PHENOLOGICAL LITERACY

UNDERSTANDING THROUGH SCIENCE & STEWARDSHIP

Module 7
Phenological Responses To Climate Change II: Demographic and Geographic Range Shifts

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Goals For Student Learning

This module was created to help students:

- Familiarize themselves with meta-analytic methods used to test scientific hypotheses
- Understand how scientists use meta-analysis to test hypotheses regarding geographic range shifts
- Understand how researchers empirically determine whether phenological shifts and/or climate change promote range shifts

Phenology and Range Shifts

Changes in species geographic ranges have been have been widely predicted as a response to changing climate. This prediction seems logical, given that many terrestrial ecosystems have experienced increased temperatures in recent years and that the geographic distribution of many species is determined, in part, by climatic factors. Organisms that can migrate to higher elevations or cooler latitudes may thus be able to survive by colonizing new regions. Parmesan and Yohe (2003) were among the first researchers to use meta-analysis to determine whether species ranges were shifting in a manner that is consistent with a response to global climate change. They synthesized data from studies of 99 species to evaluate phenological responses to climate change and changes in geographic range boundaries. Their finding that the onset of spring is advancing and that species ranges are indeed shifting northward provided compelling evidence that climate change is currently affecting biological systems.

While range shifts may enhance species' survival or promote their persistence in some cases, range shifts may also have negative consequences. For example, invasive and/or pest species may spread into new regions, threatening the species that are native to or restricted to the invaded habitats. In northern Scandinavia, sub-Arctic birch trees are often defoliated by native herbivorous moths, which are considered forest pests. In a recently published study by Jepsen et al. (2011), researchers used a combination of field monitoring and laboratory experiments to show that the northern expansion of the scarce umber moth, an exotic birch herbivore, is attributable to recent spring warming events, which have promoted increased phenological matching between scarce umber moth emergence and birch bud break.

Articles To Read

- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37-42.

Jepsen, J. U., L. Kapari, S. B. Hagen, T. Schott, O. P. L. Vindstad, A. C. Nilssen, and R. A. Ims. 2011. Rapid northwards expansion of a forest insect pest attributed to spring phenology matching with sub-Arctic birch. Global Change Biology 17:2071-2083

Suggested Discussion Questions

1. Describe the general conclusions reached by Parmesan and Yohe (2003) with respect to phenological shifts and geographic range boundary changes.

2. Deciding upon the criteria for including or excluding studies from meta-analyses is an important part of the synthetic research process. How did Parmesan and Yohe (2003) decide which studies to include in their meta-analysis?

3. How do Parmesan and Yohe (2003) define a "fingerprint of climate change"? Do you agree with their definition?

4. What are the challenges of relating changes in species abundances and distributions to climate change? How did Parmesan and Yohe (2003) address these challenges?

5. Describe how scarce umber moth populations changed in northern Norway between 2000-2008? What caused the crash in moth pest populations during the later years of this study?

6. What moth phenophases did Jepsen et al. (2011) record? What birch phenophases did they record?

7. What is the relationship between the timing of moth larval phenology and birch phenology under natural conditions? (Jepsen et al. 2011)

8. How did the researchers relate plant and moth phenological schedules to environmental climate change? (Jepsen et al. 2011)

9. What do the findings of Jepsen et al. (2011) suggest about the potential for pest outbreaks in boreal birch forests to intensify as the climate changes?

Global Change Biology

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

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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 °C, $LDT_{O.b.}$ = 1.41 °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

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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 frequency 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

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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).

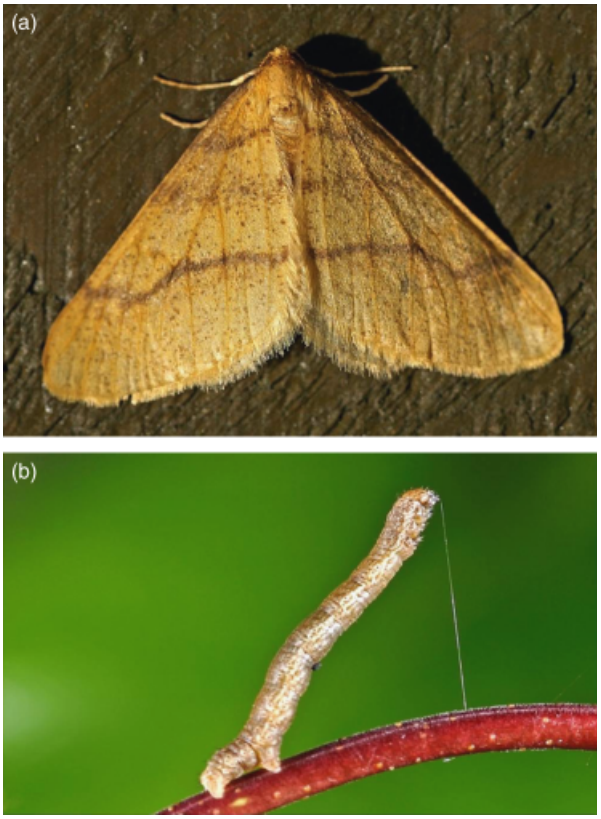

Fig. 1 Adult male (a) and larvae (b) of *Agriopis aurantiaria*. Photo: Arne C. Nilssen.

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, *Agriopis 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

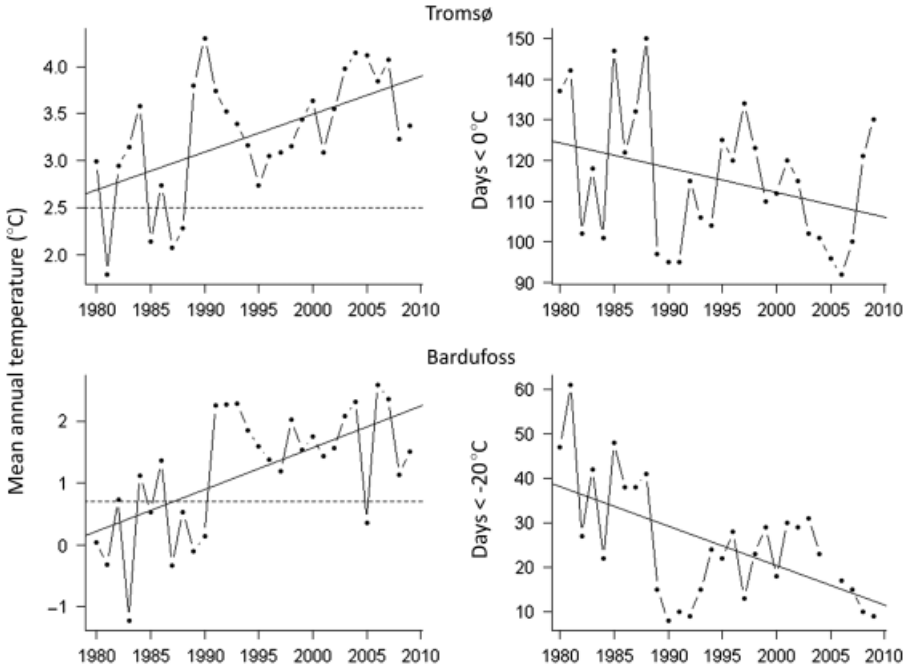

Fig. 2 Mean annual temperatures and the frequency of winter cold, expressed as the number of days below 0 °C (Tromsø; 69°40′N, 18°57′E) or −20 °C (Bardufoss; 69°05′N, 18°30′E) for the years 1980–2009. Hatched horizontal lines show the 1960–1990 normal mean annual temperature. Full straight lines show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

