

# Climate change and outbreaks of the geometrids *Operophtera brumata* and *Epirrita autumnata* in subarctic birch forest: evidence of a recent outbreak range expansion

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## Summary

1. Range expansions mediated by recent climate warming have been documented for many insect species, including some important forest pests. However, whether climate change also influences the eruptive dynamics of forest pest insects, and hence the ecological and economical consequences of outbreaks, is largely unresolved.

2. Using historical outbreak records covering more than a century, we document recent outbreak range expansions of two species of cyclic geometrid moth, *Operophtera brumata* Bkh. (winter moth) and *Epirrita autumnata* L. (autumnal moth), in subarctic birch forest of northern Fennoscandia. The two species differ with respect to cold tolerance, and show strikingly different patterns in their recent outbreak range expansion.

3. We show that, during the past 15–20 years, the less cold-tolerant species *O. brumata* has experienced a pronounced north-eastern expansion into areas previously dominated by *E. autumnata* outbreaks. *Epirrita autumnata*, on the other hand, has expanded the region in which it exhibits regular outbreaks into the coldest, most continental areas. Our findings support the suggestion that recent climate warming in the region is the most parsimonious explanation for the observed patterns.

4. The presence of *O. brumata* outbreaks in regions previously affected solely by *E. autumnata* outbreaks is likely to increase the effective duration of local outbreaks, and hence have profound implications for the subarctic birch forest ecosystem.

**Key-words:** forest defoliation, global warming, insect attacks, invasion, population cycles

## Introduction

Global warming is predicted to have a dramatic impact on many species (Thomas *et al.* 2004; Franco *et al.* 2006; Hickling *et al.* 2006; Thomas, Franco & Hill 2006). For insects, in particular, evidence of a response to long-term environmental trends, directly or indirectly linked to recent climate warming, is accumulating quickly (Bale *et al.* 2002). This includes northern and altitudinal shifts in geographical range (Parmesan 1996; Parmesan *et al.* 1999; Thomas *et al.* 2001; Root *et al.* 2003; Battisti *et al.* 2005; Battisti *et al.* 2006), increased number of generations for multivoltine species (Pollard & Yates 1993; Yamamura & Kiritani 1998), increased winter survival (Bale, Harrington & Clough 1988), and

prolonged diapause (Bale *et al.* 2002). For forest pest insects it is expected that general climate warming, as well as increased frequency of climatic anomalies, will affect both incidence and geographical extent and intensity of population outbreaks, with potentially severe economical and ecological consequences (Williams & Liebhold 1995; Fleming & Candau 1998; Neuvonen, Niemelä & Virtanen 1999; Tenow *et al.* 1999; Ayres & Lombardero 2000; Volney & Fleming 2000; Logan, Regniere & Powell 2003; Battisti *et al.* 2006). Despite this, few empirical studies address the issue, and advances are hampered by a scarcity of long-term spatio-temporal data. Further long-term studies, documenting the presence and severity of population outbreaks as well as range shifts towards the distributional limits of forest pest insects in the light of recent climate warming, would be immensely valuable in this regard.

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The geometrid moth species *Epirrita autumnata* L. (autumnal moth) and *Operophtera brumata* Bkh. (winter moth) exhibit cyclic outbreaks at  $\approx 10$ -year intervals, causing extensive defoliation and occasional mortality of mountain birch forests in northern Fennoscandia (Tenow 1972; Kallio & Lehtonen 1973; Haukioja *et al.* 1988; Lehtonen & Heikkinen 1995; Hogstad 1997; Ruohomäki *et al.* 2000; Klemola, Huitu & Ruohomäki 2006). Both species are widespread in Fennoscandia. According to Tenow (1972), the distribution range (defined as the geographical area where the species has been found to occur) of *E. autumnata* includes the entire northern Fennoscandia, while *O. brumata* has been found in all lowland districts in Norway, all over Sweden and in most of Finland except in the easternmost districts. The invasion of *O. brumata* into the northern districts of Norway is relatively recent (first recorded in Tromsø at 69°40' N in 1892; Schneider 1914 cited by Tenow 1972). The distribution range of both species is larger than the region experiencing regular outbreaks and consequent forest damage, which is hereafter termed the outbreak range (Tenow 1972; Neuvonen *et al.* 1999). While the distribution range is thought to be determined climatically, the combination of factors permitting population outbreaks in just some parts of the species' range is not well understood. Climatic conditions, competition, natural enemies, host phenology and forest age structure, as well as resource distribution, are likely to play a part (Berryman 1996; Ruohomäki *et al.* 1997; Ruohomäki *et al.* 2000; Niemela *et al.* 2001; Selås *et al.* 2001). Of particular recent interest is the potential effect of a warming climate: how climate warming will affect the outbreak dynamics and distribution of the outbreak range of these insects is a much-debated issue yet to be resolved (Bylund 1999; Neuvonen *et al.* 1999; Neuvonen, Bylund & Tømmervik 2005).

