

Population Ecology at the Range Edge

Survival and Dispersal of a High-Density Lepidopteran
Population

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Abstract

Outbreaks of pest species can cause extensive damage to arable crops and to forest production. Some pests also present severe health hazards to humans and animals. A recent outbreak of the Northern pine processionary moth *Thaumetopoea pinivora* on Gotland, southern Sweden, has caused concern for the welfare of local residents as this species is known to cause itching rashes in most people that come in contact with infested areas

This thesis examines larval traits that are important to the fitness of *T. pinivora*, and may thus be a factor in explaining why the species sometimes reaches outbreak levels. As there has been much concern that the outbreak will lead to the moth expanding its range, I have also studied the species' dispersal patterns on a local scale on Gotland and its distribution and colonization history on a global scale.

Colony size was found to be important for the growth and survival of the gregarious larvae of *T. pinivora*. The number of individuals in a colony determines the benefits gained from both predator protection and thermoregulation, indicating that high population densities are favourable for larval survival.

The larvae of *T. pinivora* hatch early in the spring. This enables them to evade predators that do not become active until later in the season. Predator activity increases later in the spring, and early hatching larvae have then had time to grow and are therefore better defended from predation than larvae that hatch later.

Although several populations were found outside the outbreak area on Gotland, none of these populations were founded recently and the migration level between the populations was low. This indicates that there is little or no expansion of the outbreak range.

The distribution of *T. pinivora* populations is globally fragmented. Genetic studies show that the colonization history is recent, which is surprising considering the limited dispersal ability of the species. The pattern could possibly be due to a loss of habitat patches that have previously been available for colonization in a stepping-stone fashion.

Keywords: outbreaks, gregariousness, hatching date, microsatellites, gene flow

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For Erik

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List of Publications

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

- I Ronnås, C., Larsson, S., Pitacco, A. and Battisti, A. (2010). Effects of colony size on larval performance in a processionary moth. *Ecological Entomology* 35, 436-445.
- II Ronnås, C. and Dalin, P. Evergreen foliage allows early hatching in a pine processionary moth and escape from ant predation. (manuscript).
- III Ronnås, C., Cassel-Lundhagen, A., Battisti, A., Wallén, J. and Larsson, S. (2011). Limited emigration from an outbreak of a forest pest insect. *Molecular Ecology* 20, 4606-4617.
- IV Cassel-Lundhagen, A., Ronnås, C., Battisti, A., Wallén, J. and Larsson, S. Genetic evidence of recent expansion from unknown glacial refugia of the northern pine processionary moth (*Thaumetopoea pinivora*). (manuscript).

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1 Introduction

When an insect population drastically increases in density and remains high for some time, this is referred to as an outbreak. Most studies on outbreaks have focused on pest species, i.e. those that negatively affect humans. Some insect species are of economic importance, for example because they feed on crops or woody plants. Others are considered pests because they can have harmful effects on human health, for example by releasing urticating hairs. In general, population densities fluctuate around an average, but the magnitude of the fluctuations differs from species to species. When the fluctuations are particularly pronounced, the density may occasionally reach outbreak levels but it usually returns back to normal given time. While the exact causes for an outbreak rarely are known, it can be assumed that some, or several, of the factors that maintain populations at low densities have been overcome. For example, a species colonizing a new area can escape the controls imposed by predation present in the old range if its predators do not colonize as fast as the focal species (Colautti *et al.*, 2004; Liu and Stiling, 2006; Menéndez *et al.*, 2008). Changes in other trophic levels such as an increase in resource availability or a decrease in the density of predators or parasitoids can also cause a population to grow (Berryman, 1987). Some species are known to reach outbreak densities often, while others never or rarely do so. Populations of species that rarely, or never, reach outbreak densities generally fluctuate much less than outbreak species (Mason, 1987). Those species appear to have life history strategies that keep them near their equilibrium density (MacArthur, 1960). Some characteristics are unusually common among outbreak species; notably, they often exhibit high diet breadth and fecundity. Outbreak Lepidopterans are more often gregarious in their larval stage and are usually spring-feeders (Hunter, 1991). The studies described in this thesis were inspired by the recent outbreak of *Thaumetopoea pinivora* on Gotland, southern Sweden.

Social Lepidoptera

Within the Lepidoptera (butterflies and moths), species with social larvae are more prone to outbreaks than those with solitary larvae (Nothnagle and Schultz, 1987; Hunter, 1991). However, most lepidopteran larvae are solitary feeders. For example, only about 5% of North American butterfly species form larval aggregations (Stamp, 1980), while 8% of forest-inhabiting moths in Canada feed in groups for at least part of the larval stage (Herbert, 1983). Social behaviour has several benefits that may affect a population's tendency to reach outbreak densities. The most important of these are: improved thermoregulation, feeding facilitation, and better defence against enemies. Thus, larvae that live in groups may suffer less predation than solitary larvae (e.g. Lawrence, 1990; Denno and Benrey, 1997; Hunter, 2000). If the larvae construct communal nests, they can retreat to these for protection (Fitzgerald, 1993). Other ways for colonies of larvae to protect themselves include antipredator group displays (Prop, 1960; Stamp and Bowers, 1988; Lawrence, 1990) and more efficient aposematic traits (Stamp, 1980; Nothnagle and Schultz, 1987; Gamberale and Tullberg, 1998).

Furthermore, some gregarious species thermoregulate by massing together in colonies in sunny locations. This may be especially important under cold weather situations, such as in early spring, or at high latitudes and altitudes (Joos *et al.*, 1988), under which temperature conditions can reduce feeding and digestion (Frid and Myers, 2002). Larger aggregations benefit more than smaller ones due to reduced convective heat exchange (Joos *et al.*, 1988). Thermoregulation is important in tent-building species, such as certain tent caterpillars and processionary moths (Knapp and Casey, 1986; Battisti *et al.*, 2005), as well as in species that do not build tents (Sullivan & Wellington, 1953; Klok and Chown, 1999).

Colony living can also allow larvae, especially the very young ones, access to plant tissues that would otherwise be unavailable. For example, some leaf surfaces are very tough; this obstacle can be overcome if several larvae feed together on the same spot (Lyons, 1962; Shiga, 1976; Clark and Faeth, 1997). Similarly, larvae feeding in groups may be more efficient at removing trichomes protecting the leaf surface (Young and Moffet, 1979).