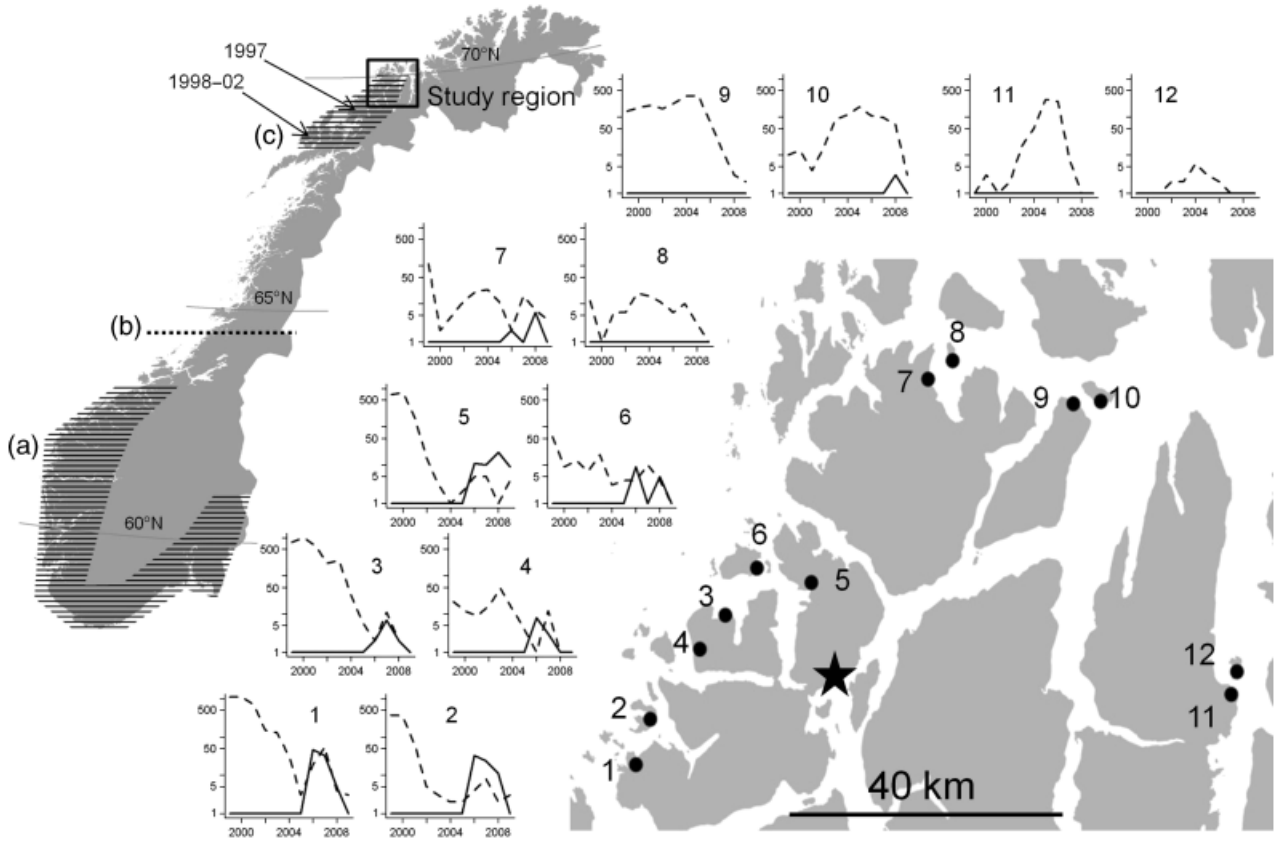

Fig. 3 Left: A map of Norway showing the current known distribution of *Agriopis aurantiaria*. Hatched area A: main distribution before year 2000 in Norway, horizontal line B: approximate Northern limit for establishment in Fennoscandia as a whole before year 2000, and hatched area C: mass outbreak area 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 km^2 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. Unfertile (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. aurantaria* and *O. brumata* were calculated from the regression between development rate ($R = 1/\text{days in lab}$ until egg hatch) and mean incubation temperature ($R = aT + b$, $\text{LDT} = -b/a$) 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 ration 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.

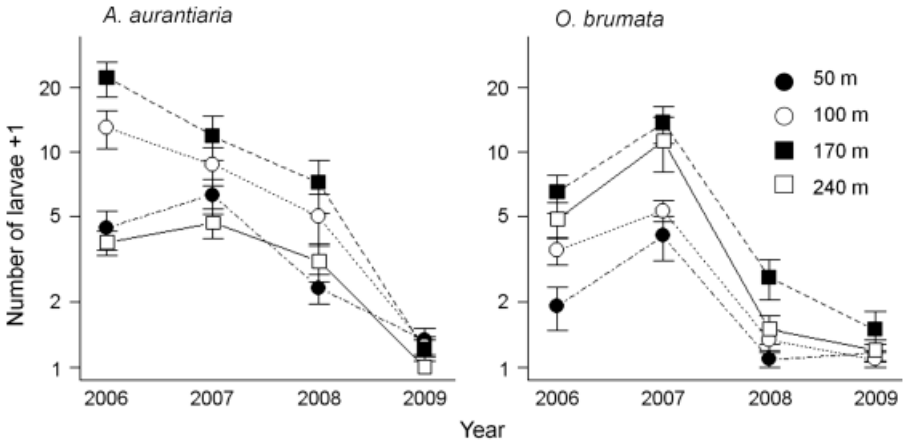

Fig. 4 Population trajectories of *Agriopis aurantiaria* and *Operophtera brumata* in the altitudinal gradients during the years 2006–2009. Year and altitude specific abundances are given as mean number of larvae on a logarithmic scale (a constant value of 1 added to account for zero values). Bars give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

