

Rapid northwards expansion of a forest insect pest attributed to spring phenology matching with sub-Arctic birch

JANE U. JEPSEN*†, LAURI KAPARI†, SNORRE B. HAGEN†‡, TINO SCHOTT†, OLE PETTER L. VINDSTAD†, ARNE C. NILSSEN§ and ROLF A. IMS†

*Norwegian Institute for Nature Research, Fram Centre, N-9296 Tromsø, Norway, †Department of Arctic and Marine Biology, University of Tromsø, N-9037 Tromsø, Norway, ‡Bioforsk Soil and Environment, Svanhovd, N-9925 Svanvik, Norway, §Tromsø University Museum, N-9037 Tromsø, Norway

Abstract

Species range displacements owing to shifts in temporal associations between trophic levels are expected consequences of climate warming. Climate-induced range expansions have been shown for two irruptive forest defoliators, the geometrids *Operophtera brumata* and *Epirrita autumnata*, causing more extensive forest damage in sub-Arctic Fennoscandia. Here, we document a rapid northwards expansion of a novel irruptive geometrid, *Agriopis aurantiaria*, into the same region, with the aim of providing insights into mechanisms underlying the recent geometrid range expansions and subsequent forest damage. Based on regional scale data on occurrences and a quantitative monitoring of population densities along the invasion front, we show that, since the first records of larval specimens in the region in 1997–1998, the species has spread northwards to approximately 70°N, and caused severe defoliation locally during 2004–2006. Through targeted studies of larval phenology of *A. aurantiaria* and *O. brumata*, as well as spring phenology of birch, along meso-scale climatic gradients, we show that *A. aurantiaria* displays a similar dynamics and development as *O. brumata*, albeit with a consistent phenological lag of 0.75–1 instar. Experiments of the temperature requirements for egg hatching and for budburst in birch showed that this phenological lag is caused by delayed egg hatching in *A. aurantiaria* relative to *O. brumata*. *A. aurantiaria* had a higher development threshold ($LDT_{A.a.} = 4.71\text{ °C}$, $LDT_{O.b.} = 1.41\text{ °C}$), and hatched later and in less synchrony with budburst than *O. brumata* at the lower end of the studied temperature range. We can conclude that recent warmer springs have provided phenological match between *A. aurantiaria* and sub-Arctic birch which may intensify the cumulative impact of geometrid outbreaks on this forest ecosystem. Higher spring temperatures will increase spring phenological synchrony between *A. aurantiaria* and its host, which suggests that a further expansion of the outbreak range of *A. aurantiaria* can be expected.

Keywords: *Agriopis aurantiaria*, *Epirrita autumnata*, geometrid moth, global warming, invasion, *Operophtera brumata*, phenology mismatch, range expansion

Received 15 September 2010; revised version received 5 November 2010 and accepted 6 November 2010

Introduction

Forest insect pests are both important indicators of climate change (Logan *et al.*, 2003) and forceful inducers of climate-related ecosystem state shifts. Their geographical distribution is largely defined by temperature, and they are responsive to even small changes in their thermal environment. Over the next century, mean annual land temperatures are projected to rise by 3–5 °C across the sub-Arctic and Arctic region (north of 60°N, ACIA, 2004) and with a milder climate, insect pest outbreaks are expected to increase in both fre-

quency and intensity (Volney & Fleming, 2000; Dale *et al.*, 2001). A more benign thermal environment will promote the polewards expansion of native forest pests, as well as facilitate the establishment of nonnative pest species (Ayres & Lombardero, 2000; Harrington *et al.*, 2001; Logan *et al.*, 2003; ACIA, 2004). Over the last century, climatic isotherms over Europe have been displaced by an average of 120 km northwards (Beniston & Tol, 1998), resulting in northwards range shifts in a number of insect taxonomic groups (Parmesan & Yohe, 2003; Hickling *et al.*, 2006). The most compelling evidence that climate-mediated range shifts are occurring, come from nonpest species, such as butterflies and dragonflies (Parmesan *et al.*, 1999; Hickling *et al.*, 2005; Wilson *et al.*, 2005; Pöyry *et al.*, 2009). However, a latitudinal and altitudinal expansion has been documented

Correspondence: Jane U. Jepsen, Norwegian Institute for Nature Research, Farm Centre, N-9296 Tromsø, Norway, e-mail: jane.jepsen@nina.no

in several important forest pest species in the northern hemisphere, for instance *Dendroctonus ponderosae* (mountain pine beetle), in western Canada (Carroll *et al.*, 2006; Robertson *et al.*, 2009) and *Thaumetopoea pityocampa* (pine processionary moth) in central Europe (Battisti *et al.*, 2005, 2006). In the mountain birch forest zone in Fennoscandia, the two native species of geometrid moth, *Operophtera brumata* (winter moth) and *Epirrita autumnata* (autumnal moth) have increased their outbreak ranges into more northern, alpine and continental areas, causing region wide devastation of the birch forest during the last decade (Hagen *et al.*, 2007; Jepsen *et al.*, 2008; Post *et al.*, 2009).

The mechanisms behind the range displacements of forest pest insects in the face of climate warming are often more elusive than their effects. At the northern distributional border, an increase in temperature can be expected to increase the climatically suitable geographical range. This in itself may permit a range expansion given that suitable hosts are available. The spread of *D. ponderosae* in western Canada, for example, has been shown to mirror the shifts in climatically suitable habitats over the last three decades (Carroll *et al.*, 2006). A more favorable thermal environment will directly affect physiological processes related to growth and development, reproduction and movement, which may lead to increased survival and dispersal capability (see Bale *et al.*, 2002 for a review). The success of many forest pest insects depends on maintaining close phenological synchrony between the feeding stage (typically larvae) and the host plants (Harrington *et al.*, 2001; Walther *et al.*, 2002). Rapid climate warming may disrupt or establish temporal associations between trophic levels, if insect and host plant development responds differently to temperature change (Stenseth & Mysterud, 2002; van Asch & Visser, 2007). This is of particular relevance for spring feeding species such as *O. brumata*, which is becoming established as a prime example of the consequences of climate warming for the phenology and trophic interactions of a spring feeding pest insect. Studies from temperate European populations show that an increase in temperature tends to cause an increased temporal disassociation between egg hatch and budburst in the local host tree (mainly oak), as egg hatch advances more rapidly than budburst (Buse *et al.*, 1999; Visser & Holleman, 2001; Both *et al.*, 2009). However, at the northern and alpine distributional border of a species, the effect of elevated temperatures could be the reverse, namely an increased match between egg hatching and budburst permitting altitudinal and latitudinal range expansions. The effects of phenological shifts on animal–plant interactions has just been reviewed in Miller-Rushing *et al.* (2010).

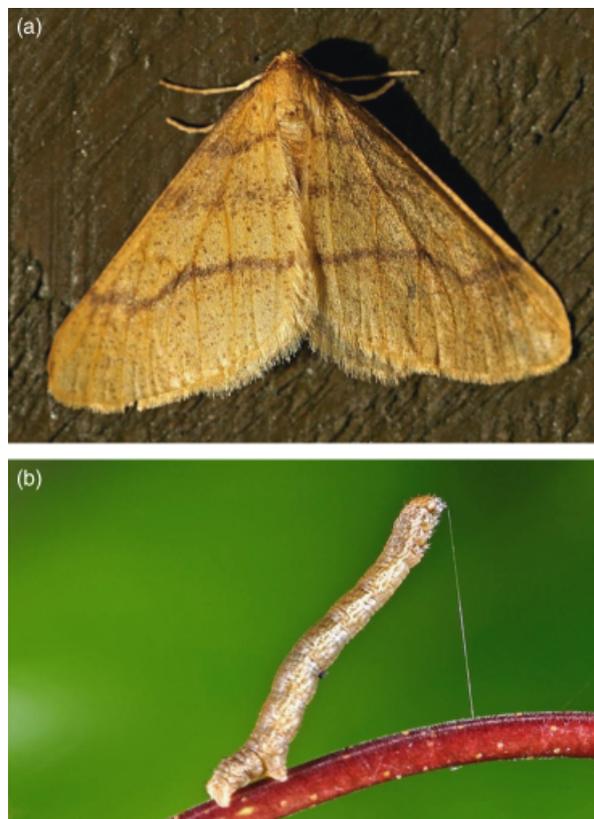


Fig. 1 Adult male (a) and larvae (b) of *Agriopsis aurantiaria*. Photo: Arne C. Nilssen.