Spatial dynamics on a local and global scale

When a population reaches an unusually high density, overpopulation can lead to resource depletion and starvation, which may have drastic effects on fitness

(e.g., Klomp 1966). When this happens, emigration to new areas can be expected according to the ideal free distribution theory (Fretwell and Lucas, 1970) to avoid starvation. This phenomenon, known as density-dependent dispersal (Berryman, 1987; Matthysen, 2005), is commonly associated with outbreaks (Denno and Peterson, 1995; Bowler and Benton, 2005). Thus, an increase in density can result in a higher emigration rate (Otronen and Hanski, 1983; Bengtsson *et al.*, 1994; Herzig, 1995; Rieske and Townsend, 2005; De Meester and Bonte, 2010), and may result in new populations being established (Nair, 1988; Benzie and Stoddart, 1992). When the high-density population is situated at the edge of the species' range, the dispersal can result in an extension of its distribution (Travis *et al.*, 2009; Wilson *et al.*, 2010). However, the spread of individuals from high-density areas will also depend on the dispersal traits of the species (Montgomery and Wallner, 1988; Pöyry *et al.*, 2009). While highly mobile insects are expected to have outbreaks covering large geographic areas, the area affected by outbreaks of poor dispersers is more likely to be restricted (Berryman, 1987; Harrison, 1994; Harrison, 1997).

The outbreak on Gotland

The northern pine processionary moth *Thaumetopoea pinivora* (Treitschke) (Lepidoptera, Notodontidae) was once considered a rare species in Sweden and was until recently red-listed (Gärdenfors, 2000). There were a few known populations at Sudret on southern Gotland and at Böda on Öland. However, the density of the population at Sudret recently increased dramatically, peaking in 2004 and 2006 (Larsson *et al.* 2008). Since this species has urticating setae that can cause severe allergic reactions in humans and animals, (Battisti *et al.*, 2011), this outbreak has been the cause of great concern for people living in the area.

2 Study System

The northern pine processionary moth *T. pinivora* is generally monophagous on Scots pine (*Pinus sylvestris* L.), although it can occasionally be found on other pine species. On Gotland, the species has a two-year development cycle (Fig. 1).

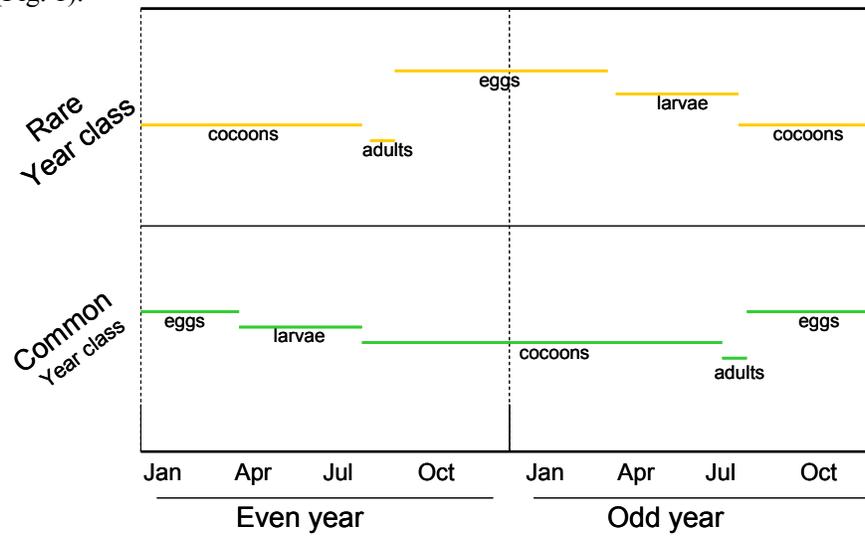


Figure 1. The life cycle of *Thaumetopoea pinivora*. The species has a two-year life cycle with parallel year classes. The population density differs between year classes, with the density of larvae being highest in even years.

The flying time of the adults is in mid July, and the females lay all their eggs (100-200) in one or two batches on pine needles (Fig. 2). Adults do not feed and do not survive for more than a few weeks. The eggs over-winter, and larvae hatch early in the following spring (by mid April on Gotland). The larvae live together in colonies throughout the larval period (five instars),



Figure 2. A *Thaumetopoea pinivora* egg batch.

which takes about three months (Schwenke, 1974). All larvae in these colonies start as full siblings, but colonies often merge at high population densities, forming groups of up to 1,000 individuals (Larsson et al., 2008). During the first two instars the larvae spend the days basking in the sun to increase their body temperature. This helps them digest the food that they eat during the nights. Whenever the colony moves, they walk in the head-to-tail procession for which they are named. In late July, the colonies leave the trees in long processions, which can be several meters long, to spin cocoons in the soil.

In Sweden, reproducing populations are only found on Gotland and northern Öland, although flying males are sometimes caught in light traps on the mainland (e.g. Palmqvist, 1984; Franzén, 2004). There is no reliable information on how long *T. pinivora* has been present on Sudret, but local residents report that the larvae have been there since at least the 1930s. In the early 2000s, the population density increased dramatically, reaching outbreak levels. The Sudret population has a tendency to have discrete year-classes with high larval densities in even years and lower densities in the odd years, although this pattern seems to have become less pronounced as the outbreak has proceeded (probably due to prolonged diapause in the cocoons).

Thaumetopoea pinivora larvae, like the larvae of the other European species *T. pityocampa* and *T. processionea*, have microscopic hairs (setae) that are released into the air and are noxious to humans and animals (Battisti et al., 2011). When the setae come into contact with (penetrate) the skin, they cause itching rashes that may last for up to three weeks (Vega et al. 2003; Fagrell et al., 2008). Contact with the setae can also cause general symptoms such as fever, tiredness, or erythema (Fagrell et al., 2008). If the setae are inhaled, they can cause asthma (Holm et al., 2009). The release of the setae is considered to have evolved as a defence against predators, but the target(s) of this defence response is unknown (Battisti et al., 2011). The larvae moult in the trees and leave their discarded skins in the canopy, where they continue to release setae, which drift in the air like pollen, for several months after being discarded. The recent outbreak at Sudret has caused much concern as the setae pose a risk to

people living nearby. Tourism is also affected as there are many summer houses in the area.