The two birch forest geometrids in question have very similar biology, but exhibit some distinct differences in their outbreak range, which are usually attributed to a difference in cold tolerance. *Epirrita autumnata* outbreak cycles are most prevalent in the northernmost and continental birch forests, whereas the outbreak range of the somewhat less cold-tolerant *O. brumata* (Tenow & Nilssen 1990; Bylund 1999) has been climatically restricted to more southern and near-coastal locations (Tenow 1972). Outbreaks of *E. autumnata* may be locally restricted by low temperatures (Virtanen, Neuvonen & Nikula 1998; Neuvonen *et al.* 1999). Thus, assuming that the outbreak range of *O. brumata* is strongly temperature-limited compared with *E. autumnata*, climate warming is expected to cause an extensive north-eastern expansion of *O. brumata* outbreaks into areas previously affected only by *E. autumnata* outbreaks, whereas outbreaks by *E. autumnata* are expected to occur more frequently in the most continental regions previously protected by extreme winter temperatures.

By analysing historical outbreak records for both species covering more than a century in northern Fennoscandia (Tenow 1972; Nilssen, Tenow & Bylund 2007), we here provide support for the expected north-eastern outbreak range expansion in *O. brumata*. In addition we observe an increase in the occurrence of *E. autumnata* outbreaks in the most

continental regions. We advocate that recent climate warming is the most parsimonious explanation for the observed patterns. The presence of *O. brumata* outbreaks in regions previously affected solely by *E. autumnata* is likely to increase the effective duration of local outbreaks and hence have profound implications for the moth–birch forest ecosystem.

