in regional and local moth dynamics in Fennoscandia. The strongest contributions at both scales were made by Finnish researchers. In 1999, Tanhuanpää and colleagues found evidence supporting the hypothesis that southern non-outbreking populations of the autumnal moth were regulated by generalist pupal predators. No such effect was found in northern outbreking moth populations. Some years later, this study was implemented in a broader context in the specialist/generalist predation hypothesis, which proposed that relatively higher abundance of specialist predators (i.e. parasitoids) in comparatively low productive habitat in the North resulted in cyclicality in northern moth populations, while relatively higher abundance and diversity of generalist predators (i.e. voles) in high productive southern habitats lead to a gradual dampening of moth outbreak amplitude from North to South (Klemola et al. 2002). The observed local outbreak patterns, i.e. that moth outbreaks preferentially occurred at high altitudes, were explained by temperature inversion (i.e. accumulation of cold air in landscape depressions), which resulted in high mortality of moth eggs during winter (Tenow & Nilssen 1990, Virtanen, Neuvonen & Nikula 1998). However, by following this logic, researchers completely ignored the fact that high altitude moth outbreaks were also common in coastal regions of Fennoscandia where temperatures never became lethal to moth eggs (Tenow 1972, Hagen et al. 2007).

Hence, forest phenology and especially the potential risk of a phenological mismatch between hatching moth larvae and tree bud burst was explored as an alternative explanation for moth outbreaks. Many of these studies were magnificently discussed in a review by van Asch & Visser, published in 2007. The hypothesis derives from the perspective that moth larvae are highly dependent of gaining access to high quality food (i.e. fresh tree foliage) directly after hatching from eggs during early spring. The quality of

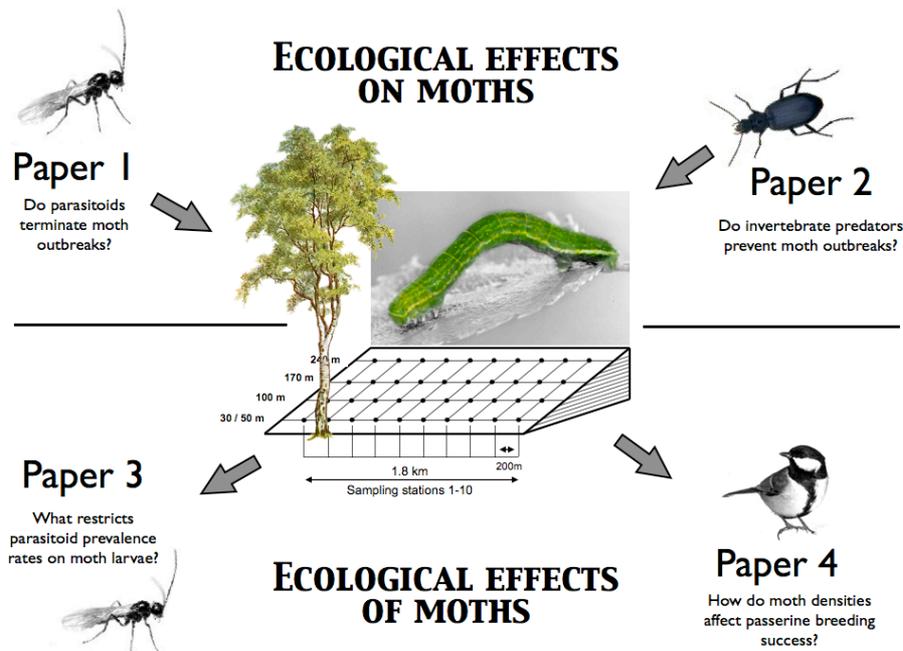


Fig. 1: Graphical summary of the structure of this PhD-thesis with a model of the altitudinal design in the center.

leaves quickly deteriorates after unfolding from buds. That is, the amount of tannins increases and the leaves toughen within a few days, which makes it increasingly difficult for newly hatched larvae to chew and feed on tree foliage if their hatching is delayed with respect to bud burst. Conversely, larvae hatching before the buds burst are prone to starve to death without having access to tree foliage. At present, this interaction between moth and tree phenology has been linked to moth outbreak dynamics, but the specific mechanism resulting in increased moth population growth is still unknown (Hagen *et al.* 2008, Jepsen *et al.* 2011, Jepsen *et al.* 2009).