While *T. pinivora* has so far been largely unstudied, much more is known about one of its relatives, the winter pine processionary moth, *T. pityocampa*. *Thaumetopoea pityocampa* has a much more widespread distribution than *T. pinivora* and is common in southern European countries such as Spain, France, and Italy. *Thaumetopoea pityocampa* frequently reaches outbreak levels and its range has been expanding for several decades, probably due to climate change (Battisti *et al.*, 2005). The life cycle of *T. pityocampa* is different from that of *T. pinivora*. While *T. pinivora* has a two-year life cycle, *T. pityocampa* completes its cycle in one year. Both species are gregarious throughout the larval stage, but *T. pityocampa* constructs silk nests where the larvae stay when resting. These nests provide protection against predators, and the structure also aids in the thermoregulation of the colonies (Battisti *et al.* 2005). Like *T. pinivora*, *T. pityocampa* feeds on *Pinus* spp. needles. In the mountainous areas of Spain where both species occur within the same geographic region, *T. pinivora* occurs at higher altitudes than *T. pityocampa*. Another significant characteristic of *T. pityocampa* is that it is winter-feeding. The larvae hatch in early autumn and have usually reached the third instar when winter begins. The substantial body of information available regarding *T. pityocampa* is useful when studying the occurrence and behaviour of *T. pinivora* because it can be used to analyze the similarities and differences between the two species and to understand why one species often reaches outbreak densities while the other does so only rarely, and why one has a continuous distribution pattern while the other has a scattered global distribution, even though both feed on the same type of host plant.

3 Study Area

The area in Sudret that is populated by *T. pinivora* is relatively limited (approximately 3,000 ha). The larvae are found in widely spaced pine stands on nutrient-poor soil ('alvar'). Due to the nature of the soil, these trees grow slowly and they are not managed for wood production. The larvae prefer trees that are exposed to the sun and are rarely found in dense stands (Fig. 3). The studies for papers I and II were performed within the high-density area at Sudret. In addition to this population, there are a few small, scattered populations further north on Gotland, and two small populations on Öland. The global distribution is very scattered, with populations found in Spain (Montoya and Robredo, 1972), central Germany (Gäbler 1949; Koch, 1953), France (Frerot and Démolin 1993), Denmark, Poland and Russia (Larsson, 2006).



Figure 3. Scenery from Sudret, southern Gotland.

4 Aims of the Thesis

The general aim of this thesis was to add to the understanding of the ecology of *T. pinivora* in order to further our knowledge about the outbreak situation of this species, and of insect outbreaks in general. *Thaumetopoea pinivora* forms colonies during the larval period, occasionally reaches outbreak levels, and causes severe harm to humans and animals due to its release of urticating setae. Therefore, there is a pressing need to better understand its biology in order to limit its harmful effects.

Specifically, I addressed the following questions:

1. How does colony size affect the growth and survival of larvae?
2. How does the predation pressure on larvae vary over the seasons, and is early hatching a way to evade predation?
3. Has the ongoing outbreak of *T. pinivora* larvae on southern Gotland lead to range expansion?
4. What is the global distribution and colonization history of *T. pinivora*?

5 Methods

The studies reported in this thesis combined field experiments and population genetics analyses with the aim of studying both the ecology and the history of *T. pinivora*. For example, I manipulated the sizes of colonies and the hatching dates of the larvae in order to understand the effects of different life history traits. In general, experiments conducted under field conditions are important because the larvae are in their natural environment and the influence of unnatural lab conditions is avoided. However, such studies are also risky since no two field seasons are identical in terms of weather conditions or predator activity. Despite these risks, I chose to perform field experiments because I wanted to study the effects of environmental factors such as naturally occurring predators and solar radiation.

Genetic studies were performed to study migration levels on a local scale within Gotland, and also to determine the historic distribution and colonization history of *T. pinivora*. While migration is sometimes investigated by performing catch-mark-recapture trials, this approach would have been less suitable for the studied species because the adults are relatively short-lived (females live for only a few days after eclosion) and the recapture of marked individuals would have been unlikely. Genetic studies also make it possible to measure the gene flow between populations, which can be used to determine whether or not migrating individuals successfully contribute to the gene pool. Population genetic data are useful for determining the causes of current distribution patterns and elucidating colonization histories, especially in cases such as this where little is known about the studied species' former distribution.

The importance of colony size

In 2007, we compared the growth and survival of *T. pinivora* larvae in colonies of different sizes (paper I). Because gregariousness can be beneficial to the larvae in several ways, the aim of this study was to examine the influence of colony size on larval performance. Newly hatched larvae were arranged in colonies of 10, 100, and 300 larvae each, and these colonies were attached to trees in the field. Because we wanted to know how much of the observed mortality was attributable to predation, ten colonies of each size were placed on trees that were protected from predators and the same number of colonies were placed on trees where predators had access to the larvae (Fig. 4).

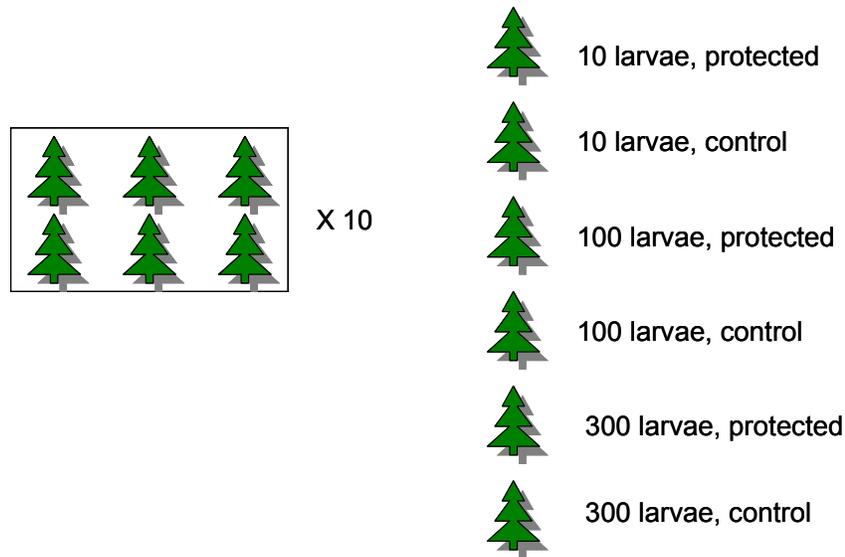


Figure 4. The experimental setup for the experiment performed in 2007.

All colonies were inspected every third day to determine when individuals moulted to the second or third instar, and whether the colony had split into smaller groups. The experiment was terminated at the end of the second instar, at which point the colonies were collected and brought to the laboratory. The larvae were counted and then frozen, dried at 100°C, and weighed.

Because *T. pinivora* larvae are highly social, it is unlikely that individual larvae would leave the colony of their own volition (cf. Aimi *et al.*, 2008). Larvae that had disappeared were therefore assumed to have died during the experiment. In addition, because the experimental trees were small enough to

be easily surveyed (2 meters) and were inspected regularly over a long period, and because the larval colonies were situated at the tips of branches, it was considered unlikely that any colony would go undetected in any given check. We therefore concluded that any missing larvae on the experimental trees had been lost due to mortality rather than dispersal.



Figure 5. The temperature of larval colonies of *Thaumetopoea pinivora* measured by Andrea Battisti.