## Materials and methods

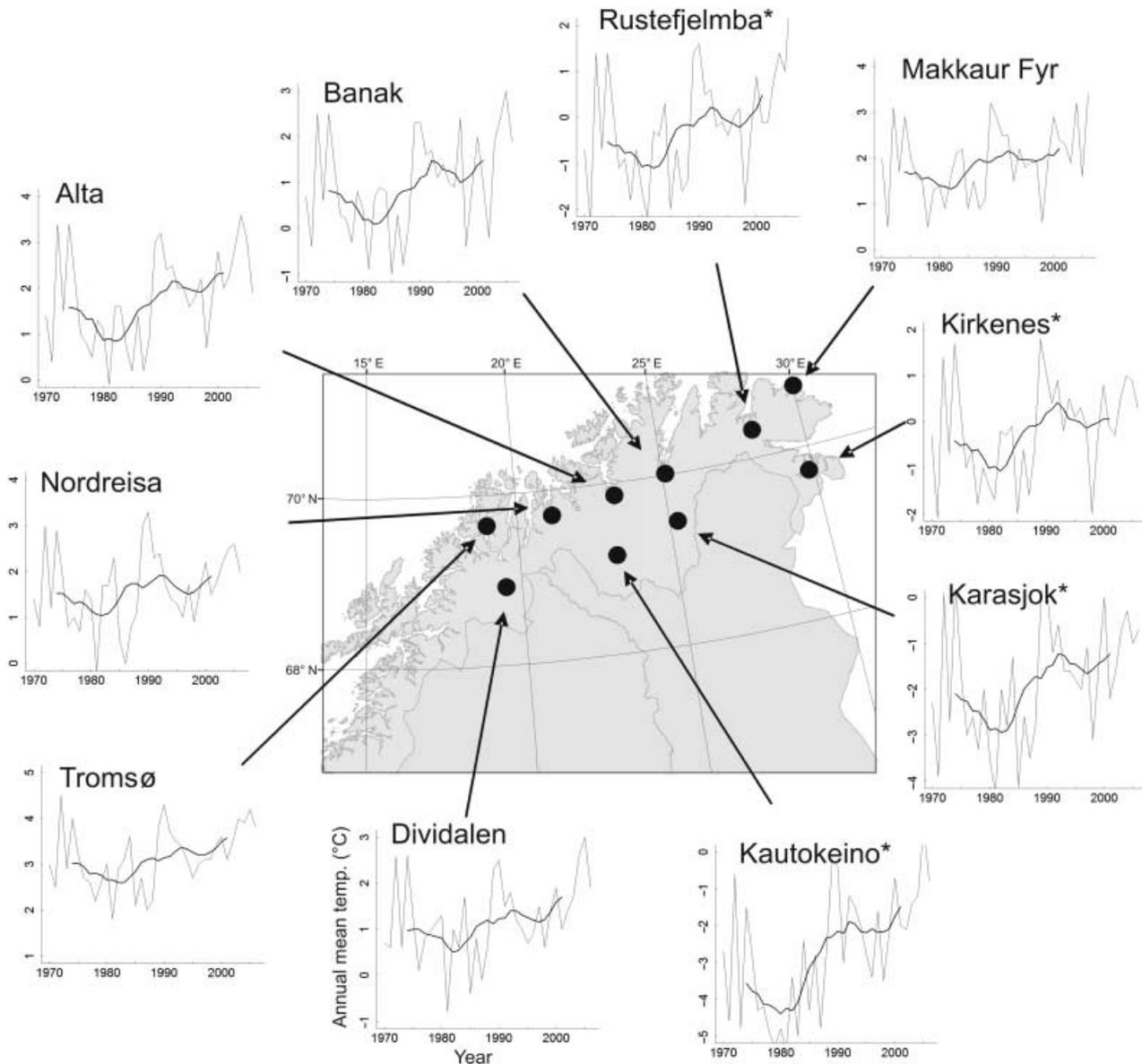
### STUDY SYSTEM

Northern Fennoscandia includes the northern parts of Norway, Sweden and Finland. For the purpose of the current study, we focused on outbreak range shifts towards the northern distribution limit. The Scandinavian mountain chain divides the region into a mild oceanic part along the western coast and a colder, more continental part to the north and east. The entire region has experienced a pronounced increase in mean annual temperatures during the past 15 years (Fig. 1). The increase is most pronounced in the northern and continental eastern parts. Only these coldest regions experience winter temperatures potentially lethal to the overwintering eggs of *E. autumnata* and *O. brumata* (approx.  $-35$  °C; Macphee 1967; Tenow & Nilssen 1990). The frequency of occurrence of extreme winter cold has decreased markedly during the same period (Fig. 2). The natural forest is dominated by pubescent and mountain birch (*Betula pubescens* Ehrh.; *Betula pubescens czerepanovii* Orlova) (Hämet-Ahti 1963) in the west and at the northern and alpine tree limit, and boreal mixed and coniferous forest to the east (parts of Finland and Sweden). Birch is the main host tree of both *O. brumata* and *E. autumnata* in the region.

### MOTH OUTBREAK DATA

To test for a (differential) expansion of the core outbreak range of the two geometrid species, we used historical records of the location of moth outbreaks in Fennoscandia originally compiled by Tenow (1972). This data set covers the period 1862–1968. Records for the period 1969–2001 are described by Tenow *et al.* (2007); Nilssen, Tenow & Bylund (2007). The historical data were compiled from various sources such as forest damage reports, national inquiries to state district forest officers, Scandinavian entomological periodicals and personal communication with researchers and foresters. A detailed description of the sources used for each country is given by Tenow (1972). We refer to Tenow *et al.* (2007); Nilssen *et al.* (2007) for a summary. The qualitative nature of the historical documentation does not allow any gradation of outbreak severity. Nevertheless, it is safe to assume that for outbreaks to be noted and reported, they will have been sufficiently severe to cause conspicuous forest damage and/or mass occurrences of swarming adults. As the Tenow data are updated only until 2001, and new occurrences of *O. brumata* outbreaks have been documented further east since then, we included two additional records in the *O. brumata* data set. These two locations represent the easternmost and northernmost confirmed outbreak in 2006 (County Governor of Finnmark; authors' observations).