However, the match/mismatch hypothesis has also been lifted up to a higher trophic level. In this, researchers acknowledged moth larvae as an important resource for a range of predator species, predominantly passerine birds (Both *et al.* 2009). This interrelationship quickly became an often-cited example of phenological mismatch across trophic levels caused by elevated temperatures (Visser *et al.* 1998, Buse *et al.* 1999, Siikamäki 1998). It also called for evolutionary studies, such as on the timing of breeding in birds with respect to prey availability (van Noordwijk *et al.* 1995) and on mechanisms for passerine birds to synchronize their hatch date with the availability of insect prey (Cresswell & McCleery 2003). Apart from these phenological studies, moth larvae were recognized as the main diet for many species during the breeding season, which, in specific systems, resulted in close dependencies between moth and bird population dynamics (Hogstad 2005, Lindström *et al.* 2005). Consequently, one moth cycle ago, in spring 2004, when I joined the moth population dynamics project at the University of Tromsø, I got confronted with an ecological system of outbreaking moth populations, which had produced a wide range of exciting hypotheses over time. Nonetheless, the cause of the outbreaks was still unknown and studies on what effects these huge resource pulses might have on the ecological system in Fennoscandia were just emerging.

The project I joined at the University of Tromsø had originally been established in 1999. As part of this approach, spatially replicated sampling stations had been set up within an altitudinal gradient (see below). Data on parasitoid impact on moth larvae and corresponding larval densities had been collected since 2001 and I got the chance to proceed with this work. Over the years the data accumulated and finally spanned over late increase (2001-2003), peak (2003-2005) and crash phases (2006-2008) for both moth species. The corresponding larval density data for both moth species allowed me to test if the larval parasitoids found during the years of study were able to effectively regulate their hosts as predicted from a great bulk of mainly theoretical literature (Paper 1). By this I was able to contribute to the research on the enigma of what might or might not cause population outbreaks and cyclic dynamics in these moth populations. My second contribution aimed at the same research issue, although related to the spatial distribution of outbreaking moth densities within altitudinal gradients (see above, Hagen *et al.*, 2007). Since the work by e.g. Roland and Embree on winter moth in Canada, it had been clear that pupal predators can have a strong effect on moth densities by consuming and killing moth pupae in the soil (Roland 1994, Roland & Embree 1995). Although this hypothesis had been tested for the effect of shrews (Hansen, Hagen & Ims, 2009), it had never been addressed for the effect of invertebrate predators on

Fennoscandian moth populations. The very large spatial variation of local moth populations within altitudinal gradients provided an excellent opportunity to test if densities of moth larvae and invertebrate pupal predators may be inversely correlated. If so, the finding could suggest that moth outbreaks at high altitudes were a result of predation release from pupal predators (Paper 2).

The dataset derived from the first parasitoid study (Paper 1) comprised a total of 4282 larvae of the autumnal moth and 11 832 larvae of the winter moth. This yielded very detailed information on the interrelationship of larval parasitoids and their host populations. In the perspective of viewing moth larvae as a resource, we re-analyzed these data from the parasitoid's point of view. That is, we tested not only if parasitoids might regulate their host populations (Paper 1) but also if the guild of larval parasitoids may be submitted to variations in host density or other parameters (Paper 3). The aim of this approach was to try to entangle if larval parasitoids may be limited by bottom-up forces such as host density or environmental features hidden in predictors such as year and altitude. This study was a direct consequence of the results found in Paper 1. It was an attempt to explain why top-down regulation of the winter moth and autumnal moth populations in coastal northern Norway was found to be outside the scope of interactions with larval parasitoids. The novelty of this study lay in regarding moth larvae as a resource for parasitoids and not to focus on the predatory effect of parasitoids on moth populations. Similarly, the last paper tested how important moth larvae were for breeding success in passerine birds (Paper 4). However, here we applied altitudinal variation in breeding parameters more target-oriented by testing the contribution of prey density to breeding success in passerine birds versus the importance of forest and tree phenology along three altitudinal gradients. The aim of this study was to highlight the strength of dependency of breeding passerine birds to the highly varying moth densities in contrast to the importance of phenology in the short sub-arctic summer. Additionally, we wondered if phenological variation across altitude might serve to counteract the risk of mismatch between bird breeding and larval hatching.