The larvae hatch at relatively low temperatures. The average temperature during the development of the first instar in 2008 was 8.4°C (15 April to 10 May). The effect of basking behaviour on colony temperature was studied in the late first- and early second-larval instars in a field experiment conducted between the 27th of April and the 9th of May in 2007 (paper I). Using a micrometeorological station, the temperature inside small (fewer than 30 larvae), medium (between 40 and 99 larvae), and large (more than 100 larvae) colonies was measured. The temperature of the colonies was determined using precision-fine wire chromel-constantan, Teflon-insulated thermocouples (model TT-E-36, by Omega Engineering Inc.) (Fig. 5). The small diameter of the thermocouple wire (about 0.13 mm) made it possible to measure the temperature inside the colonies by keeping the thermocouple completely covered by larvae. The probes were checked at regular intervals (2-4 hrs) throughout the experiment.

Larval performance in relation to the phenology of egg hatching

The effect of hatching time on the growth and survival of *T. pinivora* larvae was studied in a field experiment in 2008 (paper II). The objective was to determine the optimal hatching date for *T. pinivora* in relation to predation pressure. Larval colonies were exposed on pine trees on three occasions during the spring. Egg batches were manipulated to hatch at specific times, and the dates for exposure were chosen so that the first set of egg batches hatched on March 11, one month before hatching would occur naturally. The second set of eggs was hatched on April 10, which is around the normal time of hatching; third set was hatched on May 10, one month after the natural hatching date.

Colonies were inspected every second day. The larvae were collected and frozen as soon as at least one larva had moulted to the third instar. The number of remaining larvae was counted and the colonies were dried and weighed. The survival rate of the colonies was calculated by dividing the number of remaining larvae by the initial colony size.

The experiment described above was used to determine whether there is a window of time during which the hatching and development of *T. pinivora* larvae is particularly favourable. A follow-up experiment was conducted to study the temporal effect of predators on first and second instar larvae. In addition, this second experiment, performed in April and May 2009, also provided information on the relative importance of ants and spiders as predators of young *T. pinivora* larvae. The experiment included four treatments. In the Control (C) treatment, nothing was done to the trees and all predators had access to the canopy. In the Ants (A) treatment, the trees were shaken on two consecutive days before the experimental period to remove predators in the canopy but ants and other crawling predators had unhindered access to the tree. The Spiders (S) treatment involved coating the stems with Tanglefoot® glue to prevent predators from climbing them, and adding 3-6 tree-living spiders to the canopy every third day to ensure that each tree contained numerous spiders. The fourth treatment, No Predators (NP), included both shaking the trees and gluing with Tanglefoot.

Local dispersal patterns

One of the key objectives of my doctoral work was to determine whether the outbreak population of *T. pinivora* at Sudret was expanding. We therefore made an inventory and mapped all currently-known inhabited areas on Gotland

and Öland. We then actively searched all seemingly suitable pine stands in the vicinity of the high-density area in Sudret, and more than fifty other suitable habitats on Gotland outside Sudret for signs of larvae. In addition, we also asked foresters to report any sightings of the species, and searched sites where the species had previously been reported, or could be expected to occur (paper III). We found seven sites outside the outbreak area, six of which had not been reported to be colonized prior to the outbreak. In total, larvae were sampled from nine sites within the outbreak area and from all seven sites outside the outbreak area (Fig. 6).

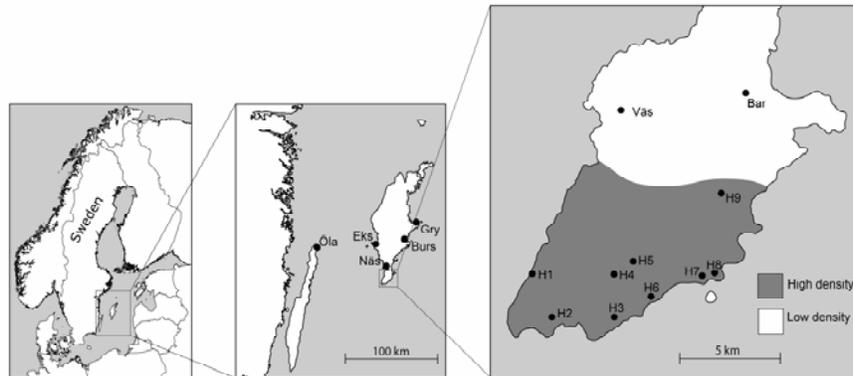


Figure 6. Location of the sampling sites (black dots) of *Thaumetopoea pinivora* on the islands of Öland and Gotland in the Baltic Sea.

In order to determine whether the populations outside the high density area had been recently established by individuals migrating from the outbreak, genetic studies were performed. DNA was extracted from larvae collected at each different site (16 sites in total) and all samples were genotyped at 12 microsatellite loci that had previously been developed for *T. pinivora* (Cassel-Lundhagen *et al.* 2009). All PCR (Polymerase chain reaction) amplifications were performed using a thermocycler (Eppendorf AG, Hamburg, Germany). PCR is a method for multiplying the amount of specific DNA sequences by targeting a specific sequence using so-called primers (starting sequences that are complementary to regions at each side of the target sequence). The two strands of the DNA double helix are separated through heating to form two single stranded DNA fragments. An enzyme thereafter builds two new double stranded fragments of the two single strands. This is repeated until a desired concentration of DNA has been achieved. Microsatellites are short, repetitive sequences of a few base pairs (usually 2-4) found within nuclear DNA. They

are highly variable due to their high rate of mutation. Population and dispersal studies typically focus on the lengths of the target sequences because mutations usually result in the addition or reduction of a repeat. The information from such genetic markers can be used to compare populations within the same species to determine their relative ages and the level of dispersal between inhabited sites. The lengths are viewed as peaks on a chromatogram. We used the PeakScanner software package (Applied Biosystems, Stockholm, Sweden) and manual editing to determine the allele lengths. Any locus and sample that did not produce clear peaks were reanalyzed at least once, as were all individuals that had unique alleles, to make sure that all allele lengths were correctly identified. The dataset was then analysed in terms of the amount of variation within and between populations. Unique alleles (i.e. allele lengths that were observed in only one population) were recorded, as was the level of homozygosity (i.e. number of loci in which both alleles had the same length) in all individuals and averaged over all individuals within and across all populations. We also searched for signs of genetic structuring between the populations by studying the similarities/dissimilarities of all studied individuals to determine their relationship to each other. This is, for example, done by analysing the frequency of each allele in all populations. The frequency of specific alleles changes gradually over time due to genetic drift, and if dispersal between two populations are low then they will diverge. Current migration patterns were also studied by searching for first generation migrants.