Northern Fennoscandia represents the northern distributional limit in Europe for *O. brumata* as well as its close relative, *E. autumnata*. While *E. autumnata* is a 'true' native species, *O. brumata* spread northwards quite recently [first recording around Tromsø at 69°40'N in 1892; Schneider (1914) cited in Tenow (1972)]. Here we report that a third spring feeding geometrid, *Agriopsis aurantiaria* (scarce umber moth, Fig. 1), has established itself in the same region simultaneously with the latest extended outbreak of the two native geometrids. The recent extensive forest devastation caused by the rapid expansion in the outbreak ranges of *O. brumata* and *E. autumnata* in the region (Jepsen *et al.*, 2009a) raises concern as to which role *A. aurantiaria* will fill in the geometrid–mountain birch forest system. The mechanism underlying the range expansion of either of the species is unclear. While the thermal ecology of *A. aurantiaria* is entirely unknown, a difference in frost tolerance (Niemela, 1979; Tenow & Nilssen, 1990) of the overwintering eggs of *O. brumata* and *E. autumnata* has been proposed as an explanation for the historical difference in geographical distribution of the two native species (Bylund, 1999; Neuvonen *et al.*, 1999). We have previously speculated that milder springs, possibly in combination with a lack of extreme

winter cold, has relaxed the thermal constraints in particular on *O. brumata* and, in part at least, permitted the rapid range expansion (Jepsen *et al.*, 2008). Increased winter survival of eggs is however not able to account for latitudinal and altitudinal expansions also occurring in regions (especially coastal areas) that never experience sublethal winter temperatures (Hagen *et al.*, 2007). Recent analysis of the spatio-temporal dynamics of outbreaks in the region (Jepsen *et al.*, 2009b) suggests that the spring phenology of the primary host tree, mountain birch [*Betula pubescens* subsp. *czerepanovii* (Orlova)] plays a decisive role in the regional synchronization of moth outbreaks. Fennoscandia has experienced a warming trend and an advancement of spring particularly during the last decade (Pudas *et al.*, 2008; Karlsen *et al.*, 2009; Callaghan *et al.*, 2010) in line with the general trend across Eurasia (Myneni *et al.*, 1997; Ahas *et al.*, 2002; Menzel *et al.*, 2006; Delbart *et al.*, 2008).

In the present study, we document the recent rapid northward expansion of *A. aurantiaria* leading to outbreak densities and local defoliation of birch forest in Northern Norway. To our fortune, the geographical extent of our monitoring area of native forest geometrids included the invasion front of *A. aurantiaria* such that we can provide a quantitative description of the invasion. In order to investigate whether advancement of spring could be an underlying cause permitting the observed spread into novel habitat, we examined spring

phenology of *A. aurantiaria* larvae in a natural climatic gradient during the invasion, with the native *O. brumata*, as a point of reference. We present complimentary data on the spring phenology of the primary host, mountain birch. Further, we experimentally determine the relative temperature requirements for (i) egg hatching in *A. aurantiaria*, *O. brumata* and *E. autumnata* and (ii) budburst of mountain birch, in temperature-controlled chambers in order to investigate (i) whether differences in spring phenology observed between the species under field conditions can be attributed to differences in temperature-dependent egg hatching and (ii) the degree of temporal synchrony in host tree budburst and egg hatch in *A. aurantiaria* relative to *O. brumata*.

Materials and methods

Study system

Northern Norway is divided by the Scandinavian mountain chain into a humid oceanic part along the western coast and a dryer, more continental part to the north and east. The entire region has experienced a significant increase in mean annual temperatures and a decrease in the frequency of extreme winter cold particularly in continental areas [Fig. 2, see also Figs 1 and 2 in Jepsen *et al.* (2008)]. The natural forest is

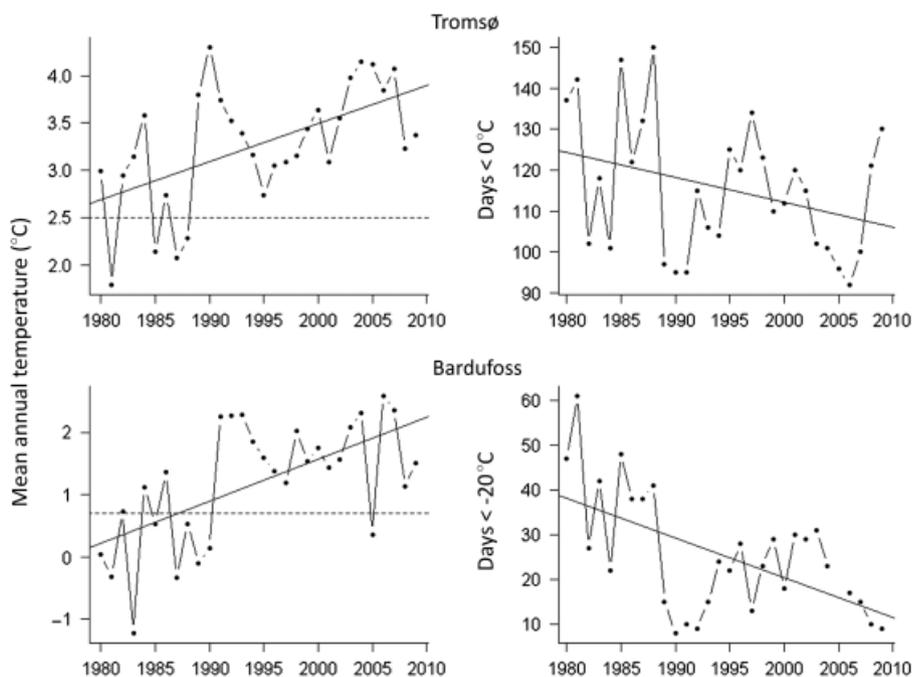


Fig. 2 Mean annual temperatures and the frequency of winter cold, expressed as the number of days below 0°C (Tromsø; 69°40'N, 18°57'E) or -20°C (Bardufoss; 69°05'N, 18°30'E) for the years 1980–2009. Hatched horizontal lines show the 1960–1990 normal mean annual temperature. Full straight lines show fitted linear regressions (mean annual temperature, Tromsø: $R^2 = 0.31$, $P = 0.001$, Bardufoss: $R^2 = 0.38$, $P < 0.001$; frequent winter cold, Tromsø: $R^2 = 0.11$, $P = 0.08$, Bardufoss: $R^2 = 0.33$, $P = 0.001$).