Methods

Study species

The winter moth and autumnal moth are two polyphagous geometrid species whose larvae, in Fennoscandia, mainly feed on foliage of the mountain birch. Despite the fact, that the autumnal moth has a holo-arctic distribution and the winter moth is a very common species in the whole of Europe, cyclic high density outbreaks, which cause large scale defoliation of forests are only known from Fennoscandia (Tenow 1972) and seem to occur more often at harsh environments such as found at e.g. high altitude and latitude (Klemola 2002). Since the beginning of the 21st century, a third species, the scarce umber moth (*Agriopis aurantiaria*, Hübner), is invading northern Norway. This species, invading northern Norway from the southern and interior parts of Fennoscandia, is steadily spreading northwards, but little is known, yet, of what kind of population dynamics it will develop in the North in the future (Jepsen *et al.* 2011). The scarce umber moth is included in the more community-based studies Paper 2 & 4. All three species resemble each other in phenology and ecology. The autumnal moth is slightly larger than the winter moth and can be called native to Fennoscandia while the winter moth invaded northern Fennoscandia approximately 100 years ago (Tenow 1972). The scarce umber moth is the largest of the three species, given that it grows up under favorable conditions. Despite the misleading names, the autumnal moth is the more cold tolerant species and consequently found also in the interior of Fennoscandia where winter temperatures drop lower than along the Norwegian coast (Jepsen *et al.* 2011). Eggs of the moth species are deposited by females during September (autumnal moth, scarce umber moth) and October (winter moth) and overwinter on tree trunks. The moth eggs hatch during spring (May) and the tiny larvae (approx. 1 mm in length) start to feed on buds and developing birch leaves. The phenological timing of egg hatch and birch bud burst seems to be essential for larval development, as too early hatched larvae starve on the snow, while delayed hatching may result in decreased food quality for newly hatched larvae (van Ash & Visser 2007). It has been shown that the autumnal moth seems to cope better with low spring temperatures, as its spring development is enhanced compared to the winter moth (Mjaaseth *et al.* 2005).

Moth larvae undergo five instars between May-July, depending on altitude at the location of this study. During this time, the larvae are exposed to avian and invertebrate predators such as spiders, harvestmen and parasitoids. After approximately 2 - 4 weeks (depending on temperature), the larvae drop to the forest floor and pupate in the soil. The pupal stage lasts approximately three (autumnal moth, scarce umber moth) to four (winter moth) months. Male moths eclose first during autumn, closely followed by female moths. Females of the scarce umber and winter moth are wingless and perch on tree trunks where they use pheromones to attract males. In contrast, females of the autumnal moth do have wings, but are considered to be bad flyers due to their heavy egg load. The number of eggs laid by each female is dependent on body size and may vary between 100 - 130 eggs per female (Klemola *et al.* 2004). Adult moths die after deposition of eggs, which overwinter until spring.