Phylogeography

The global distribution of *T. pinivora* is highly fragmented. If we could determine the history behind this pattern, including the colonization pathways from the glacial refugia, this could help in determining how the species will spread in the future (paper IV). We therefore mapped the global incidence of *T. pinivora* by examining reports of its presence in the literature. Each report was checked against the following criteria: 1) there had to be no chance of confusion with other *Thaumetopoea* species associated with *Pinus* spp., and 2) it had to originate from an area where the host plant is present. In addition, records that were later dismissed by the original authors or by others were also rejected. In addition to the survey, we collected larval samples from a representative number of the currently known *T. pinivora* populations across its entire range (Fig. 7).

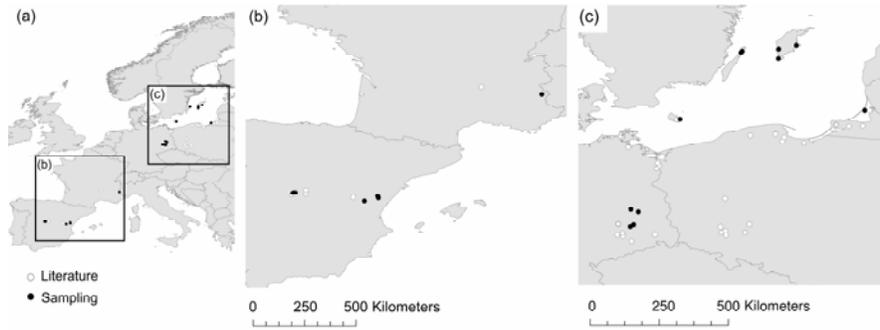


Figure 7. Locations of the sites where the northern pine processionary moth (*Thaumetopoea pinivora*) has been observed (all circles), and sites included in study IV (black circles).

In order to determine the distribution history and historical dispersal pattern of *T. pinivora*, we analysed the genetic variation in two types of genetic markers: microsatellites (see description above) and a 633 bp long region of the mitochondrial genome that lies within the gene encoding cytochrome oxidase I (COI). We chose the mitochondria (mt) and this sequence because the mtDNA molecule is maternally inherited and lacks recombination, and because its mutation rate is much lower than that of microsatellites. Sequences of this type are useful to trace colonisation patterns for populations that have been separated for a long time. The fragment was amplified using PCR and detected on a 1 % agarose gel stained with ethidium bromide to verify that the PCR reaction had generated a detectable amount of DNA. The PCR product was then cleaned from the remaining traces of primers and unincorporated nucleotides and sequenced. All sequences were compared to identify differences caused by mutations. The dataset was analysed in terms of the amount of variation in the mitochondrial DNA and the microsatellites within and between populations. Mutations in the mitochondrial DNA and unique alleles in the microsatellites were recorded for all populations. We also searched for signs of structuring among the populations by examining the similarities/dissimilarities of all studied individuals to determine their relationship to one-other.

6 Results and Discussion

The importance of colony size

The experiment described in paper I indicated that there is a positive relationship between colony size and the growth and survival of *T. pinivora* larvae. Since we wanted to determine whether larger colonies are better protected from predators, we compared colonies on unprotected trees to others on trees whose stems had been coated with glue to deny predators access. Protection had a positive effect on survival for all tested colony sizes, but the effect was greatest for the smaller colonies (Fig. 8). Spiders (Araneae) and ants (Formicidae) are both common predators on young *T. pinivora* larvae. Because gluing trees does not prevent ballooning spiders from entering the canopy, most of the observed difference in mortality between protected and unprotected trees was attributed to a difference in the level of ant predation.

Colony size also had a positive effect on the temperature within the colonies (Fig. 9b). Young larvae spend the days basking in the sun and the temperature of the colonies can be as much as ten degrees higher than the air temperature (Fig. 9a). The colony temperature decreased rapidly, however, when the sun was blocked by clouds. Because the temperature of the larvae affects the rate at which they can digest food, the ability to thermoregulate is very important in maintaining growth during cool periods. The higher thermal gain of the larger colonies was probably due to their higher ratio of mass to surface area, i.e., they had a lower surface area to volume ratio than smaller colonies and thus lost heat less rapidly (Schmidt-Nielson, 1984). Several studies on the effects of thermal gain in tent-living larvae have been reported (Joos *et al.*, 1988; Ruf and Fiedler, 2000, 2005; Frid and Myers, 2002; Battisti *et al.*, 2005) but few

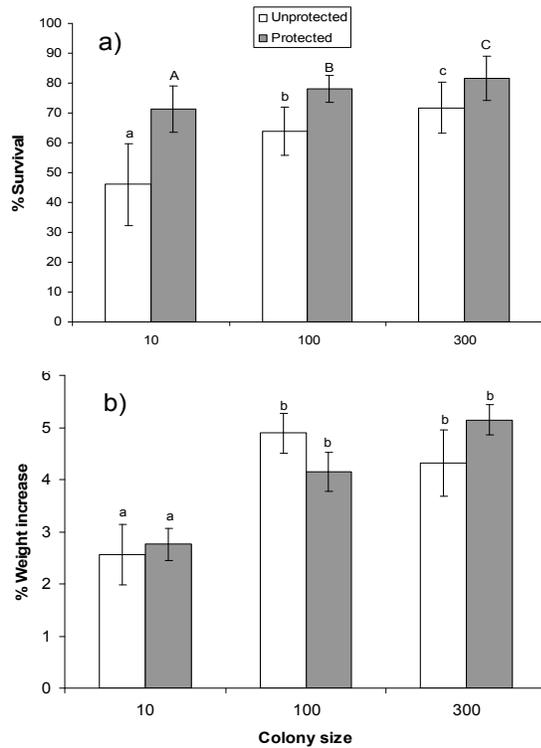


Figure 8. a) The percentage surviving *Thaumetopoea pinivora* individuals per colony at the end of the experiment. b) Growth rate of young *T. pinivora* larvae shown as % weight increase for protected and unprotected late second instar larvae belonging to different colony sizes. Error bars indicate standard errors. Different letters indicate differences between colony sizes; small and capital letters indicate differences between treatments.

have examined free-living species (but cf. Sullivan and Wellington, 1953). Our study was the first to show that large colonies of young, non tent-living larvae achieve greater temperature gains than smaller colonies and that this influences their rate of growth.

These results suggest that the number of larvae in the colonies of gregarious insects determine the extent to which they benefit from their gregariousness. This has implications for population dynamics because the potential colony size is determined not only by the number of eggs a female can lay in a batch, but also by subsequent events such as the growth and survival of the larvae. The population density itself also affects colony sizes, since small groups of larvae can merge together to form a larger colony. As such, there may be a positive feedback from high population densities that can lead to a population outbreak.