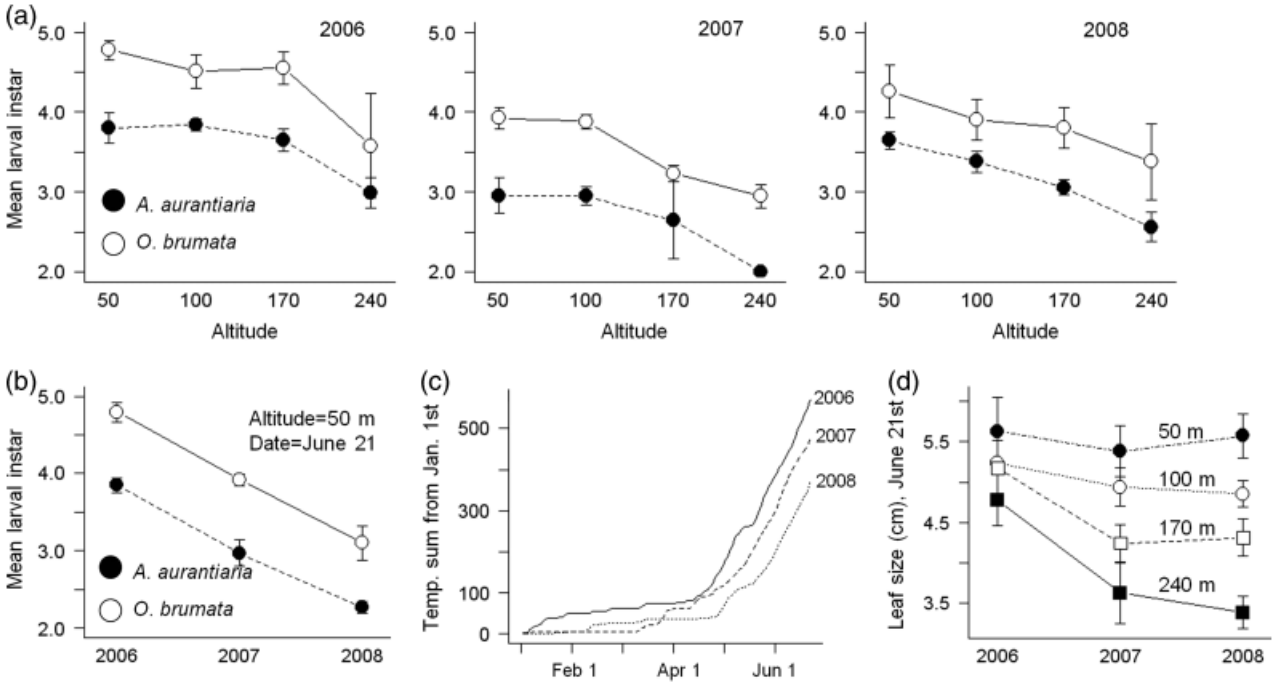

Fig. 5 Phenology of moth larvae and host plant along the altitudinal gradient. (a) Mean instar structure of both moth species per year and altitude, (b) mean instar structure of both moth species collected at the same date each year (June 21, 50 m only), (c) cumulative temperature above 0 °C from January 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'

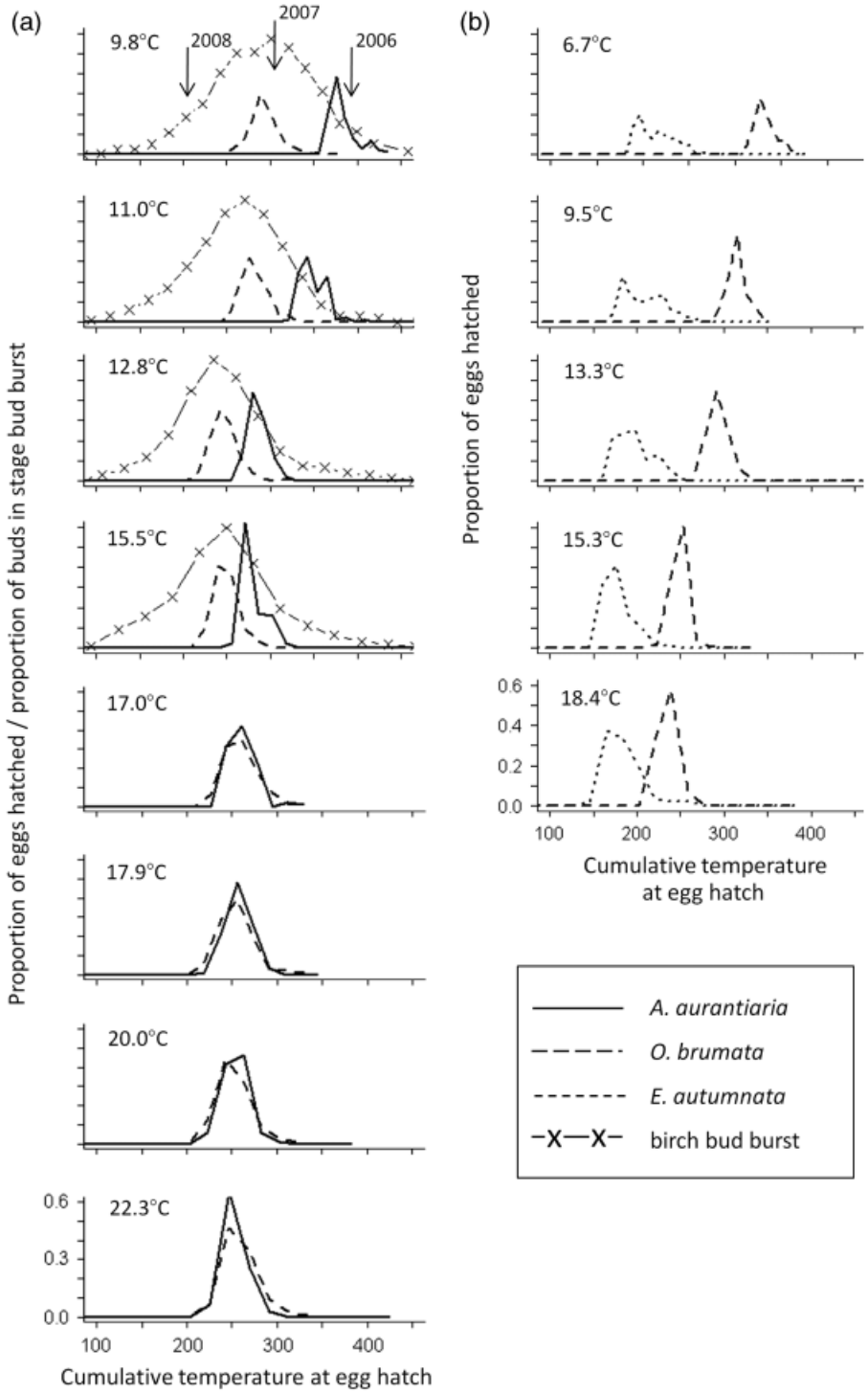

Fig. 6 Hatching curves for (a) *Agriopis aurantiaria* and *Operophtera brumata* and corresponding bud burst curve for birch (2009 experiment) and (b) hatching curves for *O. brumata* and *Epirrita autumnata* (2010 experiment). Mean temperature in the incubation room is given in the upper left corner 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