Recent records of outbreak locations (1969 onwards) are referenced by map coordinates, while older records (1861–1968) are described by place name only. To obtain coordinates for the older records, place names were located on detailed maps and the specificity of the place name was evaluated. Based on this specificity, locations were grouped according to their presumed accuracy. For instance, a very



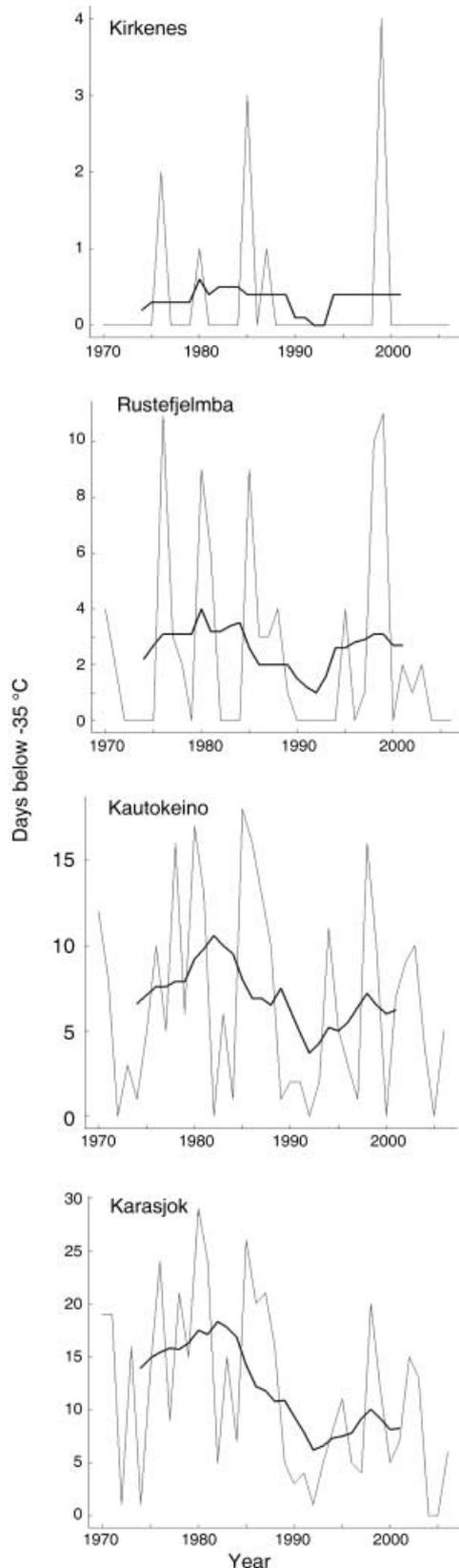
**Fig. 1.** Annual mean temperatures (°C) for the period 1970–2006 for climate stations throughout northern Norway. Bold lines, centred 10-year running averages. The four climate stations marked with an asterisk experience winter temperatures below  $-35^{\circ}\text{C}$  (Fig. 2). Source: Norwegian Meteorological Institute, [www.met.no](http://www.met.no).

specific place name such as a small island or valley was assigned to a high-accuracy group, while a large or poorly defined region was assigned to a low-accuracy group. The least specific records, with accuracy estimates more than  $\pm 50$  km, were omitted from the analysis. As we were interested in changes occurring at the northern outbreak range of the species, we included only those records located north of the Arctic Circle (*O. brumata* 116 records; *E. autumnata* 312 records).