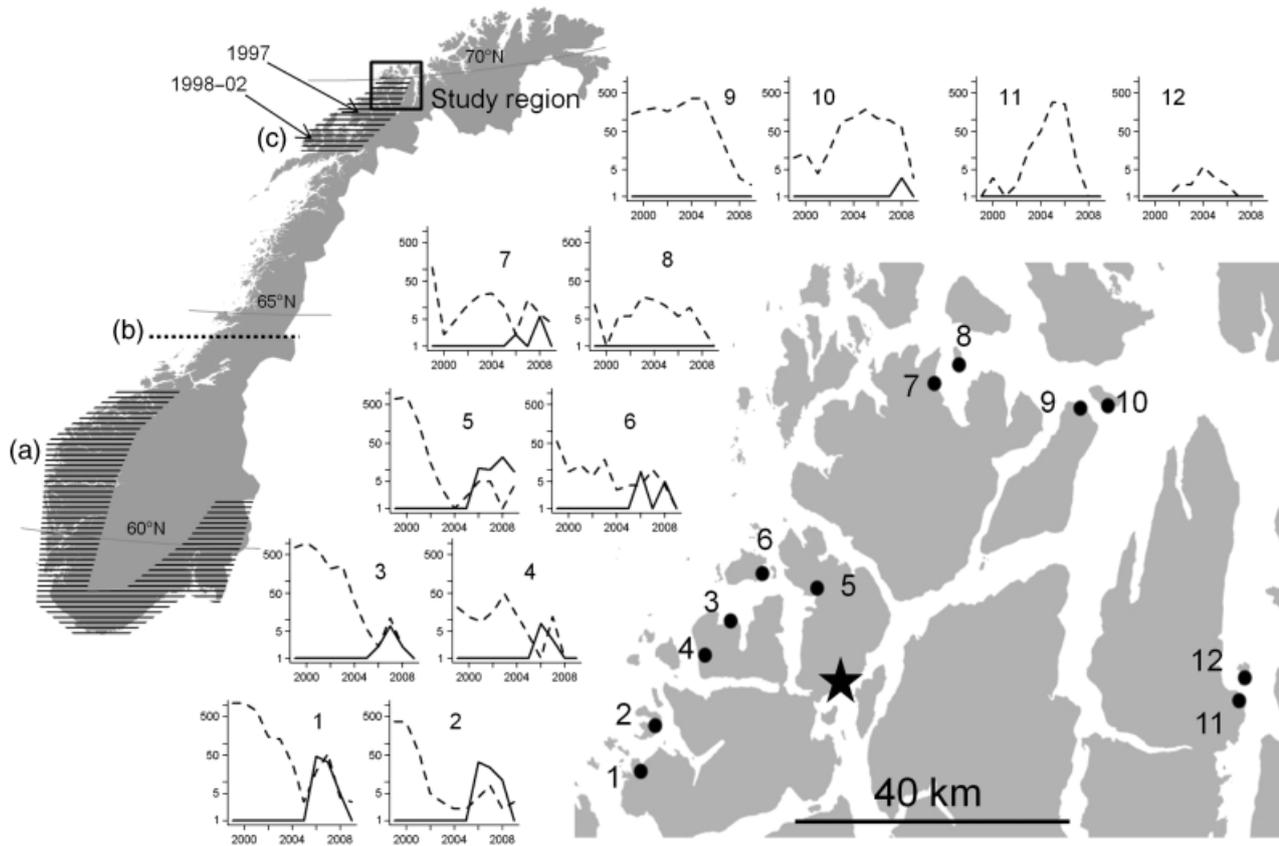


Fig. 3 Left: A map of Norway showing the current known distribution of *Agriopis aurantiaria*. Hatched area A: main distribution before year 2000 in Norway, horizontal line B: approximate Northern limit for establishment in Fennoscandia as a whole before year 2000, and hatched area C: mass outbreak area during 2004–2007. The arrows indicate place and year of founds of single larvae individuals in Northern Norway before the year 2000 (see text for details). Right: map of the study region in the coastal districts of Troms with the 12 sites where geometrid populations have been monitored since 1999. The star denotes the location of the altitudinal gradient for studying phenology of host plant and geometrid larvae during 2006–2009. Middle: population trajectories per site (the number of larvae on 100 branches of mountain birch) for both species (full line: *A. aurantiaria*, hatched line: *Operophtera brumata*) shown on a log scale.

dominated by pubescent and mountain birch, which is the main host tree of all three geometrids in the region.

The two native geometrids, *O. brumata* and *E. autumnata*, have a circumpolar distribution and are the most important pest species in the sub-Arctic birch forest ecosystem in Fennoscandia. In high latitude/altitude birch forest zones they exhibit pronounced decadal population cycles, with local outbreak densities that may result in forest death following multiyear defoliation (Tenow, 1972). *A. aurantiaria* is a Eurasian species and is known to have outbreaks in southern and Eastern Europe. Before the here reported northern invasion, *A. aurantiaria* was known to be established south of approximately 63°30'N in Norway (Area 'A' and line B, Fig. 3), with just a few earlier reports further north. This was also the approximate distributional limit further east in Sweden and Finland. Two reports exist of larvae found further north in the climatically benign region along the Norwegian west coast (Fig. 3): A single larvae was found on the island Senja (approximately 69°15'N) in 1997 (A. Nilssen unpublished results), and larvae were found at two study sites in the

archipelago Vesterålen (approximately 68°30'N) in 1998–2002 (Tenow *et al.*, 2007). The ecology of *A. aurantiaria* is not well known, but it can be expected to resemble *O. brumata* and *E. autumnata* in many aspects. Dispersal in all three species is restricted to the larval stage (ballooning) as females are flightless with stunted wings. All three species overwinter in the egg stage and hatch in spring (late May–early June), in approximate synchrony with bud burst of their host tree and nourish on birch leaves. In *O. brumata* and *E. autumnata* the feeding period lasts for 4–8 weeks, depending on temperature and forage quality, after which they drop to the ground and pupate in the soil (Tenow, 1972; Bylund, 1999). The two species, when occurring in sympatry within their outbreak range, exhibit largely synchronous dynamics with *O. brumata* dominating at termination of the cyclic outbreaks (Tenow *et al.*, 2007; Klemola *et al.*, 2009). During 2002–2008, an outbreak of unprecedented extent and duration has swept through the mountain birch forest belt of northern Fennoscandia, affecting an estimated 10 000 km² or one-third of the forested area (Jepsen *et al.*, 2009a).

Invasion and abundance of A. aurantiaria

Since 1999, we have monitored the dynamics of geometrid populations (larval densities) in 12 study sites (Fig. 3) in the coastal birch forests of Troms county, northern Norway [for methods; see Ims *et al.* (2004)]. Coincidentally, the extent of the monitoring area encompassed the northern limit of the *A. aurantiaria* invasion. *A. aurantiaria* was first recorded with a few specimens at some of the sites in 2004 and 2005. As species identity was not ascertained until later, we are only able to provide approximate numbers per site for the two first years after the invasion commenced. From 2006 and onwards, *A. aurantiaria* was monitored quantitatively in the same manner as for the two native species. Here we present the quantitative monitoring data during the course of the invasion and compare the population trajectories of *A. aurantiaria* with *O. brumata*. During the *A. aurantiaria* invasion, Tromsø University Museum received numerous reports from local people also allowing us to provide a more qualitative account of the extent of the invasion on a larger scale.

Larval and host plant phenology in natural populations

Larval phenology in natural populations of *A. aurantiaria* was investigated using *O. brumata* as a point of reference. The observational substudy took place over three phenologically contrasting years (2006–2008) at a coastal site within the region of our population monitoring (Kvaløya, 69°38'N, 18°57'E). Using altitude as the focal design variable, we selected an area with mountain birch forest from sea level to the forest limit (at approximately 250 m asl), where both *A. aurantiaria* and *O. brumata* occurred at sufficiently high densities to allow sampling of larvae for determination of phenology at all altitudes. Altitudinal transects consisted of 12 sampling stations at 50 and 100 m and 10 sampling stations at 170 and 240 m (44 stations in total). Within altitudes, sampling stations were spaced at 200 m intervals.

Sampling of larvae for investigation of phenological development was conducted at all 44 sampling stations on June 21 in each of the 3 years. In 2008, additional sampling took place on July 1, because larvae size was insufficient for sampling on all but the lowest altitude on June 21. A direct comparison between all years on the same date was thus possible only for the lowest altitude (50 m). Obtaining an additional sample from all altitudes on July 1, 2008 was nevertheless important to provide insight from a phenologically delayed year. Larvae (*A. aurantiaria*: 162–759 larvae yr⁻¹, *O. brumata*: 124–532 larvae yr⁻¹) were collected haphazardly from branches at all sample stations and frozen at –18 °C until measurements were taken. In order to determine larval phenology (i.e., instars), head capsule width was measured under a magnifying lens with a measuring ocular and converted to millimeters. The width of the head capsule of the larvae was compared graphically to an empirical distribution, smoothed using density estimation based on a nonparametric kernel to separate the five instars according to Mjaaseth *et al.* (2005) (see Appendix S1). Parallel to larvae collection (June 21), as a relative index of birch phenology, we measured leaf size of six undamaged leaves from three different trees (i.e., 18 leaves in

total) at all transect stations. The leaf size was measured as the length from the base to the tip of the leaf with a precision of 1 mm. In addition, the abundance of larvae was estimated at all transect stations each year (2006–2009) using the standard methodology described in Ims *et al.* (2004), for the population dynamics monitoring programme.

Geometrid egg hatching and host plant bud burst in climate chambers

Temperature sum requirements for egg hatching. To investigate the temperature sum requirements for egg hatching in *A. aurantiaria* relative to the two native moth species, we carried out a set of incubation experiments in temperature controlled chambers. Geometrid eggs for the experiment were obtained during the year before the experiment by collecting larvae under natural conditions in the monitoring area and rearing them into adults in the laboratory. The adults were mated in plastic boxes and allowed to lay their eggs on plastic mesh aligning the inside of the boxes. The eggs were left undisturbed in the boxes outdoors at ambient temperatures from laying until the experiment was initiated postdiapause the following spring. The temperature experienced by the eggs when kept outdoors was logged continuously at 4 h intervals (Thermochron iButton, <http://www.maxim-ic.com>). Immediately before initiating the experiment, the geometrid eggs were detached from the mesh and counted. Unfertilized (green) eggs were removed.