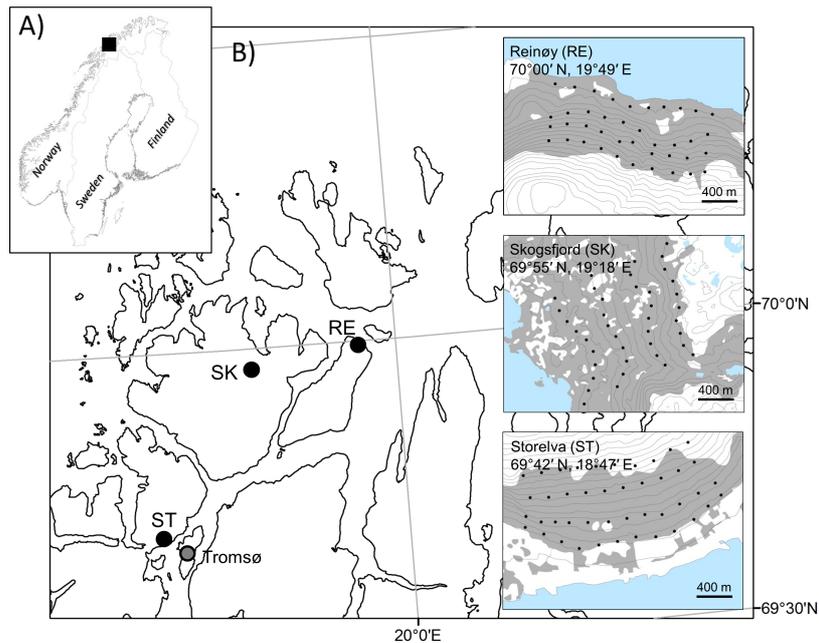


Fig. 2: Overview over the geographic placement of the study sites and the study design.

Study area and altitudinal design

All fieldwork of this PhD-project was conducted in the coastal district of northern Norway (Fig. 2). The landscape in this region is very heterogeneous, characterized by mountains of 600 m - 1200 m altitude, intersected by deep valleys, fjords and sounds. The climate is oceanic with mean winter temperature of -4.4 C (January, daily mean) and mean summer temperature of 11.8 C (July, daily mean, city of Tromsø, Norwegian Meteorological Institute). The lowest ever measured temperature in Tromsø is -20.1 C (1985, Norwegian Meteorological Institute) which is far from the lethal limit for moth eggs, which earlier had been measured to be ~ -35 C (MacPhee 1967, Tenow & Nilssen, 1990). Spring at this location starts at the lowest altitudes in early May where winter generally returns during October. In contrast to altitudinal slopes of more southern localities such as in the European Alps, the forest belt between sea level and the altitudinal tree line, which is the natural forest limit at approximately 250 – 300 m a.s.l. is very condensed. Altitudinal gradients have been recognised as natural, experimental set-ups to test the ecological importance of environmental parameters as e.g. temperature, wind velocity and moisture (Körner, 2007).

This PhD-thesis is based on fieldwork and data from three study sites; Reinøya (established in 1999), Storelva (2005) and Skogsfjord (2008, Fig. 1). The study design at all sites incorporated altitudinal gradients but differed slightly (Figs 1 & 2, see below). At each of four successive altitudes (30 m at Reinøya but 50 m at Skogsfjord and Storelva, 100 m, 170 m and 240 m a.s.l.), four transects consisting of 10 sampling stations were established. The sampling stations within transects were spaced by 200 m to avoid correlating moth densities due to dispersal (i.e. Edland [1971] measured that dispersal in the form of ballooning of moth larvae occurred over a distance of 30 m). Consequently, each study site measured approximately 1.8 km in length and ranged from close to sea level to the altitudinal tree line (Fig. 1). The 30 m transect at two study sites had to be moved to 50 m a.s.l. due to urban areas (Storelva) and a lake at the base of the slope (Skogsfjord). In addition, because of the funnel-shaped extension of the slope towards the lower altitudes at Storelva, the 50 m and 100 m transects at Storelva consisted of 12 sampling stations instead of 10 (Fig. 2).

Sampling methods

Larval moth density and altitude were the main parameters, which entered all four studies of this thesis. To ensure a reliable density measure over time and a large number of field assistants, we adapted a standard method introduced by Hagen et al. 2003. Accordingly, in a radius of approximately 20-30 m around each sampling station, 10 branches of equal size (~ 70 cm) were cut from 10 haphazardly chosen birch trees and shaken within a large plastic box. Larvae of both species feeding freely on the birch leaves consequently detached from the leaves and could be counted in the box. Until approximately their third instar, young winter moth larvae feed between birch leaves, which are spun together. Hence these larvae may quickly be overseen by this method and care was taken to time density measurements at best possibility with the fourth instar of winter moth larvae.

In papers 1 & 3, the relationship between moth larvae and larval parasitoids was tested. To obtain samples for estimation of the prevalence of parasitoids, larvae of the autumnal and winter moth were sampled by the same method as described above. However, for this purpose, branches were not cut from the trees but the researchers roamed freely around the sampling stations, shaking all available tree tops and branches into the boxes. Larval sampling for parasitoid rearing never interfered with density measurements. All larvae were consequently transported to the lab where up to 20 larvae were stored in 1 litre plastic boxes and fed every third day. The boxes contained sieved sand for pupation and a layer of peat moss (*Sphagnum* spp.) for moisture maintenance. All emerging larval parasitoids (i.e. parasitoids that attack the larval stage of their host) were recorded. When the larval stage had ceased in the samples, the boxes were stored under natural conditions until autumn. Then all emerging moths were recorded and the sand was sieved to find and check intact pupae for late larval parasitoids (i.e. larval parasitoids that emerge within pupae).