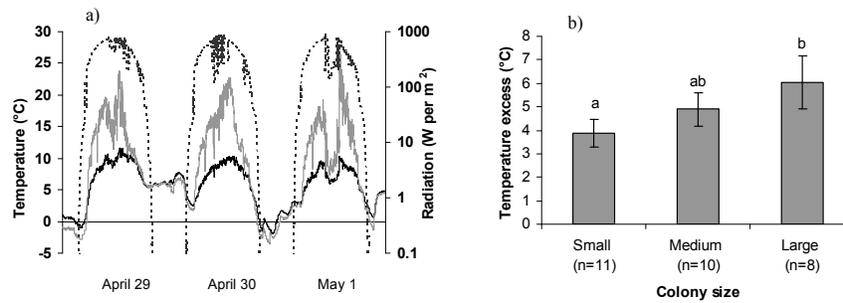


Figure 9. a) Example of the temperature of the ambient air (black line) and the inside of a medium-size ($n = 92$ larvae) colony of first-instar larvae of *Thaumetopoea pinivora* (grey line) and solar radiation (dashed line) measured at the experimental site. b) Temperature excess of different-sized colonies tested between April 28 and May 9, 2007, measured when the insolation was higher than 100 W/m^2 .

Larval performance in relation to the phenology of egg hatching

Thaumetopoea pinivora appears to be well adapted to develop at relatively low temperatures. The larvae are able to thermoregulate and can tolerate starvation for several days if the temperature drops below suitable feeding levels. In general, insect eggs hatch after exposure to a given temperature sum and after experiencing a certain number of hours above the given temperature; the eggs of *T. pinivora* accumulate temperature hours even during cold periods, with a limit temperature of 3-5 degrees C (unpublished data). This means that during unusually warm winters, eggs can hatch in the middle of the winter; this actually happened in the winter of 2007-2008. Thus, this type of hatching behaviour is risky, although it ensures an early hatching date. We therefore expected to find that the larvae benefited from hatching early in the spring. When comparing individuals that hatched earlier or later than normal to those that hatched with normal timing, we found that those that hatched later than normal had a lower survival rate (Fig. 10). This occurred despite the fact that the larvae that hatched at normal dates developed more slowly and were therefore exposed to predators for a longer period of time. In the follow-up experiment where different predators were excluded, we found that ants fed on the larvae that hatched in May but were much less active in the trees in April. Since ants are able to wipe out entire colonies once they have found them, early hatching appears to be very beneficial for larval survival.

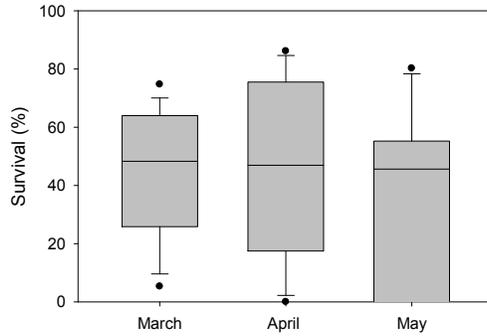


Figure 10. The percentage of surviving individuals per colony at the beginning of the third instar. Larvae that hatched in May had a significantly lower survival rate than those that hatched in March or April. Box-plots show median values, quartiles and interquartile ranges of the data.

Thaumetopoea pinivora larvae feed on year-old pine needles; a food source that is relatively stable in quality and present all year around. This means that larvae do not have to synchronize their hatching with budburst as do many other leaf-feeding insects. *Thaumetopoea pinivora* larvae also have several behavioural adaptations (e.g. thermoregulation) that enable them to survive and grow at low temperatures. When the larvae grow bigger, they become more difficult for the ants to handle, and it appears that the larvae have evolved an ability to exploit the enemy-free time before the ants start hunting in the trees. By hatching at an early date, they have an opportunity to grow significantly before the ants begin climbing the trees, which protects them from predation.

Local dispersal patterns

The high density of *T. pinivora* on Gotland was expected to cause density-dependent dispersal and we also found several colonies of *T. pinivora* outside the outbreak area. However, three aspects of our results suggest that none of these populations were recently established. First, there was significant genetic structuring in the populations located further away from the high density population (Fig. 11). Second, the distant populations exhibited similar levels of genetic variation to the high-density ones, and unique alleles were found in the isolated sites. Finally there were no signs of founder events or genetic bottlenecks, indicating that these populations were not recently established. This is surprising, because we expected the outbreak to spread as a consequence of density-dependent dispersal. Instead, the data suggest that the outbreak occurred due to changes in the local environment that made the environment within the outbreak area preferable to surrounding areas, even though the population density was high (Berryman 1987). An alternative

explanation is that because the pre-outbreak population had been small and local for a long time, there may have been selective pressure against tendencies to migrate (Bonte *et al.*, 2011).

Females of *T. pinivora* are not very good dispersers because they are heavy and short-lived (A. Battisti, pers. obs.). However, males are strong fliers and are often caught in light traps far away from their hatching site (Palmqvist, 1984; Franzén, 2004). Therefore, it was expected that migrating males should prevent significant genetic differentiation of the isolated populations. This was not found. We hypothesise that immigrating males may have difficulties finding a mate because females are mated very soon after emerging from their cocoons, when resident males are already present and therefore outcompete immigrants.

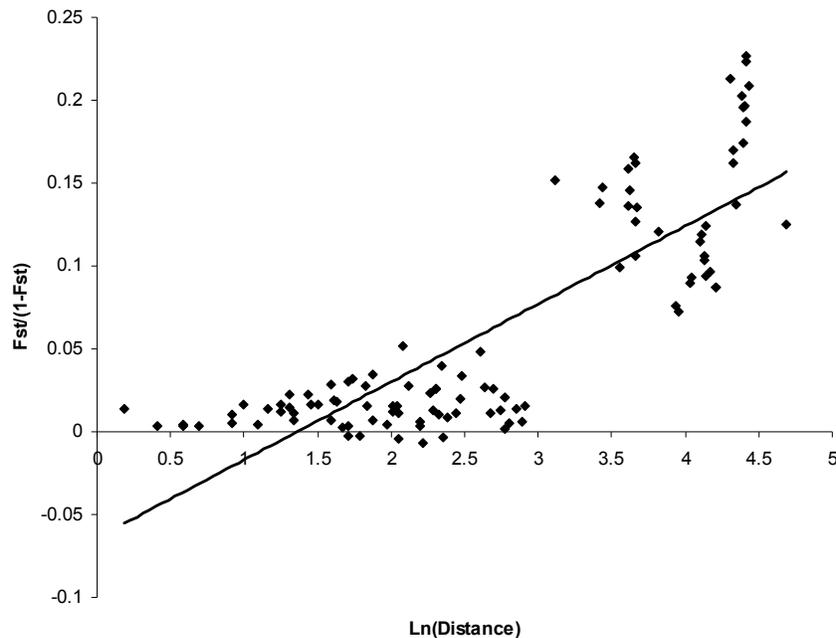


Figure 11. A plot of pairwise F_{ST} (Weir and Cockerham 1984) values against log geographic distance revealed significant genetic isolation by geographic distance.