The experiment was conducted in temperature-controlled rooms under continuous light conditions at the University of Tromsø. The ambient temperature in the incubation rooms was logged continuously (4 h intervals). Owing to a lack of *E. autumnata* eggs during the first year of study, we were forced to divide the experiment into two separate parts. The temperature requirements for hatching in *A. aurantiaria* relative to *O. brumata* were investigated during the first year, whereas the temperature requirements of *O. brumata* relative to *E. autumnata* were investigated during the second year. We used eight different incubation temperatures in 2009 and five in 2010, covering a range of 6–22 °C. The lower half of the range represents realistic spring temperatures in Northern Norway over the last decade (May temperature in Tromsø 2000–2010: average = 6.1 °C, average range = –1.5–16.7 °C, Norwegian Meteorological Institute, <http://www.met.no>).

Unequal availability of eggs led to slight differences in the lab protocol and sample sizes during the first and second year. In 2009, a haphazard sample of eggs, derived from a large number of different females, was used in the experiment. Sample sizes were approximately 90 *A. aurantiaria* eggs and 300 *O. brumata* eggs per temperature. Eggs were kept in small glass vials with 15 and 30 eggs per vial for *A. aurantiaria* and *O. brumata*, respectively. Owing to a limited number of incubation rooms available, we first incubated eggs at four temperatures at the higher end of the temperature range (March 13–April 4), and then at four temperatures at the lower end of the range (April 8–May 31). While the high temperature trials were in process, the eggs to be used for the low temperature trials later were left outdoors, while temperatures were continuously logged (4 h intervals) in order to determine

the precise temperature sum accumulated before the onset of the experiment in the lab. In 2010, a single sample containing an equal mix of eggs from five different females was used for both species at each incubation temperature. Sample sizes were approximately 100 *E. autumnata* eggs and 150 *O. brumata* eggs per temperature. Eggs at all temperatures were incubated simultaneously in the period April 16–May 4, 2010. During all experiments, each egg vial was examined once a day by the same person and the number of hatched larvae was recorded.

Temperature sum requirements for birch bud burst. The temperature sum requirements for budburst in mountain birch were investigated simultaneously to the egg hatching experiment in 2009, using the same incubation rooms [see Karlsson *et al.* (2003) for a similar approach]. On the same day as we initiated the egg hatching experiment (April 8, 2009), four birch branches (50–70 cm in length) were collected from 20 different mature birch trees in a natural forest stand in the vicinity of the egg storage facility. One branch from each tree was placed in a water-filled glass container in each of the four coldest incubation rooms. On each branch, 20 short shoot buds were marked in order to follow their phenological development throughout the experiment. During the experiment, the glass containers were refilled and the branches sprayed with water daily. A thin slice was cut from the base of each branch once a week to optimize water supply to the branches. Every 2 days, the buds were classified to phenological stage, always by the same observer. The phenological bud stages used were as follows: Dormant bud with bud membrane intact (0), breaking bud with bud membrane broken and leaf tip visible (1), opening bud with leaf tips elongated but not yet separated (2), leaf tips separated, but leaf only partly unfolded ('a mouse ear') (3), the whole leaf visible (4). For the sake of the current analysis, the bud stages were regrouped into three bud stages: 'Pre-budburst' (0), 'Budburst' (1 and 2) and 'Post-budburst' (3 and 4). Buds that for some reason never completed development (e.g. reached the last bud stage) were excluded before analysis.

Data analysis

Larval and host plant phenology in natural populations. Altitude and year-specific mean stages of the larval phenology and host plant phenology in altitudinal gradients were estimated using linear mixed-effects models (library 'lme' in R, R Development Core Team, 2008). The variation in larval phenology between sample stations was analyzed using 'year', 'species' (categorical) and 'altitude' (continuous), as well as all possible interactions between them as fixed effects and 'station' as categorical random effect. Data were entered in the model as sampling station specific mean instar, i.e. the arithmetic average instar based on all larvae sampled at a station per year. Data from the two sampling dates (June 21 and July 1) were considered equal in the analysis. Postponing the 2008 sampling could have result in longer development times for larvae compared with the 2 previous years, but the fact that the temperature sum on July 1, 2008 (459) was still below that of June 21, 2006 (570) and 2007 (475), suggest that

this is probably not the case. Analysis of mean birch leaf size per station were done by the same approach as for larval phenology using 'year', 'altitude' and all possible interactions as fixed effect and 'station' as random effect. Although larval instar is a nominal variable, using sample station mean values (with decimal values) as entries (i.e. replicates) provided model residuals that did not deviate notably from the requirements of linear models. The model selection criteria AICc and evidence ratios were used to find the most parsimonious models (Johnson & Omland, 2004).

Temperature sum requirements for egg hatching and birch bud burst. The temperature sum requirements for egg hatch between species and incubation temperatures were assessed by calculating mean daily temperature sums above 0 °C from January 1 until egg hatch for each replicate egg vial. This was done by weighting the proportion of eggs hatched in a vial on a given day in relation to the accumulated temperature sum on that day. The difference in egg hatch in *A. aurantiaria* relative to *O. brumata* and in *O. brumata* relative to *E. autumnata* was expressed in 'day equivalents', as the difference in cumulative temperature at egg hatch between the two species divided by the mean temperature in the incubation rooms. Similarly, the temperature sum requirements for budburst was calculated for each incubation temperature, as the mean daily temperature sums above 0 °C from January 1 until budburst. This was done by weighting the proportion of buds on each branch that had reached bud stage 'Budburst' on a given day in relation to the accumulated temperature sum on that day. A measure of mean bud stage on a given day in each incubation room was calculated by assigning a value of 1–3 to buds in the stages 'Pre-budburst', 'Budburst' and 'Post-budburst', respectively, and calculating the average score over all buds. The delay in egg hatch in *A. aurantiaria* relative to *O. brumata* at the four coldest temperatures could hence be expressed directly as a difference in mean bud stage at the time of hatching. Experimental effects were assessed statistically by regressing the pairwise species differences in egg hatch (in terms of both day and bud stage equivalents) against temperature treatments. Lower development thresholds (LDT, the temperature below which no egg development takes place) for *A. aurantiaria* and *O. brumata* were calculated from the regression between development rate ($R = 1/\text{days}$ in lab until egg hatch) and mean incubation temperature ($R = aT + b$, $LDT = -b/a$) according to Honek (1996).

Results

Invasion and regional dynamics of A. aurantiaria

The first indication of an incipient invasion in northern Norway (Area A, Fig. 3) was obtained during the fall of 2004, when observations of phototaxic adults were reported from multiple sites in Troms County (approximately 70°N). In later years, reports from the public to Tromsø University Museum certified to high abundances of larvae on particularly birch, rowan and *Rosa*,

with a peak in 2006. Locally outbreak densities resulted in severe defoliation. Mapping the outbreak region based on the reports showed that our area of quantitative geometrid monitoring included the northern border of the invasion. However, the highest abundances appeared to be south of the monitoring area.

The quantitative monitoring of *A. aurantiaria* that commenced in 2006, showed that the invasion reached the highest abundances in the southwestern sites (site 1–6), while none or scattered specimens were recorded in the northern and eastern sites (Fig. 3). The peak of the invasion/outbreak was in 2006–2007, followed by a population crash in 2008–2009. The southwestern sites, where *A. aurantiaria* occurred in highest abundance, had all experienced a peak in abundance of *O. brumata* in the preceding years (2000–2004), after which some years of very low abundance were expected (see Ims *et al.*, 2004), following the pattern of a 10-year outbreak cycle. Curiously, *O. brumata* displayed a second, much smaller, peak in abundance during the years and sites where *A. aurantiaria* was most abundant (2005–2009). The population trajectories of *A. aurantiaria* and *O. brumata* in the altitudinal gradient show that the two species displayed similar dynamics, but with some differences in the timing of the peak and crash phase (Fig. 4). *A. aurantiaria* was most abundant in 2006 and reached the highest abundance at intermediate altitudes (100 and 170 m), whereas *O. brumata* peaked the following year, and generally had higher abundance at higher altitudes (170 and 240 m). Populations of both species had crashed by 2009.