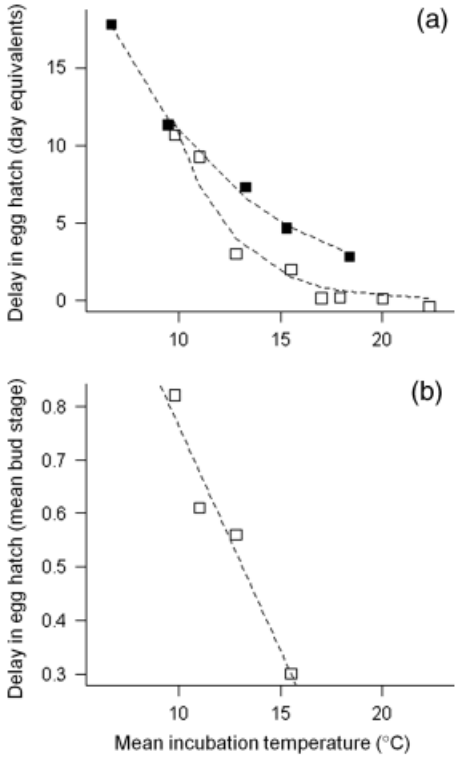

Fig. 7 Delay (i.e. difference) in mean egg hatch as a function of incubation temperature in *Agriopis aurantiaria* relative to *Operophtera brumata* (open squares) and *O. brumata* relative to *Epirrita autumnata* (filled squares). The delay in egg hatch is expressed as (a) day equivalents (number of 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 (*Agriopis–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 ($R^2 = 0.92$, $P = 0.027$).

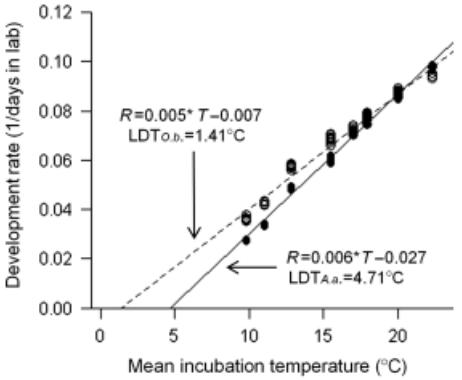

Fig. 8 The lower development threshold (LDT) calculated from the regression between development rate ($R = 1/\text{days in lab}$ until egg hatch) and mean incubation temperature ($R = aT + b$, $\text{LDT} = -b/a$) following Honek (1996). *Agriopis aurantiaria* (filled circles, full line) and *Operophtera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

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 development 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. auratiaria–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.

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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. brumata* 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.

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A globally coherent fingerprint of climate change impacts across natural systems

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Causal attribution of recent biological trends to climate change is complicated because non-climatic influences dominate local, short-term biological changes. Any underlying signal from climate change is likely to be revealed by analyses that seek systematic trends across diverse species and geographic regions; however, debates within the Intergovernmental Panel on Climate Change (IPCC) reveal several definitions of a 'systematic trend'. Here, we explore these differences, apply diverse analyses to more than 1,700 species, and show that recent biological trends match climate change predictions. Global meta-analyses documented significant range shifts averaging 6.1 km per decade towards the poles (or metres per decade upward), and significant mean advancement of spring events by 2.3 days per decade. We define a diagnostic fingerprint of temporal and spatial 'sign-switching' responses uniquely predicted by twentieth century climate trends. Among appropriate long-term/large-scale/multi-species data sets, this diagnostic fingerprint was found for 279 species. This suite of analyses generates 'very high confidence' (as laid down by the IPCC) that climate change is already affecting living systems.

The Intergovernmental Panel on Climate Change[1] (IPCC) assessed the extent to which recent observed changes in natural biological systems have been caused by climate change. This was a difficult task despite documented statistical correlations between changes in climate and biological changes[2–5]. With hindsight, the difficulties encountered by the IPCC can be attributed to the differences in approach between biologists and other disciplines, particularly economists. Studies in this area are, of necessity, correlational rather than experimental, and as a result, assignment of causation is inferential. This inference often comes from experimental studies of the effects of temperature and precipitation on the target species or on a related species with similar habitats. Confidence in this inferential process is subjective, and differs among disciplines, thus resulting in the first divergence of opinion within the IPCC.

The second impasse came from differences in perspective on what constitutes an 'important' factor. Anyone would consider a currently strong driver to be important, but biologists also attach importance to forces that are currently weak but are likely to persist. In contrast, economic approaches tend to discount events that will occur in the future, assigning little weight to weak but persistent forces. Differences of opinion among disciplines can therefore stem naturally from whether the principal motivation is to assess the magnitude of immediate impacts or of long-term trajectories. Most field biologists are convinced that they are already seeing important biological impacts of climate change[1–4,6–9]; however, they have encountered difficulty in convincing other academic disciplines, policy-makers and the general public. Here, we seek to improve communication, provide common ground for discussion, and give a comprehensive summary of the evidence.

How should a 'climate fingerprint' be defined? A straightforward view typical of an economist would be to conclude that climate change was important if it were principally responsible for a high proportion of current biotic changes. By this criterion a climate fingerprint appears weak. Most short-term local changes are not caused by climate change but by land-use change and by natural fluctuations in the abundance and distribution of species. This fact has been used by non-biologists to argue that climate change is of little importance to wild systems[10]. This approach, however, effectively ignores small, systematic trends that may become important in the longer term. Such underlying trends would be confounded (and often swamped) by strong forces such as habitat loss. Biologists have tended to concentrate on studies that minimize confounding factors, searching for trends in relatively undisturbed systems and then testing for significant associations with climate change. Economists have viewed this as biased (nonrandom exclusion of data) whereas biologists view this as reducing non-climatic noise. Thus, economists focus on total direct evidence and apply heavy time discounting; biologists apply a 'quality control' filter to available data, accept indirect (inferential) evidence and don't apply time discounting.

The test for a globally coherent climate fingerprint does not require that any single species show a climate change impact with 100% certitude. Rather, it seeks some defined level of confidence in a climate change signal on a global scale. Adopting the IPCC 'levels of confidence'[11] and applying the economists' view of a fingerprint, we would have "very high confidence" in a fingerprint if we estimated that more than 95% of observed changes were principally caused by climate change, "high confidence" between 95% and 67%, "medium confidence" between 33% and 67%, and "low confidence" below 33%. In contrast, the biologists' confidence level comes from the statistical probability that global biotic trends would match climate change predictions purely by chance, coupled with supporting experimental results showing causal relationships between climate and particular biological traits.