Phylogeography

The inventory of the global occurrence of *T. pinivora* revealed that its distribution is very fragmented (Fig. 7). A fragmented distribution can indicate

that the observed populations are remnants of a more widespread distribution (Habel and Assmann 2010). Alternatively, they can occur when the species has a narrow habitat requirement paired with a high aptitude for dispersal, enabling it to track rare suitable habitat patches (Schroeder *et al.*, 2007). *Thaumetopoea pinivora* was found to exhibit very little mitochondrial diversity across its whole range. Only nine sites within the analysed region of the mitochondrial COI gene were polymorphic and 90% (116 out of 129) of the analysed individuals shared the same haplotype. In total, eight unique haplotypes were found; three in the northern region and four in Spain. This indicates that the populations have not been present in their current locations long enough for a significant number of mutations to emerge. It also indicates that the species does not exist as a single continuous population, as such a population should have accumulated genetic diversity over time (Bromilow and Sperling, 2010). The number of mutations depends on both the length of time that a population has existed and the effective population size (N_e). Thus, all of the analysed populations appear to have a recent history.

The diversity of microsatellite alleles was highest in the Spanish samples, intermediate in the German samples, and lowest in the northern populations; however, the differences between the populations were not great (Fig. 12). This indicates a gradual colonization from south to north, and that most of the variation has been retained at the colonisation front (Ibrahim *et al.*, 1996). The absence of unique alleles in the northern samples also supports our conclusions that the colonization was recent (Slatkin, 1985). The study performed on the outbreak on Gotland showed that the dispersal ability of this species is limited (paper III). Therefore, the global pattern is very surprising as we would expect the colonization of widely spaced populations to be a much slower event. Although we have not been able to determine the exact cause of the distribution pattern, a possible explanation could be recent habitat loss. Studies conducted in Sweden (Aimi *et al.*, 2008; Larsson *et al.*, 2008), as well as our observations at the sampled sites across Europe, give the impression that *T. pinivora* has rather narrow habitat requirements. The species is only found in stands with slow-growing trees on poor soils; we know of no *T. pinivora* populations in pine stands on rich soils managed for timber production. It is possible that pine stands of this type were more common in the past when the species expanded from the refugia, but have since disappeared from many regions due to intensified forestry and agriculture.

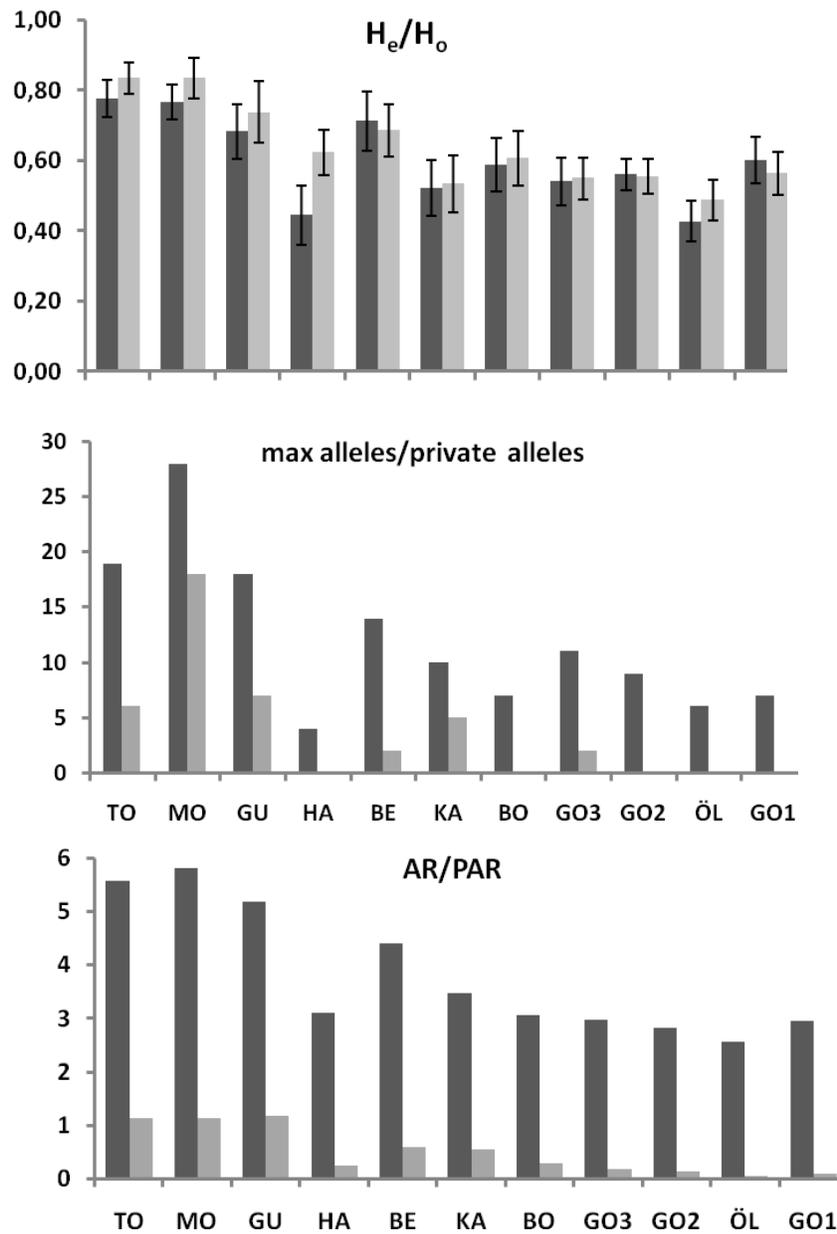


Figure 12. Diversity estimates for nine microsatellite markers in *Thaumetopoea pinivora* populations at 11 locations across its whole range. a) Expected (H_e) and observed (H_o) heterozygosity with bars indicating standard errors; b) maximum numbers of alleles and number of private alleles; c) allelic richness (AR) and private allelic richness (PAR).