#### DATA ANALYSIS

To analyse the change in northern and eastern outbreak range borders over time, we extracted the year an outbreak was first recorded on each locality. Classical linear models focusing on the mean values of latitude (northward expansion) or longitude (eastward expansion) are unlikely to be sensitive to change in range borders. On the other

hand, extreme values (largest latitude or longitude) are too sensitive to outliers. We used quantile regression models (Koenker & Bassett 1978; Cade & Noon 2003) that directly relate specific quantiles of the cumulative distribution function to covariates (here, years). A reasonable compromise between robustness and sensitivity to changes is obtained by using the 0.10 and 0.90 quantiles: the values delimiting the lower 10% and higher 90% of the spatial distribution of outbreak observations. We also estimated changes in the median (0.50 quantile) to assess any shift in the overall distribution. We used both latitude and longitude quantiles, as the geography of northern Fennoscandia favoured these two directions. Quantile regression was carried out using the *Quantreg* library for R (R Development Core Team 2005; Koenker 2006). The statistical procedure is based on a simplex procedure described by Koenker & d'Orey (1987). We used nonparametric paired bootstrapping to estimate robust standard errors of regression coefficients (Koenker 2006).



**Fig. 2.** Number of days with temperatures below  $-35^{\circ}\text{C}$  for the period 1970–2006 for the four coldest climate stations. Compare with Fig. 1 for geographical locations. Temperatures below approx.  $-35^{\circ}\text{C}$  are lethal to the overwintering eggs of both *Epirrita autumnata* and *Operophtera brumata*.

**Table 1.** Quantile regression coefficients and confidence intervals (in parentheses) for the regression lines shown in Fig. 2

Species	Quantile	Longitude/east	Latitude/north
<i>Operophtera brumata</i>	90	0.091 (0.090; 0.095)	0.010 (0.008; 0.016)
	50	0.057 (0.033; 0.086)	0.012 (0.002; 0.016)
	10	0.038 (0.017; 0.046)	0.001 (-0.005; 0.020)
<i>Epirrita autumnata</i>	90	0.061 (0.055; 0.069)	0.004 (0.003; 0.007)
	50	0.016 (-0.014; 0.043)	-0.006 (-0.010; -0.0004)
	10	-0.019 (-0.023; 0.010)	0.002 (0.001; 0.006)

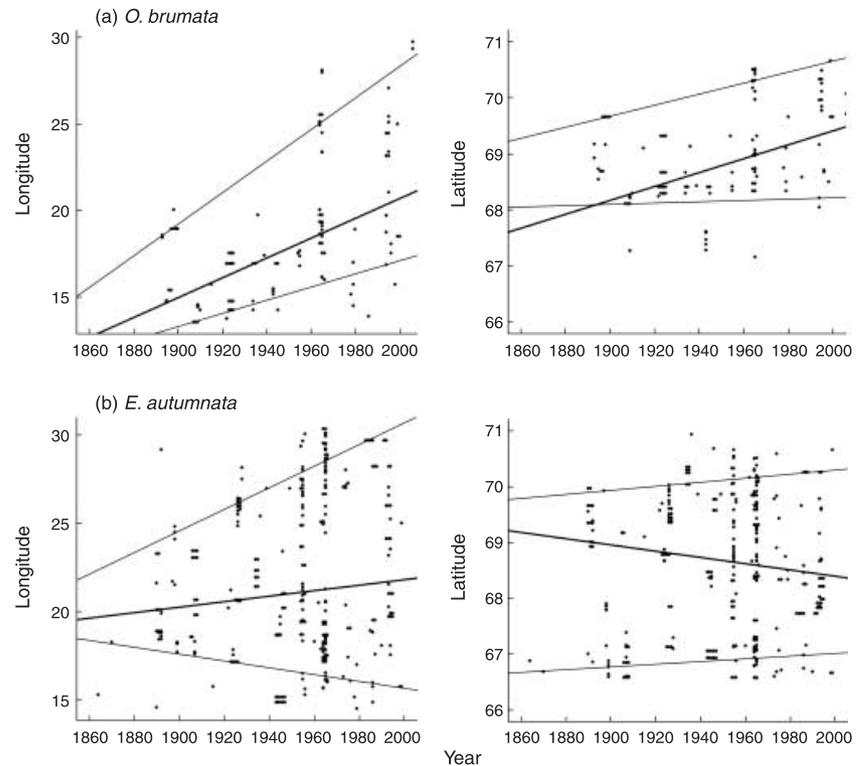
The spatial and temporal changes in outbreak distribution pattern of the two geometrid species were visualized through contour plots tracking the year an outbreak of each species was first recorded for a given locality. Based on the original records indicating the year of the first recorded outbreak at each locality, we interpolated a continuous surface using natural neighbour interpolation (Sibson 1981). Contour lines for the natural neighbour surface were extracted at 10-year intervals. Surface interpolation and contour lines were calculated using ARCGIS 3D-ANALYST (ESRI Inc., Redlands, CA, USA).