Larval and host plant phenology in natural climatic gradients

The analysis of the mean instar structure of the two species along altitudinal gradients showed that the most parsimonious statistical model included the main

effects of the three focal variables ('year', 'altitude' and 'species'; AICc = 173.48, evidence ratio between best and second best model = 44.3, see Appendix S2 for details of the best models). The phenology of *A. aurantiaria* lagged consistently (i.e. independently of year and altitude) behind that of *O. brumata* by 0.75–1 instar (Fig. 5a and b). Both species showed a gradual decline in mean instar structure with increasing altitude, with populations at the highest altitude lagging 0.75–1 instar behind populations inhabiting the lowest altitude (Fig. 5a). Moreover, larvae collected on 50 m on the same date in all 3 years (Fig. 5b) showed that mean instar structure decreased significantly from 2006 to 2007 (nonoverlapping 95% confidence intervals), and then again with an equivalent decrease from 2007 to 2008, as expected from local temperature data (Fig. 5c). The difference in instar structure between the coldest and warmest year (2006 and 2008), was approximately 1.5 instars within each species.

There was a systematic delay in birch leaf phenology with increasing altitude along the altitudinal gradient (Fig. 5d). The most parsimonious statistical model explaining birch leaf phenology included not only the main effects ('altitude', 'year'), but also the interaction between them (AICc = 165.6, evidence ratio between best and second best model = 883601, see Appendix S2 for details of the best models). The significant interaction was a result of the, otherwise strong, altitudinal delay in leaf phenological development being less apparent in the warmer year (2006) than in the 2 colder years (2007–2008). While the delay in larval development was significant (Fig. 5b) for both species in the coldest year (2008), there was no apparent delay in host plant phenology, indicating a more pronounced temporal disassociation between larval and host plant phenology in 2008 compared with the previous years.

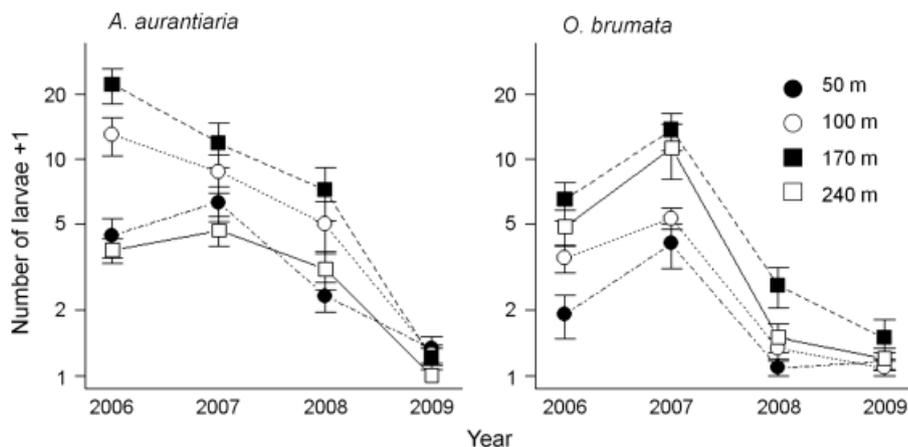


Fig. 4 Population trajectories of *Agriopsis aurantiaria* and *Operophtera brumata* in the altitudinal gradients during the years 2006–2009. Year and altitude specific abundances are given as mean number of larvae on a logarithmic scale (a constant value of 1 added to account for zero values). Bars give standard error of the estimated means.

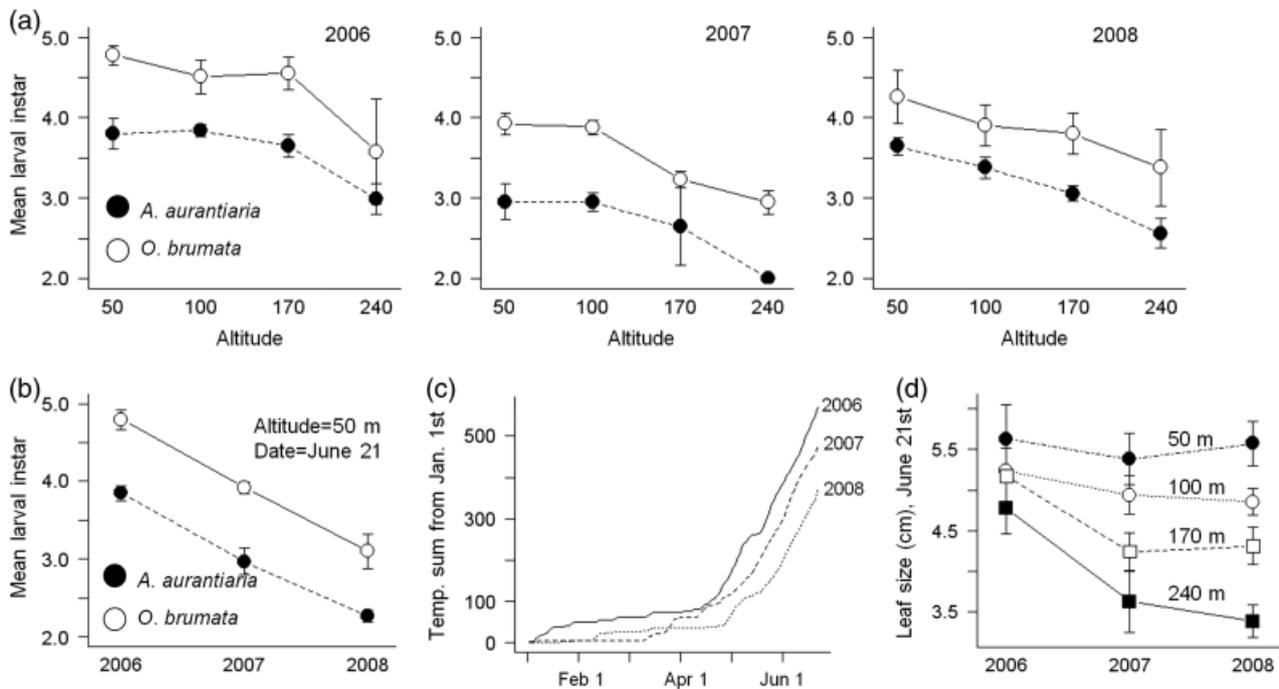


Fig. 5 Phenology of moth larvae and host plant along the altitudinal gradient. (a) Mean instar structure of both moth species per year and altitude, (b) mean instar structure of both moth species collected at the same date each year (June 21, 50 m only), (c) cumulative temperature above 0 °C from January 1 until June 21, and (d) phenology of birch leaves in the altitudinal gradient. All estimates of phenology (larval instar and birch leaf size) are based on a linear model where the data entries are sampling station specific mean values (see section on ‘Data analysis’).

Experiments in climate chambers

The relative temperature requirements for egg hatch differ greatly between the three species. Our results show that the general sequence of hatching is *E. autumnata* followed first by *O. brumata* and subsequently by *A. aurantiaria*. *A. aurantiaria* requires higher temperature sums for hatching than *O. brumata* at all temperatures in the colder part of the temperature range (Fig. 6a). The difference between the two species diminishes gradually at higher temperatures and at temperatures above 16–17 °C the hatching curves of *A. aurantiaria* are indistinguishable from those of *O. brumata*. In comparison, *E. autumnata* has substantially lower temperature requirements for hatching at all temperatures relative to *O. brumata* (Fig. 6b). There was a clear temporal disassociation between hatching in *A. aurantiaria* and birch budburst, which diminished with increasing temperature. This was in sharp contrast to *O. brumata*, which hatched in close synchrony with budburst at all temperatures included in the experiment.

The delay in mean egg hatch of *A. aurantiaria* relative to *O. brumata* at a given temperature is similar or slightly less than the one observed between *O. brumata* and *E. autumnata* (Fig. 7a) and corresponds to a substantial difference in birch bud development at the time

of hatching (Fig. 7b). The LDT in *A. aurantiaria* is substantially higher than in *O. brumata* (Fig. 8).