Here, we present quantitative estimates of the global biological impacts of climate change. We search for a climate fingerprint in the overall patterns, rather than critiquing each study individually. Using the biologists' approach, we synthesize a suite of correlational studies on diverse taxa over many regions to ask whether natural systems, in general, have responded to recent climate change. Furthermore, we attempt a cross-fertilization by applying an economists' measure—the estimated proportion of observed changes for which climate trends are the principal drivers—to data sets chosen using biologists' criteria. We call this a 'global coherence' approach to the detection of climate change impacts.

First, we explore a biologists' confidence assessment with two types of analyses of observed change: statistical meta-analyses of effect size in restricted data sets and more comprehensive categorical analyses of the full literature. Second, we present a probabilistic model that considers three variables: proportion of observations matching climate change predictions, numbers of competing explanations for each of those observations, and confidence in causal

attribution of each observation to climate change. These three variables feature equally in a model that explores an economists' 'confidence' assessment. Finally, we explore diagnostic 'sign-switching' patterns that are predicted uniquely by climate change.

The evidence

A few studies indicate evolutionary responses of particular species to climate change[12–14], but the generality of evolutionary response remains unknown. Here, we focus on phenological (timing) shifts, range boundary shifts, and community studies on species abundances (Table 1).

Meta-analyses

We developed databases suitable for meta-analysis[15] on two phenomena: range-boundary changes and phenological shifts. To control for positive publishing bias, we used only multi-species studies that reported neutral and negative results as well as positive (see Methods).

For range boundaries, suitable data spanned 99 species of birds[16], butterflies[17] and alpine herbs[18,19] (see Methods). The meta-analysis showed that the range limits of species have moved on average 6.1 ($\pm$2.4) km per decade northward or m per decade upward, significantly in the direction predicted by climate change (bootstrapped 95% confidence interval of the mean (CI_{mean}) = 1.3–10.9 km m^{-1} per decade; one-sample *t*-test, degrees of freedom (d.f.) = 98, $t = 2.52$, $P = 0.013$; Table 2).

For phenologies, suitable data were reported for herbs[20–23], shrubs[20–25], trees[20,23–25], birds[20,21], butterflies[26] and amphibians[27,28], a total of 172 species (see Methods). There was a mean shift towards earlier spring timing of 2.3 days per decade, with a bootstrapped 95% CI of 1.7–3.2 days advancement per decade (significant at $P < 0.05$).

Categorical analyses

The remaining studies were not included in the meta-analyses, either because they were on single species or because they did not present data in the raw form of *x* unit change per *y* time units per species. These less-detailed data were simplified into four categories: changed in accord with or opposite to climate change predictions, changed in some other fashion or stable (see Methods).

As with previous studies[17], analyses ignore species classified as 'stable'. This category does not represent a single result, as apparent stability could arise from a diversity of situations[17] such as: 1) the phenology, abundance or distribution of the species is not driven by climatic factors; 2) the species is actually changing, but poor data resolution could not detect small changes; and 3) the phenology, abundance or distribution of the species is driven by climatic factors, but fails to respond to current climate change. Such failure could stem from anthropogenic barriers to dispersal (habitat fragmentation) or from a lag in response time. Lags are expected when limited dispersal capabilities retard poleward/upward colonization[29], or when a necessary resource has slower response time than the focal species[17].

Phenological shifts. We quantitatively assessed 677 species reported in the literature (Table 1). Over a time period range of 16–132 years (median 45 yrs), 27% showed no trends in phenologies, 9% showed trends towards delayed spring events, whereas the remaining 62% showed trends towards spring advancement. Observed trends include earlier frog breeding[27,28], bird nesting[30–32], first flowering[20–25], tree budburst[23–25], and arrival of migrant birds and butterflies[20,21,26,33] (Table 1). Shifts in phenologies that have occurred are overwhelmingly (87%) in the direction expected from climate change ($P < 0.1 \times 10^{-12}$; Table 2).

Distribution/abundance shifts. In a quantitative assessment covering >1,046 species, we were able to categorize 893 species, functional

Table 1 **Summary of data studying phenological and distributional changes of wild species**

Taxon	Ref. number	Total no. of species (or species groups)	Spatial scale			Time scale (range years)	Change in direction predicted (*n*)	Change opposite to prediction (*n*)	Stable (*n*)	No prediction (*n*)
			L	R	C					
Phenological changes										
Woody plants	20,23,24*,25*	*n* = 38 sp		2	1	35–132	30	1	7	–
Herbaceous plants	20,21*	*n* = 38 sp	1	1		63–132	12	–	26	–
Mixed plants	22*	*n* = 385 sp	1			46	279	46	60	–
Birds	20,21*,30,31,32,33	*n* = 168 sp	2	3	1	21–132	78	14	76	–
Insects	26	*n* = 35 sp		1		23	13	–	22	–
Amphibians	27,28	*n* = 12 sp	2			16–99	9	–	3	–
Fish	20	*n* = 2 sp		1		132	2	–	–	–
Distribution/abundance changes										
Tree lines	54,55,56*	*n* = 4 sp + 5 grps	2	1		70–1,000	3 sp + 5 grps	–	1	–
Herbs and shrubs	18,19,41*,42*	*n* > 66 sp, 15 detailed		3		28–80	13	2	–	–
Lichens	36	4 biogeographic grps (*n* = 329 sp)	1			22	43	9	113	164
Birds	8*	*n* = 3 sp		1		50	3	–	–	–
	16,57*	N sp (*n* = 46 sp)		2		20–36	13	15	18	
		S sp (*n* = 73 sp)		2		20–36	36	16	21	6
	43*	Low elevation (>91 sp)	1			20	71	11	9	–
		High elevation (>96 sp)	1			20	37	27	32	–
Mammals	37	*n* = 2 sp		1		52	2	–	–	–
Insects	17,49*	*n* = 36 sp		1	1	98–137	23	2	10	1
	17	N boundaries (*n* = 52 sp)		1		98	34	1	17	–
		S boundaries (*n* = 40 sp)		1		98	10	2	28	–
Reptiles and amphibians	43*	*n* = 7 sp	1			17	6	–	1	–
Fish	39	*4* biogeographic grps (*n* = 83 sp)	1			–	2 grps	–	1 grp	1 grp
	40*	N sp (*n* > 1 sp)		1		70	>1	–	–	–
		S sp (*n* > 1 sp)		1		70	>1	–	–	–
Marine invertebrates	34*,40*	N sp (*n* > 21)	1	1		66–70	>19	2	–	>1 sp not classified
		S sp (*n* > 21)	1	1		66–70	>20	1	–	
		Cosmopolitan sp (*n* = 28 sp)	1			66	–	–	–	28
Marine zooplankton	40*	Cold water (*n* > 10 sp)		1		70	>10	–	–	>8 sp not classified
		Warm water (*n* > 14 sp)		1		70	>14	–	–	
	35	6 biogeographic grps (*n* ≥ 36 sp)			1	39	6 grps	–	–	–

N, species with generally northerly distributions (boreal/arctic); S, species with generally southerly distributions (temperate); L, local; R, regional (a substantial part of a species distribution; usually along a single range edge); C, continental (most or the whole of a species distribution). No prediction indicates that a change may have been detected, but the change was orthogonal to global warming predictions, was confounded by non-climatic factors, or there is insufficient theoretical basis for predicting how species or system would change with climate change.