## Results

Our results clearly support the hypothesis that *O. brumata* has experienced a strong northward and eastward expansion of the core outbreak area, while *E. autumnata* outbreaks appears to have expanded into colder, more continental regions. Most noticeably, this has happened during the past 15 years. A pronounced increase in both mean annual and minimum winter temperatures has occurred during the same period, in particular in the continental parts of Fennoscandia (Figs 1 and 2).

Quantile regression of the year an outbreak was first recorded against latitude and longitude (Table 1; Fig. 3) for each species show a greater rate of change (higher regression coefficient) in eastern and northern range over time in *O. brumata* than in *E. autumnata*. The fact that 0.90 quantiles tend to be steeper than 0.10 quantiles, in particular in an easterly direction, indicates that changes have been most pronounced at the eastern range border. The non-significant eastern 0.50 quantile for *E. autumnata* shows that no directed eastern expansion has occurred, while the significant negative slope of the northern 0.50 quantile actually points to a recent southern expansion of *E. autumnata* (northern coast to inland).

Contour plots reveal two strikingly different patterns of outbreak occurrence in *O. brumata* and *E. autumnata*, respectively (Fig. 4), and support the results of the quantile regression. Outbreaks of *O. brumata* show a gradual northern and particular eastern advance (20–70 km between the 1990 and 2000 contour lines). In contrast, *E. autumnata* outbreaks have spread from both the north-western Atlantic coast and the south-east into the coldest continental regions.



**Fig. 3.** Quantile regression plots of the year an outbreak was first recorded against longitude and latitude (representing an eastern and northern expansion, respectively). Bold lines, median (0.50 quantile); thin lines, 0.90 (upper) and 0.10 (lower) quantiles.