In paper 2, the importance of invertebrate pupal predators (i.e. predators that attack moth pre-pupae and pupae on and in the soil) for spatial moth outbreak dynamics was tested. Pupal predators, such as ground beetles, spiders, harvestmen and carabid beetles were caught by the use of pitfall traps during a catching period of three weeks from mid-August until early September. For this purpose, each sampling station was equipped with eight pitfall traps. At the end of the catching period, the catch was transported to the lab where functional groups were recorded and identified.

In paper 4, we explored the dependencies between avian predators (i.e. great tits and pied flycatcher), phenology and moth densities. For this purpose, all sampling stations in the three altitudinal gradients were equipped with temperature loggers and two nest boxes each. These nest boxes were emptied during autumn and checked weekly from mid April. Species, number of eggs and fledglings was recorded until all birds had fledged. This was generally the case during mid-July.

Statistical analyses and data

All data analyses in this PhD-thesis were done using the statistical software R (R Development Team). According to the nature of the response variables, we applied either logistic regressions (papers 1 & 3), linear regressions (lm, papers 1, 2 & 4) or linear mixed effects models (Paper 1 & 4). Whenever necessary, we applied model selection by the use of Akaike Information Criterion (AIC). In other cases, we used predefined statistical models to estimate the effects focal to the aim of the study. According to the rule of parsimony, we presented the simplest models or analyses and, if possible, graphical display and analysis of the data instead of complex statistical modeling.

Main results and discussion

In the first paper (Paper 1), we presented data on larval densities collected on the study site Reinøya from 2001 - 2008. Additionally, data on larval parasitism were presented from 2001 - 2005. After 2005, the local population of autumnal moths had collapsed which made the attempt to collect a sufficient number of larvae for parasitoid rearing impossible. The population peak for the autumnal moth happened during the year 2003, largely simultaneously at all four altitudes (Paper 1: Fig. 3). However, for the winter moth, we found very strong variation in larval densities along the gradient. For example, the local winter moth population peaked in density at 30 and 100 m during the beginning of the study, while densities highest in the gradient appeared to increase until the peak in 2004 - 2005. This finding, i.e. outbreaks of the winter moth lagged behind autumnal moth outbreaks by 1-3 years, was in coherence with other studies and was addressed in detail during paper 3 (see also Ammuneit *et al.* 2010). Also the local variation between sampling stations within altitudes was more pronounced for the winter moth than for the autumnal moth.

First, we tested if the prevalence of larval parasitoids could predict moth population growth rate towards the subsequent years. For this test, we merged all density and parasitoid data per altitude and applied one logistic regression model for each moth species with growth rates as response and parasitism as predictor variables. Additionally, we pooled the data on parasitoid prevalence for all parasitoid species to evaluate the overall effect of larval parasitism on moth growth rates. According to the model selection tool AIC, altitude had no bearing on the results of this analysis and could hence be neglected. The models revealed that the prevalence of the larval parasitoids found in this study had no effect on the temporal dynamics of their hosts. However, when analyzing the spatial variation in moth densities along altitudinal transects (that is, in the second attempt we used density and parasitism estimates per sampling station instead of merged data per altitude and added the parameter year to the model to correct for temporal variation in the data), we found that this spatial variation in moth population growth in part could be explained by the effect parasitism.