7 Conclusions and Reflections

Somehow, now that I have reached the end of my doctoral work, I seem to have come up with more questions than answers. It remains unclear why a population of *T. pinivora* should have reached such a high density on Gotland. The species has certain characteristics that are common among outbreaking insects; it is gregarious and it feeds on a common host plant (Hunter, 1991). Still, I can only speculate on the identity of the limiting factors that were overcome to yield this increase in density. Since insect species with social larvae are over-represented among outbreak species, information on the benefits of gregariousness may help us understand why the densities of these species often fluctuate strongly. In this project, I have shown that it is not enough to simply be part of a colony, but that the size of the colony determines the magnitude of any expected benefits. As the potential colony size depends on the density of the population, the carrying capacity of a population may be increased when the density temporarily increases (Allee effect). When many colonies are close together, small colonies can find other colonies to merge with, and are thus able to minimize the penalty of being small.

One hypothesis that could explain the recent outbreak of *T. pinivora* that has not yet been examined is whether or not having two discrete year classes allows *T. pinivora* to evade enemies with a shorter life cycle. There is a specialist tachinid fly (*Blondelia pinivora*) that parasitizes larvae of *T. pinivora* occurring at Sudret (Aimi *et al.*, 2008). As the density of larvae is much lower in odd years than in even years, the parasitoid will have plenty of hosts in even years. In the next year, when the parasitoid hatches, the number of larvae is much lower and the parasitoid population could potentially crash. This hypothesis could be tested by collecting pupae from both odd- and even-year classes and hatching them to determine the level of parasitism. Unfortunately, this is easier said than done. Pupae from even-year larvae are easy to find, but in the odd years they are scarce and can only be located if the

place where they submerged has been marked. While I have attempted to perform this type of study, I have yet to succeed in finding pupae from odd-year larvae.

Thaumetopoea pinivora has several adaptations that at first seem rather odd. The hatching of the eggs is unpredictable because they start to accumulate temperature-hours before mid winter. This seems to be an adaptation to ensure early hatching. But why should it be important to hatch early when the food source is readily available all year round? I have found that although this behaviour yields a very long larval period and slow growth during the first instars, it actually increases the likelihood that the larvae will survive. Many generalist predators, such as ants, do not forage in the tree canopy until later in the spring, and thus, the *T. pinivora* larvae are able to enjoy a relatively enemy-free time until the temperature increases enough for other species to become active. By then, the larvae have grown to the point that they can more effectively defend themselves. Although young, deciduous foliage is considered a higher quality food source, there are several species that feed on year-old evergreen foliage. It would be very interesting to find out if any of these other species also exploit this enemy-free time.

The distribution pattern of *T. pinivora* is puzzling. While it is, as far as we know, a poor disperser, it also has a very scattered global distribution. Furthermore, there is an ongoing outbreak on Gotland but this has not yet resulted in any range expansion, or documented new colonisations. We do know that its colonisation history in northern Europe is relatively recent. It also seems clear that concerns regarding the possibility of a major outbreak in Sweden, with a rapid expansion from the outbreak at Sudret, can be laid to rest. It is not very common to study the population structure of outbreaks and fragmented habitat patches in the same species. Most studies on fragmented habitats are performed on endangered species with a focus on conservation. In this case, we have found that a local outbreak pattern can arise when small, isolated populations fluctuate in density. In this case, something is preventing the outbreak population from expanding to new areas; *T. pinivora* females are poor fliers, and it may be that this is what is keeping the species' expansion in check. A lack of suitable habitats is a second possible explanation. The species' global distribution pattern seems to be inconsistent with the evidence that it has undergone a recent and rapid expansion. It is difficult to determine how the species has moved so fast, but we interpret our data to support the hypothesis that the present distribution is the result of a recent stepping-stone like colonisation from a single origin after the last glaciation, followed by a devastation of suitable habitats in most of central Europe. The habitat

requirements of *T. pinivora* appear to be relatively narrow, and populations have not been found in wood production forests. Although it is not possible to reconstruct the availability of suitable habitat patches in the past, it is possible that the recent expansion of agricultural- and forest production areas has resulted in a decline in the abundance of the sparse, slow-growing pine stands that *T. pinivora* prefer.

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Populationsekologi vid yttersta gränsen

Utbrott av skadeinsekter kan orsaka omfattande skador på jordbruksgrödor och för skogsproduktionen. Vissa skadedjur kan också orsaka allvarliga hälsorisker för människor och djur. På Gotland lever nattfjärilen tallprocessionsspinnare, *Thaumetopoea pinivora*, vars larver utvecklar giftiga mikroskopiska hår (setae) som kan orsaka allvarliga allergiska besvär hos människor och djur. En population har funnits på södra Gotland (Sudret) under lång tid, men under senare år har antalet larver ökat explosionsartat. När ett sådant utbrott redan har påbörjats kan det vara svårt att studera de exakta orsakerna bakom utbrottet. Jag har studerat egenskaper i larvstadiet som påverkar arters benägenhet att få utbrott. Många utbrotsarter är kolonilevande under larvtiden, så även tallprocessionsspinnaren. Det kan finnas flera fördelar med att leva i kolonier. Flera larver i en klunga kan bättre försvara sig från rovdjur (rovinsekter), de kan höja sin temperatur genom att sola sig i grupp och de kan hjälpas åt att komma åt svårtillgänglig föda. Studier på tallprocessionsspinnarlarver visade att koloniernas storlek är viktig eftersom antalet individer i en koloni avgör de fördelar larverna kan få från både skydd mot rovdjur och termoregulering. Eftersom små larvkolonier kan slås ihop till större, kan en hög populationstäthet med många kolonier per träd vara gynnsamm för artens överlevnad.

Tallprocessionsspinnarens larver kläcks tidigt på våren. Detta ger dem möjlighet att undkomma rovdjur som inte blir aktiva förrän senare på säsongen. Myror, till exempel, blir inte aktiva i träden förrän i maj, en månad efter att larverna har kläckts. Larverna har då haft tid på sig att växa, och eftersom stora larver är bättre skyddade från myror än små, är den tidiga kläckningen gynnsamm för larvöverlevnaden, även om den innebär att larverna växer mycket långsamt under den svala våren.

TallproceSSIONsspinnarens kända globala förekomst består av ett antal splittrade populationer från Frankrike och Spanien i söder, till Kaliningrad i öster och Gotland i norr. Genetiska studier visar att artens kolonisationshistoria är relativt sentida, vilket är förvånande med tanke på dess begränsade spridningsförmåga. Resultaten visar också att arten aldrig har haft en sammanhängande utbredning över hela Europa, men det är möjligt att fler, mindre områden med en lämplig livsmiljö har funnits tidigare. Om det då var kortare avstånd mellan lämpliga områden, kan detta ha underlättat koloniseringen av norra Europa.

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