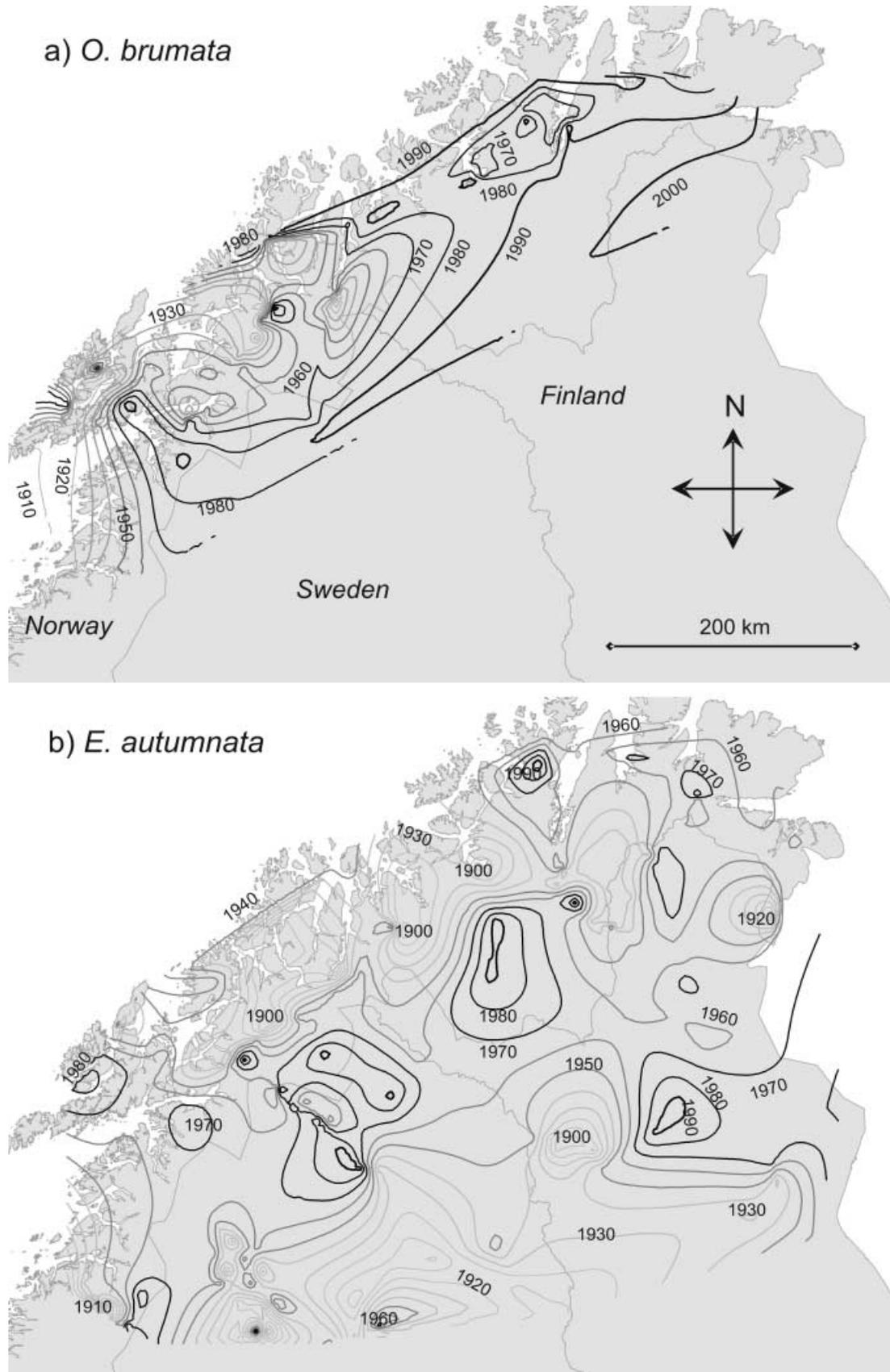
## Discussion

Climate warming is predicted to cause distributional changes for insects with a temperature-limited geographical range (Bale *et al.* 2002). This includes many species in temperate and northern regions (Parmesan 1996; Parmesan *et al.* 1999; Bale *et al.* 2002; Battisti *et al.* 2005; Battisti *et al.* 2006). While examples of climate-related range expansions are currently numerous, studies showing that outbreaks of native species expand into new regions within their general distribution range are very rare (Williams & Liebhold 1995). Tenow (1996) noted that the occurrence of *E. autumnata* outbreaks in previously unaffected areas of Finnmark in 1993–94 followed a sequence of unusually warm years in 1987–94 (Fig. 1). In the case of cyclic geometrid moth species in subarctic birch forest, large-scale analyses relating climate conditions to the spatial patterning of outbreaks are virtually absent.

Our study demonstrates a likely major role of regional climatic trends in large-scale outbreak dynamics in the geometrid–mountain birch system. Our most important finding is a clear difference in the pattern of outbreak range expansion experienced during recent warmer years in Fennoscandia by *O. brumata* as opposed to *E. autumnata*. Specifically, we found that *O. brumata* has experienced a clear eastern, and to a lesser degree northern, advance in outbreak range, whereas new outbreaks of *E. autumnata* have begun to occur even in the coldest, most continental regions. This is precisely according to expectations if the outbreak range of *O. brumata* historically has been relatively more temperature-limited than that of *E. autumnata*.