Studies on parasitoids in insect populations are a time consuming task, as the host species have to be followed through most of their life cycles. As a logistic consequence, parasitoid studies are either conducted within laboratory populations (Hassell 2000) or at relatively small scale in nature without spatial replication at an adequate scale (Klemola *et al.* 2010). Our study revealed that this mismatch between the spatial scale at which moth outbreaks occur and the scale at which ecological studies often are conducted may lead to different and potentially wrong conclusions according to how important larval parasitoids may be for shaping temporal dynamics of the autumnal and winter moth in Fennoscandia. While larval parasitoids did have an effect on small-scale variation in moth growth rates between sampling stations, parasitoids had no effect on the temporal dynamics of two moths at the scale of the whole study site (which is a more realistic spatial scale at which outbreaks in natural environments occur than between sampling stations). The same finding we reported from a related study at another locality, which followed a 70 km long transect (Hagen *et al.* 2010). Accordingly, the studies demonstrated the importance of spatial replication of study units and concluded that disagreement about the role of larval parasitoids in regulating temporal host dynamics found in the scientific literature might be attributed to conflicts in spatial replication of study units and the overall spatial scale of ecological studies.

However, also spatial patterns in the distribution and abundance of species may help to explain what factors can act to limit species' density. In northern Fennoscandia, moth larvae densities are often correlated with altitude. Along mountain slopes, outbreaks can be observed close to the tree line, with sharp distinction between forest that has been severely affected and unaffected forest habitat. While larval parasitoids were rejected as drivers of moth population dynamics in the populations of our study in Paper 1, other predators such as pupal predators had been found earlier to significantly affect moth populations (Roland & Embree 1995). Larval parasitoids attack their host during the larval stage, that is when larvae feed on tree foliage. However, during the end of the larval stage, moth larvae drop to the ground and pupate in the soil (see above). During this time, which may last between 2-3 months, moth pupae and prepupae (the larval stage just prior to pupating), moth larvae/pupae are entirely defenseless and, hence, prone to predation by vertebrate or invertebrate predators. Few years before the start of my PhD-project, Finnish researchers had found strong impacts of predation on the pupal stage of moth populations in southern Finland (Tanhuanpää *et al.* 1999). Interestingly, this profound impact of predation on pupae was absent in northern moth populations and the researchers suggested, that release from shrew predation could be the cause of high amplitude moth outbreaks in the North of Fennoscandia, a pattern, which was absent in southern populations. This hypothesis was explicitly tested by Hansen and colleagues during the years 2002 - 2003, but was rejected as shrew densities were not related to moth densities and neither to altitude in the same altitudinal gradient where the research for Paper 1 in this thesis was conducted (Hansen *et al.* 2009). But there are more predator groups than shrews that might affect moth populations.

In paper 2, we chose the invertebrate predator guild, particularly soil dwelling predators for our study. Again, we used the natural experimental setting of moth density variation across altitude to test if the absence of moth outbreaks at low altitude can be attributed to the community of invertebrate predators. In contrast, large moth densities culminating in outbreaks at higher altitudes might be explained by the larvae's escape from predation, given that the abundance or functional response of invertebrate predators is low at high altitudes. To test this hypothesis, we used pit fall traps to index abundances/activities of ground-dwelling invertebrate predators, specifically harvestmen, spiders, carabid beetles, rove beetles and other predatory beetles within two altitudinal gradients in relation to the densities of moths. Despite the characteristic altitude-dependent patterns in moth density (Paper 2: Fig. 2), predator densities neither followed their prey spatially, nor temporally (although the temporal scope of the study was short, Paper 2: Figs 5 & 6). As predator densities, additionally, were not inversely correlated with altitude, we rejected the hypothesis that invertebrate predators might cause the observed altitudinal patterning in moth densities (Paper 2). By the end of this study (Paper 2), we had not come closer to answering the question of what might cause complex temporal and spatial dynamics of moth population in northern Fennoscandia, but we had reduced the number of potential candidates of top-down regulation/limitation of moth populations by removing larval parasitoids (Paper 1) and ground-dwelling invertebrate predators (Paper 2) from the list.