*Study partially controlled for non-climatic human influences (for example, land-use change). Studies that were highly confounded with non-climatic factors were excluded. (See Supplementary Information for details of species classification.)

groups or biogeographic groups (Table 1). Less than one-third (27%) of these have exhibited stable distributions during the twentieth century. Others (24%) show changes that are impossible to relate to climate change predictions. These two types of result neither support nor refute a climate change signal, although it will be important for predictive biological models to eventually determine what proportion of these are truly stable systems.

Some range shifts have been measured directly at range boundaries, whereas others have been inferred from abundance changes within local communities. Over all of the range and abundance shift data, 434 species were categorized as changing over time periods of 17–1,000 years (median 66 years) (Table 1). Of these, 80% have shifted in accord with climate change predictions (see Methods) ($P < 0.1 \times 10^{-12}$; Table 2). New species have colonized previously 'cool' regions, including sea anemones in Monterey Bay[34] and lichens and butterflies in Europe[17,36], whereas some Arctic species have contracted in range size[35,37]. Over the past 40 years, maximum range shifts vary from 200 km (butterflies[17]) to 1,000 km (marine copepods[34]).

Probabilistic coherence

How strong is the climate change signal in the light of confounding factors and lack of experimentation? We investigate this argument in a probabilistic context. We formulated a probabilistic model to ask whether a climate change fingerprint exists in a disparate set of n observed biological changes. Let n'/n indicate the proportion of observations counter to climate change predictions and p indicate the probability that climate change is the only possible causal agent of the observed biological change in any of the $n - n'$ species that do conform to climate change predictions. In practice, this can be estimated across a set of species by assigning each species a 0 or a 1, depending on whether or not competing explanations exist; p then is the proportion of species that have no competing explanations.

Competing (non-climatic) explanations can, therefore, be expected in $\{(1 - p)(n - n')\}$ of the reported analyses. Finally, for any of the $n - n'$ climate-conforming species, let π indicate the probability, determined from previous empirical study, that climate change is the principal causal agent of a particular biological change (independent of p).

These three variables, each varying from 0 to 1, are inputs to a binomial probability model whose output estimates the proportion of all species that are, in truth, being impacted by climate change. In practice, confounding factors can never be eliminated completely from observational studies; therefore, p would normally have a low value. Here, we consider only the conservative case where $p = 0$; that is, we assume that non-climatic alternative explanations exist for every species. In the Supplementary Information, we present modelling schemes where p varies from 0 to 1.0.

The importance of non-climatic explanations should decrease with increasing scale. Most local changes are idiosyncratic and consist of noise when scaled up; however, atmospheric carbon dioxide levels have risen nearly uniformly across the globe. Increased CO_2 can directly cause earlier flowering[38], as does increased temperature, making these effects difficult to separate. However, these two effects can be viewed as different aspects of global warming, legitimizing discussion of their joint impacts.

The variable π reflects the extent to which previous study and experimentation provides clear mechanistic understanding of the links between climate variables and a species' behaviour and ecology. To understand the importance of π, consider the case of the silver-spotted skipper butterfly (*Hesperia comma*) that has expanded its distribution close to its northern boundary in England over the past 20 years. Possible ecological explanations for this expansion are regional warming and changes in land use. Comparing the magnitudes and directions of these two factors suggests that climate change is more likely than land-use change to be the cause of expansion[29]. Deeper support was provided by previous empirical studies documenting strong thermal limitation. At the northern boundary, development of offspring was restricted to the hottest microclimates (south-facing chalk slopes). Range expansion coincided with colonization of non-southern slopes. Simulation models based solely on previously measured thermal tolerances (that is, without land-use change) closely matched the observed expansion of 16.4 km (model prediction 14.4 km)[12]. Thus, mechanistic understanding of the system generates a high estimate for π.

Figure 1 shows relationships between the n'/n proportions and the minimum value of π that would be required to sustain different degrees of confidence for $p = 0$. For example, the medium confidence region shows minimum values of π that would be required across the displayed range of n'/n proportions to guarantee that about half of the observed species impacts were in truth being driven principally by climate change. Claiming a climate fingerprint with high confidence would require high minimum values for π (>0.67) regardless of n'/n.

Applying the probabilistic model

Using all of the data from Table 2 to parameterize the model, $n' = 147$ and $n = 770$, making $n'/n = 0.16$ (16% of species changing opposite to climate change predictions). We now consider π. The extent to which climate change can be isolated as the predominant driving force is extremely variable among species and systems. Such attribution results from a subjective synthesis of experimental and observational research, often conducted well before and independently of any study of long-term trends. The species for which π is high are those with a history of basic biological research, especially where research has been conducted along several axes (controlled laboratory/greenhouse experiments, field manipulations and observations).

Table 2 **Summary statistics and synthetic analyses derived from Table 1**

Type of change	Changed as predicted	Changed opposite to prediction	*P*-value
Phenological ($N = 484/(678)$)	87% ($n = 423$)	13% ($n = 61$)	$<0.1 \times 10^{-12}$
Distributional changes			
At poleward/upper range boundaries	81%	19%	–
At equatorial/lower range boundaries	75%	25%	–
Community (abundance) changes			
Cold-adapted species	74%	26%	–
Warm-adapted species	91%	9%	–
$N = 460/(920)$	81% ($n = 372$)	19% ($n = 88$)	$<0.1 \times 10^{-12}$
Meta-analyses			
Range-boundaries ($N = 99$)	6.1 km m^{-1} per decade northward/upward shift*		0.013
Phenologies ($N = 172$)	2.3 days per decade advancement*		<0.05

Data points represent species, functional groups or biogeographic groups. *N*, number of statistically or biologically significant changes/(total number species with data reported for boundary, timing, or abundance processes). The no prediction category is not included here.
*Bootstrap 95% confidence limits for mean range boundary change are 1.26, 10.87; for mean phenological shift the limits are −1.74, −3.23.