Judging from historical records, the advance of *O. brumata* outbreaks into the north-eastern region of Fennoscandia has occurred gradually, with a few records during an extensive outbreak in the mid-1960s, an increasing number during the 1990s, and finally a pronounced eastern advance along the northern forest limit in northernmost Norway during the past 5–6 years. This strongly suggests an expansion of the area experiencing regular outbreak cycles permitted by a gradual increase in temperature, rather than some occasional outbreaks beyond the core outbreak range.

A direct causal link between climate and alterations in species ranges is not easily established. Thus the relationship between even the most well documented range expansions or retractions and climate change is often more-or-less implied (Parmesan *et al.* 1999; Parmesan & Yohe 2003; Hickling *et al.* 2006). In the present case, the coarseness of the historical documentation limits the options for more rigorous spatio-temporal analysis of outbreak dynamics vs. climatic trends. Still, we consider the pronounced increase in both mean annual and minimum winter temperatures the most parsimonious explanation for the observed change in outbreak distribution by *O. brumata* and *E. autumnata*. Both species suffer substantial egg mortality below approx.  $-35^{\circ}\text{C}$ , but the freezing point of *E. autumnata* eggs is a few degrees lower than that found in *O. brumata* (Macphee 1967; Tenow *et al.* 1990). Thus it is likely that *O. brumata* historically has been more temperature-restricted than *E. autumnata*. In response to warmer temperatures, *O. brumata* is able to expand its core outbreak area further north-east, while *E. autumnata*, already reaching outbreak densities in the far north-east, expands further into



**Fig. 4.** Contour plots tracking the year an outbreak was first recorded for each of the two species, *Epirrita autumnata* and *Operophtera brumata*, in northern Fennoscandia.

colder, more continental regions previously protected by extreme winter temperatures. Even the coldest region (Karasjok) has recently experienced winters with no days below  $-35^{\circ}\text{C}$  (Fig. 2, 2004–05).

A difference in cold tolerance is the proposed explanation for the historical absence of *O. brumata* outbreaks in more continental and northern locations (Tenow 1972; Bylund 1999). Additionally, several earlier studies (Hågvar 1972; Tenow 1972) have documented an altitudinal zonation of the two species within their sympatric outbreak region, with *E. autumnata* dominating close to the tree line and *O. brumata* at lower altitudes. Hagen *et al.* (2007) recently showed that extensive outbreaks by *O. brumata* now occur at, or very close to, the tree line, suggesting a simultaneous altitudinal expansion of the outbreak region of *O. brumata*. This recent altitudinal expansion of *O. brumata*, taking place in coastal birch forest characterized by mild winters, cannot be related to egg cold-tolerance. Therefore other climate-sensitive attributes of the ecology of *O. brumata* are likely to be involved. A recent (1993–94) outbreak by *Argyresthia retinella* in north-western Norway was similarly attributed to an increase in temperature (Tenow *et al.* 1999).

The result of the outbreak range expansion in *O. brumata* is a significant increase in the area where the two species exhibit sympatric outbreaks. The implications of this for moth–birch forest dynamics in northern Fennoscandia are likely to be substantial. Of particular concern is how the increase in *O. brumata* outbreaks, with peaks often lagging 1–2 years after *E. autumnata* (Hogstad 1997; Tenow *et al.* 2007), may extend the effective length of outbreaks and, consequently, the defoliation damage afflicted on the mountain birch forest. Defoliation by moths adversely affects the growth of host trees for several years following an outbreak (Tikkanen & Roininen 2001; Karlsson *et al.* 2004), and prolonged outbreaks are known to cause forest death over large areas (Tenow 1972; Kallio & Lehtonen 1973; Lehtonen & Heikkinen 1995; Tenow & Bylund 2000). This concern is justified by the current situation at the north-eastern limit of the *O. brumata* outbreak range in Norway, where certain regions have suffered 5–6 consecutive years of outbreaks, initially by *E. autumnata* and currently by *O. brumata*. Clearly the present situation in northern Fennoscandia warrants intensified research to document further spread of the outbreak range of *O. brumata*, its mechanistic relation to climatic variables and the sympatric population of *E. autumnata*, as well as the implications in terms of the fate of the subarctic birch forest ecosystem (Tenow 1996).

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