Discussion

This study documents a rapid invasion by a novel forest pest insect, *A. aurantiaria*, into the subarctic birch forest system in Fennoscandia, coinciding with a prolonged period with warm springs from 2002 until 2007 (Fig. 2). Locally, the species attained densities causing severe defoliation of host trees. The situation today draws parallel to the invasion by *O. brumata* in the region a century ago. *O. brumata* has historically had a more southern distribution, and was first recorded in the Tromsø region in the 1890s (Tenow, 1972). About a decade later it caused severe defoliation locally. Today, *O. brumata* participates in outbreaks across the entire birch forest belt in Northern Fennoscandia, including most of the region that experience outbreaks by *E. autumnata* (Jepsen *et al.*, 2009a). The recent latitudinal and altitudinal outbreak range expansion by *O. brumata* (Hagen *et al.*, 2007; Jepsen *et al.*, 2008) has both prolonged and intensified the most recent outbreak cycle, resulting in widespread damage and die-off in the mountain birch forest. It is hence of substantial interest to investigate how the new invader, *A. aurantiaria*, ‘fits’

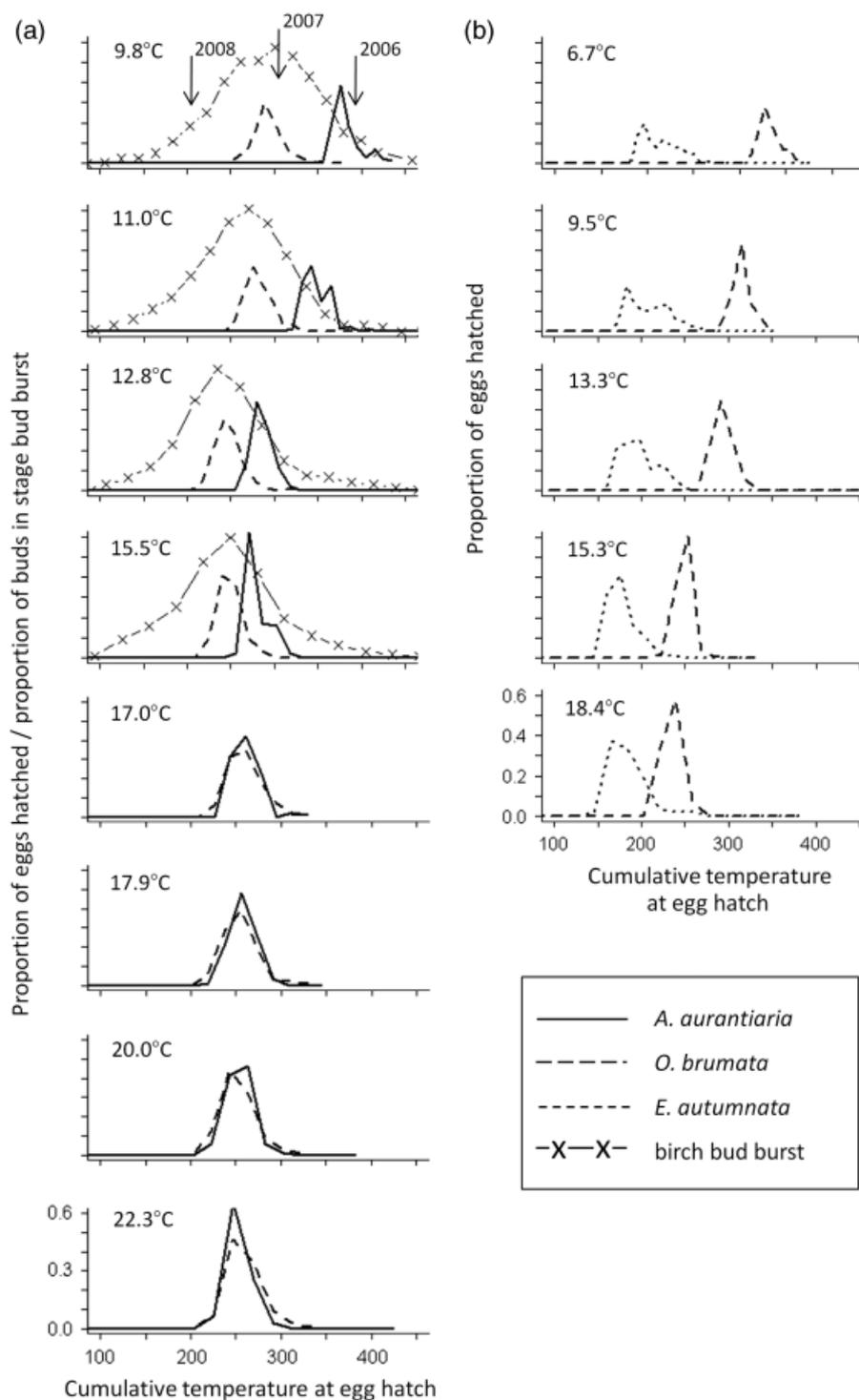


Fig. 6 Hatching curves for (a) *Agriopis aurantiaria* and *Operophtera brumata* and corresponding bud burst curve for birch (2009 experiment) and (b) hatching curves for *O. brumata* and *Epirrita autumnata* (2010 experiment). Mean temperature in the incubation room is given in the upper left corner of each figure. Arrows on top-left figure show the cumulative field temperature on June 1 during the three field years for comparison (compare Fig. 5c).

into the geometrid-mountain birch system in the region, with the aim of determining its potential for establishment and further spread.

We have shown that *A. aurantiaria* has established itself at least as far north as the Tromsø region (approximately 70°N), with higher densities in the southwestern

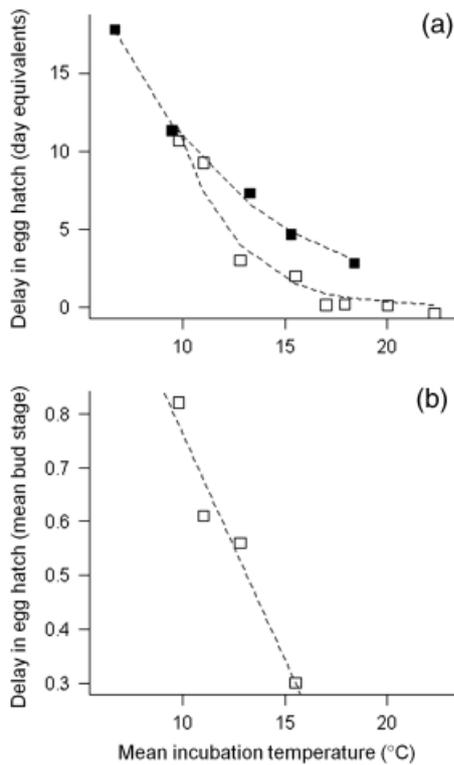


Fig. 7 Delay (i.e. difference) in mean egg hatch as a function of incubation temperature in *Agriopsis aurantiaria* relative to *Operophtera brumata* (open squares) and *O. brumata* relative to *Epirrita autumnata* (filled squares). The delay in egg hatch is expressed as (a) day equivalents (number of days at a given incubation temperature) and (b) mean bud stage of birch (the difference in mean bud stage at the time of hatching of species A and species B). Hatched lines in (a) are fitted exponential decay curves (*Agriopsis*–*Operophtera*: decay rate = 0.357, SE = 0.06, $P = 0.001$; *Operophtera*–*Epirrita*: decay rate = 0.151, SE = 0.008, $P < 0.001$). Hatched line in (b) show the fitted linear regression ($R^2 = 0.92$, $P = 0.027$).

part of the monitoring area. The scarcity of recordings further north suggests that this can be considered the front of the invasion of *A. aurantiaria* in northern Norway. The 10-year outbreak cycles of the two native species are believed to be governed by trophic feedbacks between moth, its host plants and/or natural enemies (Tenow, 1972; Ruohomäki *et al.*, 2000; Klemola *et al.*, 2002; Tanhuanpää *et al.*, 2002). During the last outbreak cycle, *A. aurantiaria* showed population dynamics very similar to *O. brumata*, with a peak in 2006 and a similarly timed crash phase. This suggests that *A. aurantiaria*, once established, will display population outbreaks in approximate temporal synchrony with the two native species.