This sort of biological detail reveals that climate and extreme weather events are mechanistically linked to body size, individual fitness and population dynamics for diverse species[3–9] (but not for all). Species for which confidence in climate as the primary driving mechanism is low are those for which long-term observational records exist, but not detailed empirical research on target species or on ecologically similar species. The black line in Fig. 1 suggests that medium confidence can be claimed for $n'/n = 0.16$ if $0.35 < \pi < 0.7$. Other contingencies, such as complications from a positive publishing bias or non-independence among confounding factors, can be considered through variations of the model (see Supplementary Information).

Differentiating diagnostic patterns

Predictions of the impacts of climate change are not unidirectional, but may show opposite trends within communities and across long time spans or large spatial scales. Alternative causal agents would therefore have to be able to switch the sign of their impacts within a study if they were to form credible competing explanations. Such differentiating patterns greatly reduce the likelihood of hidden, non-climate competing explanations, thereby increasing P and decreasing the value of π necessary to achieve a given confidence level (see Supplementary Information). High confidence could be obtained under this scheme with existing patterns ($n'/n \leq 0.33$) and poor mechanistic understanding (low π). Sufficient data to quantify the differential impacts on species' distributions or phenologies across time periods or geographic regions were available for 334 species, among which 84% showed a sign-switching diagnostic of climate change response ($P < 0.1 \times 10^{-12}$; Table 3).

Community representation sign switching

Community studies in regions of overlapping 'polar' and 'temperate' species base their climate change attribution on differential responses of these two categories. Among marine fish and intertidal invertebrates (for example, snails, barnacles, anemones, copepods and limpets) off the Californian coast[34,39] and in the North Atlantic[35,40], lichens in the Netherlands[36], foxes in Canada[37] and birds in Great Britain[16], polar species have tended to be stable or decline in abundance, whereas temperate species at the same site have increased in abundance and/or expanded their distributions. Analogous shifts are occurring even within the Arctic and Antarctic among penguins[8], woody plants[41] and vascular plants[42]. Similar patterns exist for lowland compared with highland birds in the tropics[43]. Most of these studies are local, with high variability of individual species' population dynamics. Even so, 80% of changes in community representation are in accord with climate change predictions (Tables 2 and 3).

Temporal sign switching

Long-term studies encompass periods of climate cooling as well as warming. If the distributions of species are truly driven by climate trends, these species should show opposite responses to cooling and warming periods. Such sign switching has been documented in the United Kingdom for marine fish, limpets, barnacles and zooplankton[40], in the United Kingdom and Estonia for birds[20,31,44,45], and in the United Kingdom, Finland and Sweden for butterflies[17,46–48] (see also Table 3 legend). A typical pattern includes northward range shifts during the two twentieth-century warming periods (1930–45 and 1975–99), and southward shifts during the intervening cooling period (1950–70). No species showed opposing temporal trends (Table 3).

Spatial sign switching

Whole-range, continental-scale studies, by encompassing the extremes of a species' distribution, allow testing for differential spatial impacts. In North America and Europe, detailed temporal data spanning the twentieth century were compiled for 36 butterfly species at both northern and southern range extremes[17,49]. Eight species (22%) exhibited a diagnostic pattern of northward expansion (new colonizations) and southern contraction (population extinctions). No species showed opposing range shift trends (northward contraction and southward expansion) (Table 3).

Discussion

The logic of a global focus on biological change is analogous to that for climate change itself. With climate change, attribution of recent warming trends to changes in atmospheric gases comes from analysis of global patterns, not from detailed data from individual meteorological stations. Similarly, when assessing biological

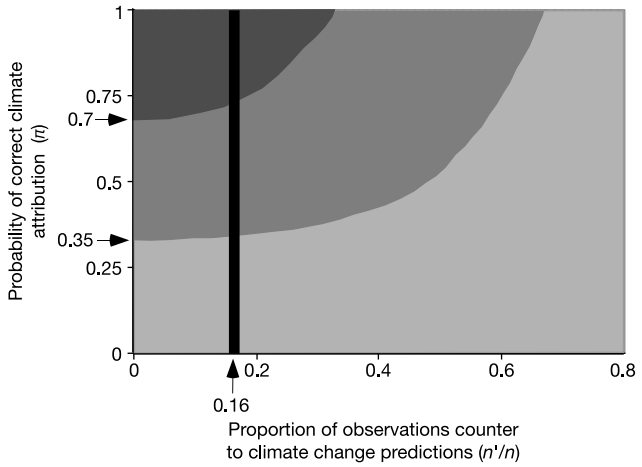

Figure 1 Probabilistic model based on parameter estimates from a review of the literature. Levels of confidence in the linkage of biological changes to global climate change are: high (dark grey), medium (mid-grey) and low (light grey). Confidence regions assume $p = 0$ (competing explanations exist for all studies). The black line indicates the region of confidence possible using the probabilistic model on the basis of the parameter estimate of n'/n from the literature review, and allowing π to vary freely.

Table 3 **Biological fingerprint of climate change impacts**

Sign-switching pattern	Percentage of species showing diagnostic pattern
Community	
Abundance changes have gone in opposite directions for cold-adapted compared with warm-adapted species. Usually local, but many species in each category. Diverse taxa, $n = 282$*.	80%
Temporal	
Advancement of timing of northward expansion in warm decades (1930s/40s and 1980s/90s); delay of timing or southward contraction in cool decades (1950s/60s), 30–132 years per species. Diverse taxa, $n = 44$*.	100%
Spatial	
Species exhibit different responses at extremes of range boundary during a particular climate phase. Data are from substantial parts of both northern and southern range boundaries for each species. All species are northern hemisphere butterflies, $n = 8$*.	100%

Differential sign-switching patterns diagnostic of climate change as the underlying driver.
*Numbers of species represent minimum estimates, as not all species were described in sufficient detail in each study to classify. A few species showed two types of sign switching, and so are included in more than one cell. Data are from references in text and from raw data provided by L. Kaila, J. Kullberg, J. J. Lennon, N. Ryrholm, C. D. Thomas, J. A. Thomas and M. Warren.

impacts, the global pattern of change is far more important than any individual study.

The approach of biologists selects study systems to minimize confounding factors and deduces a strong climate signal both from systematic trends across studies and from empirically derived links between climate and biological systems. This deduction is made even if climate explains only a small part of the observed biological change. The meta-analyses of 334 species and the global analyses of 1,570 species (or functional/biogeographic groups) show highly significant, nonrandom patterns of change in accord with observed climate warming in the twentieth century, indicating a very high confidence (>95%) in a global climate change fingerprint (Table 2).