During the next two studies (Papers 3 & 4) we changed our focus; instead of viewing moth population dynamics as a result of the impact of ecological interactants, we regarded larvae as a resource for two groups of consumers, parasitoids and passerine birds. This was a new approach especially for paper 3, in which data on larval parasitoids from paper 1 were reanalyzed from a new perspective. Despite the lacking capability of larval parasitoids to rule moth growth rates, the high prevalence rates of up to 74% in some cases had been surprising (Paper 1: Table 1). The aim of paper 3 was to understand why the larval parasitoids were not able to launch a stronger impact on temporal moth dynamics than could be expected from such high prevalence rates. Additionally, one earlier formulated hypothesis on the temporal lag between autumnal moth and winter moth dynamics (Klemola *et al.* 2009, see above) suggested that dissimilar vulnerability of the two moth species to parasitism might cause the time lag between winter moth and autumnal moth outbreaks. According to the hypothesis, the autumnal moth would suffer higher

parasitism, leading to an earlier population crash. Meanwhile, the winter moth could escape parasitism and cumulate to peak densities in the wake of an autumnal moth population peak (Klemola *et al.* 2009).

First, we used logistic regression analyses to test if the dynamics of the four most important parasitoid species were depending on host density or if other parameters imbedded in the models in the form of year and altitude could explain the spatio-temporal patterning of larval parasitoid prevalence rates. Some parasitoid species displayed tendencies for a spatial and temporal response to host densities, but, surprisingly, these effects were entirely outweighed by the importance of year and altitude in explaining variation in parasitism prevalence. However, parameters such as year and altitude cannot be easily attributed to specific ecological mechanisms without demonstrating the underlying cause and effects (e.g. unfavorable temperature which might impede search efficiency of parasitoids during certain years or/and at certain altitude). Consequently, we did not succeed in identifying the particular driver of parasitoid dynamics as they were mirrored in the prevalence rates of their hosts, but our data showed clearly that the effect magnitude of altitude and year strongly overrode host (moth larvae) density as the explanatory variable for spatio-temporal variation in parasitism. Hence, we concluded that unknown aspects of the larval parasitoid ecology, which co-vary with year and altitude, decouple the effect of larval parasitoids from the population dynamics of their hosts. What these "unknown aspects" may include is a matter of speculation but pathogens and/or phenological issues should be evaluated (see below). Additionally, parasitism rates for the two generalists at Reinøya in fact were higher for the winter moth and not for the autumnal moth, as might be expected from the lag - hypothesis. Instead, we found no differences among the two host species in total parasitism rates (Paper 3: Fig. 2) and the lag - hypothesis based on larval parasitoids was rejected.

The last investigation in the scope of this PhD-thesis, which incorporated moth populations as a resource, was conducted on the breeding success of two passerine bird species, the great tit (*Parus major*, Linnaeus) and the pied flycatcher (*Ficedula hypoleuca*, Pallas). Also this study was designed with particular emphasis on ecological variation along altitudinal gradients. From an insectivorous bird's perspective, altitudinal gradients may act to pose a conflict of interest for birds when being confronted with the selection of breeding habitat. Moth larvae constitute a large portion of the bird's diet, especially during the breeding season (Bel'ski & Bel'skaya 2009; Burger *et al.* 2012). But while highest densities of moth larvae often occur at high altitude in forested mountain slopes in northern Fennoscandia, spring, as reflected by bud burst and snow melt, starts on the base of mountain slopes, slowly progressing upwards. Taking the relative shortness of sub-arctic summers into consideration, we were interested to highlight the possible trade-off between prey resource access (moth larvae abundance) and forest phenology.

Our analyses showed that phenology was the main explanatory variable in bird breeding parameters. Birds of both species significantly preferred nest boxes at lower altitude, where spring arrived first, and also egg-laying date was either positively correlated with altitude (pied flycatcher) or birch bud burst (great tit). Additionally, nest box occupancy was significantly correlated with moth larvae density. Despite the fact that great tits laid their clutches up to two weeks earlier than pied flycatchers, the predicted peak date for egg laying with respect to breeding success varied only by two days between the species. This indicates that great tits are able to adjust their egg incubation period to counteract the potential risk of phenological mismatch with their Lepidoptera prey. On the other hand, this strategy may be paid for by a higher failure rate in breeding success compared to the later breeding pied flycatcher. This failure rate can most likely be explained by a higher degree of variation in (possibly more unfavorable) weather conditions during the first spring days at sub-arctic regions when great tits commence breeding. However, as great tits, by their early start of breeding, gain the advantage of being able to lay a second clutch within the short time frame of the sub-arctic summer, failure during the first breeding attempt may be compensated for later in the season.