The field studies along natural climatic gradients confirm that *A. aurantiaria* displays a larval develop-

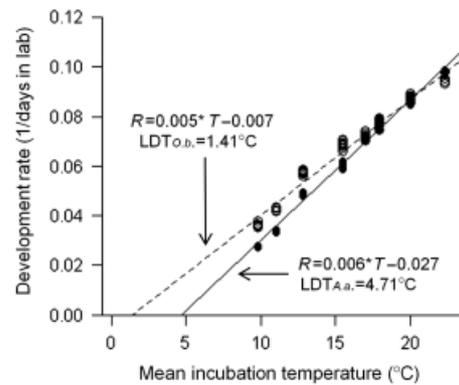


Fig. 8 The lower development threshold (LDT) calculated from the regression between development rate ($R = 1/\text{days in lab}$ until egg hatch) and mean incubation temperature ($R = aT + b$, $LDT = -b/a$) following Honek (1996). *Agriopsis aurantiaria* (filled circles, full line) and *Operophtera brumata* (open circles, hatched line). The lines show the fitted linear regression.

ment similar to *O. brumata*, albeit with a consistent phenological lag of 0.75–1 instar. This is in close correspondence with the observed delay in larval phenology in *O. brumata* relative to *E. autumnata* in a comparable altitudinal gradient (Mjaaseth *et al.*, 2005). There is hence a clear sequence in larval phenology between the three species under field conditions. Larval phenology (mean instar distribution at a given date) is a function of hatching date, growth rate and survival rate of the early instars (before sampling), all of which are temperature dependent processes. The cause of the observed sequence in larval phenology is hence not easily elucidated from the field records. Mjaaseth *et al.* (2005) found no differences in growth rate of third–fifth instar larvae to account for the observed delay in larval phenology between *O. brumata* and *E. autumnata*. Assuming similar hatching rules for both species, the authors suggested that growth rates may differ in first and second instars, perhaps due to differences in feeding strategy of the newly hatched larvae. Our experimental results clearly point to differentiating temperature sum requirements for egg hatching in the three species, rather than differences in growth rate of larvae, as the main reason for the difference in phenology between both *A. aurantiaria*–*O. brumata* and *O. brumata*–*E. autumnata*. Firstly, *A. aurantiaria* requires higher temperature sums for hatching at the coldest end of the incubation temperature range, and the phenological delay in *A. aurantiaria* relative to *O. brumata* is of a similar magnitude as *O. brumata* relative to *E. autumnata*. This suggests that incubated simultaneously under realistic field temperatures (the lower end of the range included in our experiment), eggs of the three species would hatch in sequence. Secondly, the

within-species phenological delay observed in the field between the warmest and the coldest year is largely explained by the between-year difference in temperature sum at the date of sampling (2006 vs. 2008, Fig. 5b and c). A between-year difference in temperature sum of about 200° (2006: 570.4 vs. 2008: 372.6) results in a phenological delay of about 1.5 instars. If the phenological delay in *A. aurantiaria* relative to *O. brumata* observed in the field (= 0.75 instars) is primarily due to a difference in the time of egg hatching, we would expect temperature sum requirements in *A. aurantiaria* to be about 100° higher than in *O. brumata*. Our experimental results confirm that this is indeed the case at the lower end of the temperature range (104.5 at 9.8° and 101.7 at 11°).

The developmental response to temperature (such as the LDT and the temperature sum required for development) is known to change with latitude in many invertebrate species (Honek, 1996; Trudgill *et al.*, 2005). Specifically, northern species often have lower LDT than their more southern relatives (Honek, 1996), allowing the northern species to develop faster at low temperatures. Accordingly, we found that LDT for egg hatch in *A. aurantiaria* exceeded LDT of *O. brumata* by several degrees. However, the difference in slope of the regressions suggests that, once above LDT, the increase in development rate for a given change in incubation temperature is faster in *A. aurantiaria* than in *O. brumata*.

The observed difference in hatching in *A. aurantiaria* compared with *O. brumata* is sufficiently large to be of consequence for the degree of temporal association between larval emergence and host tree budburst. Given the coarseness of the bud classification (three stages), a difference in mean bud stage at hatching of 0.6–0.8 at the lowest temperatures is equivalent to a change from early budburst to fully unfolded leaf. The degree of tolerance of newly hatched *A. aurantiaria* larvae to temporal disassociation with host plant budburst has never been studied, but it is likely to be low, similar to what has been observed for *O. brumata* (van Asch & Visser, 2007 and references herein). This would mean that *A. aurantiaria* is likely to be substantially more asynchronous with host plant phenology in years (or localities) where *O. brumata* hatch in perfect association with budburst.

Natural invasion and range expansions of pest insects with cyclic dynamics will often go undetected for years, because of near-zero population densities between outbreaks. Moreover, if a climate-induced invasion event is going to result in outbreak densities the climatic conditions facilitating the invasion must coincide with the biotic conditions that rule the cyclic outbreak dynamics of trophically related species. We were able to document what appears to be the first outbreak by invading

A. aurantiaria in Northern Norway. Further, we have provided quantitative data on the population dynamics and phenology of the species in its new environment as well as experimental evidence for climate induced phenological matching with sub-Arctic birch as probable mechanism facilitating the outbreak. The establishment of such matches is expected to result in the kind of rapid nonlinear responses to climatic warming (Stenseth & Mysterud, 2002) that we have documented for *A. aurantiaria*. Our study provided insights into the role that the invading species may play in the mountain birch-geometrid system, today and under a future milder climate. We can conclude that with a population dynamics and larval development that is remarkably similar to *O. brumata* along natural climatic gradients, *A. aurantiaria*, once established, can be expected to show population outbreaks in approximate temporal synchrony with the two native species. The cumulative impact of these geometrids on the sub-Arctic birch forest system may thus intensify even more in the future. However, compared with *O. brumata*, *A. aurantiaria* has a higher LDT, hatches later and is phenologically delayed under a natural temperature regime at its northern distributional limit, which means that it may be more prone to temporal disassociation with birch budburst and strive to complete development in cold years. However, with increasing temperatures, *A. aurantiaria* hatches in increasing synchrony both with *O. brumata* and birch budburst, suggesting that further expansion of the outbreak range of *A. aurantiaria* can be expected in Northern Fennoscandia.

Acknowledgements

This work was funded by the Research Council of Norway, the Department of Arctic and Marine Biology, University of Tromsø and the Norwegian Institute for Nature Research (NINA), Tromsø.

References

- ACIA (2004) *Impacts of a Warming ARCTIC*. Cambridge University Press, New York, USA.
- Ahas R, Aasa A, Menzel A, Fedotova VG, Scheifinger H (2002) Changes in European spring phenology. *International Journal of Climatology*, **22**, 1727–1738.
- Ayres MP, Lombardero MJ (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of the Total Environment*, **262**, 263–286.
- Bale JS, Masters GJ, Hodkinson ID *et al.* (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, **8**, 1–16.
- Battisti A, Stastny M, Buffo E, Larsson S (2006) A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly. *Global Change Biology*, **12**, 662–671.
- Battisti A, Stastny M, Netherer S, Robinet C, Schopf A, Roques A, Larsson S (2005) Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecological Applications*, **15**, 2084–2096.
- Beniston M, Tol RSJ (1998) Europe. In: *The Regional Impacts of Climate Change: An Assessment of Vulnerability*. IPCC Working Group II (eds Watson RT, Zinyowera MC, Moss RH), pp. 149–185. Cambridge University Press, Cambridge, UK.