The approach of economists takes a broader view. In its purest form, applied to all existing data and incorporating time discounting, this approach would conclude that climate change has little total impact on wild species. We argue that this approach misses biologically important phenomena. Here we hybridize the two approaches by applying an economists' model to data that biologists would consider reasonable, and forego time discounting. A total of 74–91% of species that have changed have done so in accord with climate change predictions (Table 2) giving an estimate of $n'/n = 0.16$ for the hybrid model. Assessment of π, the probability of correct attribution to climate, is subjective and relies on the level of confidence in inferential evidence. Such evidence comes from empirical analyses and experimental manipulations, which have documented the importance of climatic variables to the dynamics, distributions and behaviour of species[3,5,8,9]. From these studies, biologists infer that expected values of π are often high. We show that moderate values of π (0.35–0.70) are consistent with medium confidence in a global climate change fingerprint.

The different approaches raise two distinct questions of the data and result in different levels of confidence in a climate change fingerprint. The questions are: (1) whether climate change can be shown to be an over-riding factor currently driving natural systems; and (2) whether there is sufficient evidence to implicate climate change as a common force impacting natural systems on a global scale. In an absolute sense, land-use change has probably been a stronger driver of twentieth century changes in wild plants and animals than has climate change (question 1). From a biological view, however, finding any significant climate signal amidst noisy biological data is unexpected in the absence of real climate drivers (question 2). Such small, persistent forces are inherently important in that they can alter species interactions, de-stabilize communities and drive major biome shifts.

A review of the literature reveals that the patterns that are being documented in natural systems are surprisingly simple, despite the real and potential complexity of biotic change. Change in any individual species, taxon or geographic region may have a number of possible explanations, but the overall effects of most confounding factors decline with increasing numbers of species/systems studied. Similarly, uncertainty in climate attribution for any particular study does not prevent the development of a global conclusion on the basis of a cumulative synthesis. In particular, a clear pattern emerges of temporal and spatial sign switches in biotic trends uniquely predicted as responses to climate change. With 279 species (84%) showing predicted sign switches, this diagnostic indicator increases confidence in a climate change fingerprint from either viewpoint.

The published IPCC conclusion stated high confidence ($P > 0.67$) in a climate signal across observed biotic and abiotic changes. Analyses presented here support that conclusion. Furthermore, a driver of small magnitude but consistent impact is important in that it systematically affects century-scale biological trajectories and ultimately the persistence of species. The climate fingerprint found here implicates climate change as an important driving force on natural systems. □

Methods

Climate change predictions

Expected phenological shifts for regions experiencing warming trends are for earlier spring events (for example, migrant arrival times, peak flight date, budburst, nesting, egg-laying, and flowering) and for later autumn events (for example, leaf fall, migrant departure times, and hibernation)[50,51]. Response to climate warming predicts a preponderance of polward/upward shifts[50,51]. Dynamics at the range boundaries are expected to be more influenced by climate than are dynamics within the interior of a species range. Thus, community level studies of abundance changes are used best to infer range shifts when they are located at ecotones involving species having fundamentally different geographic ranges: higher compared with lower latitudes, or upper compared with lower altitudes. Response to climate warming predicts that southerly species should outperform northerly species at the same site[50,51].

Selection of studies for review

This was not an exhaustive review. The studies listed in Table 1 comprise the bulk of wild species studied with respect to climate change hypotheses. Selection of papers was aimed at those with one or more of the following attributes: long temporal span (>20 years), data covering a large geographic region, and/or data gathered in an unbiased manner for a multi-species assemblage (typically species abundance data of locally well-documented communities). We excluded several high-quality studies of single species performed at local scale or highly confounded by non-climatic global change factors. The stable category represents species for which any observed changes are indistinguishable from year to year fluctuations, either from a statistical test for trend using very long time series data or from comparing net long-term movement to expected yearly variation on the basis of basic biological knowledge of dispersal/colonization abilities.

Meta-analyses

To create databases, studies were combined that made similar types of measurements and that reported quantitative estimates of change over a specified time period. All species were used; that is, even species that are categorized as stable in Table 1 were included in the meta-analysis. We treated phenological and distributional changes separately. To minimize positive publishing bias, only multi-species studies were included.

We considered each species as an independent data point, rather than each study. Only data reported in terms of change per individual species were included. This precluded use of studies that only report mean change across a set of species.

We used only distributional studies at range boundaries. We excluded equatorial and lower elevational boundaries because of a paucity of data combined with theoretical reasons for treating these boundaries separately from poleward/upper elevational boundaries[52]. Three studies met the criteria for data detail, covering 9 alpine herbs[18,19], 59 birds[16] and 31 butterflies[17]. The geographic locations of these boundaries were non-overlapping, reducing the likelihood of correlated confounding variables. Altitude was converted to latitudinal equivalent (for temperature clines, 1 km northward = 1 m upward). The United Kingdom bird data compared mean northern boundary in 1999 to that in 1972 using the ten northernmost occupied grid cells (on 10 km^2 grids) from published atlases. The Swedish butterfly data compared mean northern boundary in the period 1971–97 to mean northern boundary in 1900–20 using the five northernmost records per year. The Swiss herb data showed changes in species assemblages over the twentieth century in fixed plots up altitudinal gradients on 26 mountains.

The effect size per species was the absolute magnitude of range boundary shift, standardized across species to be in units of km m^{-1} per decade, with northward/upslope shifts positive and southward/downslope shifts negative. Data were not skewed, and n was large. Therefore, a one-sample t-test was used to evaluate the null hypothesis of no overall trends (that is, $H_ø$: mean boundary change across all species is zero). Variances were not available for all species, so we used an unweighted analysis. We performed an additional bootstrap analysis of 95% confidence limits on the mean boundary shift (10,000 iterations)[53].

The phenological meta-analysis was on spring timing events—there were insufficient studies on autumn phenology to warrant analysis. Nine studies published magnitudes of shift over a given time period (17–61 years). They included 11 trees[20,23–25], 6 shrubs[20,21,23–25], 85 herbs[20–23], 35 butterflies[26], 21 birds[21], 12 amphibians[27,28] and 2 fish[20]. This data set was inappropriate for the t-test owing to skew, but bootstrapped confidence limits provided an estimate of the probability that the true mean shift includes zero.

For both analyses, geography and taxa are confounded. For the range boundary analysis, all bird data are from the United Kingdom, all butterfly data from Sweden, and all herb data from Switzerland. For the phenological analysis, most shrub and bird data are from the United States, butterfly data from Great Britain, and trees from Europe. Therefore, it is not meaningful to split the analyses further.

Categorical analyses

Reported data from all studies listed in Tables 1 and 3 were included in the categorical analyses. The predicted direction is a change predicted by global warming scenarios[50,51]. All studies were conducted in temperate Northern Hemisphere, except for 194 species in Costa Rica[43] and 5 species in Antarctica[8,42]. Two categories showing changes either predicted by or opposite to predictions of climate change theory were tested against the random expectation of an equal probability of observing changes in either direction. Analyses were by binomial test with $H_ø$: $P = 0.5$.

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