Conclusions and future prospects

During the past 13 years, since Ruohomäki *et al.*'s review on moth population dynamics and their possible causes in Fennoscandia (Ruohomäki *et al.* 2000), many studies in addition to those presented in this PhD-thesis have produced novel insights into cause and effect relationships in this study system. Despite these efforts, the focal issue of most studies, i.e. what rules temporal and spatial moth dynamics, remains unsolved. However, rejection of hypotheses offers opportunities for new interpretations and helps to pinpoint successive hypotheses and study efforts. The unquestioned dominant effect of altitude and year in all our analyses is maybe the most striking result of this PhD-thesis. Unfortunately, we did not succeed to identify the specific mechanism(s) that might be responsible for the dominance of these two omnibus variables. However, this unexplained variation was of great help to conclude that larval parasitoids were not capable of regulating their hosts in our study areas and that the reason for this incapability has to be sought in unknown mechanisms, which co-vary with year and altitude. In that, papers 1 & 3 help to

recapitulate the traditional parasitoid regulation hypothesis in light of our extensive empirical survey. However, shortly after publication of paper 1, a Finnish study from the interior of Fennoscandia concluded into the opposite direction, stating to have found evidence for the parasitoid regulation hypothesis (Klemola *et al.* 2010). Although also this study (as very many before) suffered from inadequate spatial replication in term of scale, future efforts could be directed to test if the response of parasitoids to their hosts is habitat-specific on a regional scale. The geography of the climatically mild, heterogeneous coastal sections and the cold, homogenous interior of Fennoscandia differ profoundly, which without doubt strongly affects insect community structure between these two landscapes. The possibility that also numerical and functional responses of the two landscape-specific parasitoid guilds may differ and hence their effects on moth population dynamics could be addressed in a large scale parasitoid study crossing the borderline between these two landscapes. Along the coastline of northern Norway, where larval parasitoids are not capable of terminating moth outbreaks and where the topography is very heterogeneous with high mountains, deep valleys, fjords, sounds and islands, sharply localized moth outbreaks are evident (Ims *et al.*, 2004). These outbreaks often occur at high altitude or isolated patches of birch forest (Hagen *et al.*, 2007). At the same time, outbreak dynamics can be synchronous over thousands of square kilometers in the northernmost districts of Fennoscandia, but patchy within the outbreak region (Jepsen *et al.* 2009). Our test on the density related impact of ground dwelling invertebrate predators on moth dynamics between adjacent habitat of outbreaking and non-outbreaking moth densities high and low in the altitudinal gradients, respectively, lead to the rejection of the predator-escape hypothesis for invertebrate ground-dwelling predators. However, the extraordinary sharp delimitation of outbreak patches along altitudinal gradients strongly suggests a direct or indirect dependency between moth outbreaks and phenologically related parameters. The distinction between direct dependencies (e.g. environmental features such as temperature or moisture) on moth populations or indirect dependencies such as possible effects of environmental parameters on biotic agents such as pathogens should be targets of future studies. Specific attention should be given to address potential mechanisms on other stages of the moth's life cycle than exclusively the larval and pupal stages. That is, we still lack the elementary understanding of which specific stage in the moths development is critical for building up (or eliminate) outbreaking moth densities. Specifically targeted studies on identifying this critical stage similar to the work of Münster-Swendsen (2002) on spruce needle miners in Denmark, who followed the complete life cycle of this species, could answer important ecological questions: How many larvae successfully pupate during the late larval stage and give rise to the reproducing population of adult moths? How does fertility in adult moths relate to densities during the previous (larval) stage and which proportion of laid eggs in autumn eventually hatches during spring? May the far shorter generation time of pathogens compared to moths make pathogens an important candidate that deserves a closer look, such as suggested by Myers 25 years ago (Myers 1988)? Perhaps, researchers have focused too much on the hypothesis of moth regulation by parasitoids during the past decades. Given the clear results that lead to the rejection of the parasitoid regulation hypothesis during this PhD-thesis, I believe that stepping back to view moth dynamics from a wider angle and recollecting the contributions of Münster-Swendsen (2002) on life cycle studies and Myers (1988) on pathogens could yield valuable insights to moth population dynamics in Fennoscandia.

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Paper 1

Paper 2

Paper 3

Paper 4



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