- Both C, van Asch M, Bijlsma RG, van den Burg AB, Visser ME (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology*, **78**, 73–83.
- Buse A, Dury SJ, Woodburn RJW, Perrins CM, Good JEG (1999) Effects of elevated temperature on multi-species interactions: the case of Pedunculate Oak, Winter Moth and Tits. *Functional Ecology*, **13**, 74–82.
- Bylund H (1999) Climate and the population dynamics of two insect outbreak species in the North. *Ecological Bulletins*, **47**, 54–62.
- Callaghan TV, Bergholm F, Christensen TR, Jonasson C, Kokfelt U, Johansson M (2010) A new climate era in the sub-Arctic: accelerating climate changes and multiple impacts. *Geophysical Research Letters*, **37**, L14705, doi: 10.1029/2009GL042064.
- Carroll AL, Regniere J, Logan JA, Taylor SW, Bentz BJ, Powell JA (2006) Impacts of climate change on range expansion by the mountain pine beetle. Mountain Pine Beetle Initiative Working Paper 2006-14. Natural Resources Canada, Canadian Forest Service, Victoria, BC.
- Dale VH, Joyce LA, McNulty S *et al.* (2001) Climate change and forest disturbances. *Bioscience*, **51**, 723–734.
- Delbart N, Picard G, Le Toans T *et al.* (2008) Spring phenology in boreal Eurasia over a nearly century time scale. *Global Change Biology*, **14**, 603–614.
- Hagen SB, Jepsen JU, Ims RA, Yoccoz NG (2007) Shifting altitudinal distribution of outbreak zones of winter moth *Operophtera brumata* in sub-arctic birch forest: a response to recent climate warming? *Ecography*, **30**, 299–307.
- Harrington R, Fleming RA, Woiwod IP (2001) Climate change impacts on insect management and conservation in temperate regions: can they be predicted? *Agricultural and Forest Entomology*, **3**, 233–240.
- Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.
- Hickling R, Roy DB, Hill JK, Thomas CD (2005) A northward shift of range margins in British Odonata. *Global Change Biology*, **11**, 502–506.
- Honek A (1996) Geographical variation in thermal requirements for insect development. *European Journal of Entomology*, **93**, 303–312.
- Ims RA, Yoccoz NG, Hagen SB (2004) Do sub-Arctic winter moth populations in coastal birch forest exhibit spatially synchronous dynamics? *Journal of Animal Ecology*, **73**, 1129–1136.
- Jepsen JU, Hagen SB, Hogda KA, Ims RA, Karlsen SR, Tommervik H, Yoccoz NG (2009a) Monitoring the spatio-temporal dynamics of geometrid moth outbreaks in birch forest using MODIS-NDVI data. *Remote Sensing of Environment*, **113**, 1939–1947.
- Jepsen JU, Hagen SB, Ims RA, Yoccoz NG (2008) Climate change and outbreaks of the geometrids *Operophtera brumata* and *Epirrita autumnata* in sub-arctic birch forest: evidence of a recent outbreak range expansion. *Journal of Animal Ecology*, **77**, 257–264.
- Jepsen JU, Hagen SB, Karlsen SR, Ims RA (2009b) Phase-dependent outbreak dynamics of geometrid moth linked to host plant phenology. *Proceedings of the Royal Society B-Biological Sciences*, **276**, 4119–4128.
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends in Ecology and Evolution*, **19**, 101–108.
- Karlsen SR, Hogda KA, Wielgolaski FE, Tolvanen A, Tommervik H, Poikolainen J, Kubin E (2009) Growing-season trends in Fennoscandia 1982–2006, determined from satellite and phenology data. *Climate Research*, **39**, 275–286.
- Karlsson PS, Bylund H, Neuvonen S, Heino S, Tjøs M (2003) Climatic response of budburst in the mountain birch at two areas in northern Fennoscandia and possible responses to global change. *Ecography*, **26**, 617–625.
- Klemola N, Heisswolf A, Ammunet T, Ruohomäki K, Klemola T (2009) Reversed impacts by specialist parasitoids and generalist predators may explain a phase lag in moth cycles: a novel hypothesis and preliminary field tests. *Annales Zoologici Fennici*, **46**, 380–393.
- Klemola T, Tanhuanpää M, Korpimäki E, Ruohomäki K (2002) Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. *Oikos*, **99**, 83–94.
- Logan JA, Regniere J, Powell JA (2003) Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment*, **1**, 130–137.
- Menzel A, Sparks TH, Estrella N *et al.* (2006) European phenological response to climate change matches the warming pattern. *Global Change Biology*, **12**, 1969–1976.
- Miller-Rushing AJ, Hoyer TT, Inouye DW, Post E (2010) The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B – Biological Sciences*, **365**, 3177–3186.
- Mjaaseth RR, Hagen SB, Yoccoz NG, Ims RA (2005) Phenology and abundance in relation to climatic variation in a sub-arctic insect herbivore-mountain birch system. *Oecologia*, **145**, 53–65.
- Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, **386**, 698–702.
- Neuvonen S, Niemelä P, Virtanen T (1999) Climatic change and insect outbreaks in boreal forest: the role of winter temperatures. *Ecological Bulletins*, **47**, 63–67.
- Niemelä P (1979) Topographical delimitation of *Oporinia* damages – experimental evidence of the effect of winter temperature. Reports from the Kevo Subarctic Research Station. Vol. 15. pp. 33–36.
- Parnesan C, Ryrholm N, Stefanescu C *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.
- Parnesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Post E, Forchhammer MC, Bret-Harte MS *et al.* (2009) Ecological dynamics across the arctic associated with recent climate change. *Science*, **325**, 1355–1358.
- Pöyry J, Luoto M, Heikkinen RK, Kuussaari M, Saarinen K (2009) Species traits explain recent range shifts of Finnish butterflies. *Global Change Biology*, **15**, 732–743.
- Pudas E, Leppala M, Tolvanen A, Poikolainen J, Venäläinen A, Kubin E (2008) Trends in phenology of *Betula pubescens* across the boreal zone in Finland. *International Journal of Biometeorology*, **52**, 251–259.
- R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. Foundation for Statistical Computing, Vienna, Austria.
- Robertson C, Nelson TA, Jelinski DE, Wulder MA, Boots B (2009) Spatial-temporal analysis of species range expansion: the case of the mountain pine beetle, *Dendroctonus ponderosae*. *Journal of Biogeography*, **36**, 1446–1458.
- Ruohomäki K, Tanhuanpää M, Ayres MP, Kaitaniemi P, Tammaru T, Haukioja E (2000) Causes of cyclicity of *Epirrita autumnata* (Lepidoptera, Geometridae): grandiose theory and tedious practice. *Population Ecology*, **42**, 211–223.
- Schneider HJS (1914) Lepidopterologische meddelelser fra Tromsø stift II. *Tromsø Museums Aarshefte*, **35–36**, 179–219 (in Norwegian).
- Stenseth NC, Mysterud A (2002) Climate, changing phenology, and other life history and traits: nonlinearity and match-mismatch to the environment. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 13379–13381.
- Tanhuanpää M, Ruohomäki K, Turchin P *et al.* (2002) Population cycles of the autumnal moth in Fennoscandia. In: *Population Cycles: The Case for Trophic Interactions* (ed. Berryman AA), pp. 142–154. Oxford University Press, Oxford.
- Tenow O (1972) The outbreaks of *Oporinia autumnata* Bk. and *Operophtera* spp. (Lep., Geometridae) in the Scandinavian mountain chain and Northern Finland 1862–1968. *Zoologiska Bidrag från Uppsala*, (Suppl. 2), 1–107.
- Tenow O, Nilssen A (1990) Egg cold hardiness and topoclimatic limitations to outbreaks of *Epirrita autumnata* in Northern Fennoscandia. *Journal of Applied Ecology*, **27**, 723–734.
- Tenow O, Nilssen AC, Bylund H, Hogstad O (2007) Waves and synchrony in *Epirrita autumnata*/*Operophtera brumata* outbreaks. I. Lagged synchrony: regionally, locally and among species. *Journal of Animal Ecology*, **76**, 258–268.
- Trudgill DL, Honek A, Li D, Van Straalen NM (2005) Thermal time – concepts and utility. *Annals of Applied Biology*, **146**, 1–14.
- van Asch M, Visser ME (2007) Phenology of forest caterpillars and their host trees: the importance of synchrony. *Annual Review of Entomology*, **52**, 37–55.
- Visser ME, Holleman LJM (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London Series B – Biological Sciences*, **268**, 289–294.
- Volney WJA, Fleming RA (2000) Climate change and impacts of boreal forest insects. *Agriculture, Ecosystems and Environment*, **82**, 283–294.
- Walther GR, Post E, Convey P *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Wilson RJ, Gutierrez D, Gutierrez J, Martinez D, Agudo R, Monserrat VJ (2005) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters*, **8**, 1138–1146.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Kernel estimates of frequency distribution of different instars based on head capsule width for the two species. The limit values for head capsule width for the five instars (S1–S5) for *O. brunata* were respectively: 0–0.35 mm (S1), 0.35–0.65 mm (S2), 0.65–0.90 mm (S3), 0.90–1.25 mm (S4) and 1.25–1.80 mm (S5). The limit values for head capsule width for instars 1–5 for *A. aurantiaria* were respectively 0–0.38 mm (S1), 0.38–0.81 mm (S2), 0.81–1.19 mm (S3), 1.19–1.81 mm (S4), and 1.81–2.5 mm (S5).

Appendix S2. Model selection.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.