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Geometrid moth outbreaks and their climatic relations in northern Sweden

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Abstract

The alpine treeline in northern Fennoscandia is composed primarily of mountain birch (*Betula pubescens* ssp. *czerepanovii*), a deciduous tree that experiences episodic defoliation due to outbreaks of the autumnal moth (*Epirrita autumnata*) and winter moth (*Operophtera brumata*). Here, we use an extensive dendroecological data set to reconstruct historic defoliating outbreaks and relate them to climatic conditions. Our data are from 25 sites in eight valleys in northern Sweden. We used the computer program OUTBREAK to reconstruct moth outbreaks. The reconstructed outbreak record matches the historical record well. There is a significant, but weak relationship between the outbreak severity and temperatures in February, April, July, and August of the outbreak year. Temperatures in the previous May and November were also positively correlated with outbreak severity. For seasonally aggregated temperatures, only autumn temperatures are correlated with outbreak severity. There was no significant correlation between NAO index and outbreak severity. A spatiotemporal semivariogram analysis showed that sites within approximately 100 km of each other show similar patterns in outbreak severity. Our analyses suggest that moths are affected by climatic variations. The influence of climate on outbreaks is weak because background climatic conditions alone cannot induce an outbreak. Outbreaks also depend on nonclimatic factors, such as tree age, and the outbreak status of neighboring areas.

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Introduction

The high-elevation forests in the Scandes Mountains of northern Fennoscandia are composed almost entirely of mountain birch [*Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti]. Every 9 to 10 years, outbreaks of autumnal moth [*Epirrita autumnata* (Borkhausen)] and winter moths (*Operophtera brumata*) affect these stands, defoliating large swaths of the forest and killing many of the trees (Tenow et al., 2005; Babst et al., 2010). Autumnal moths are commonly found in continental climates and winter moths are found more in maritime climates; however, recently the winter moth has expanded into more continental areas (Tenow, 1972; Jepsen et al., 2008; Klemola et al., 2008; Ammunet et al., 2010). Outbreaks of winter moths typically occur 1–2 years after those of the autumnal moth (Tenow, 1972). Both of these disturbances induce stand regeneration, and thereby influence stand age structure and landscape patchiness (Tenow et al., 2005). They potentially help configure the alpine treeline as well (Nuorteva, 1963).

Climatic variations may contribute to moth outbreaks, though how climate contributes is not clear (Tenow et al., 2013). A number of studies have found that outbreaks occur after warm winters and cool springs and summer (Nilssen and Tenow, 1990; Neuvonen et al., 1999; Niemela et al., 2001; Nilssen et al., 2007; Yang et al., 2007). Warm winters reduce egg mortality, allowing for a large spring population density (Nilssen and Tenow, 1990; Ruohomaki et al., 1997; Neuvonen et al., 1999). Low spring and summer temperatures facilitate moths indirectly by a decrease in parasitoid and predator activity (Neuvonen et al., 1999; Virtanen and Neuvonen, 1999). However, Klemola et al. (2003) discovered a positive influence of summer temperatures on moth populations, an unexpected result that contrasts with the previous studies; the researchers were unable to provide an explanation for this result. Klemola et al. also found a positive relationship with winter temperatures, which they attributed to reduced egg mortality during warm winters.

These previous studies are limited to time periods of 1 to 5 years because they depend on sampling moth populations. Their spatial extent is also restricted, to areas of a single valley (e.g., Virtanen and Neuvonen, 1999; Yang et al., 2007). In this study, we use a dendroecological approach to detect moth outbreaks across a network of sites in northern Sweden and then investigate their climatic relationships. Tree rings record forest disturbances such as fires (Swetnam et al., 1999; Pohl et al., 2006; Margolis et al., 2007; Aldrich et al., 2010), wind throws (Frelich and Lorimer, 1991), ice storms (Lafon and Speer, 2002), and herbivory (Brubaker, 1978; Payette, 1986; Swetnam and Lynch, 1989; McLaren and Peterson, 1994; Boudreau et al., 2003). Networks of tree-ring chronologies across a landscape can be used to detect historic insect outbreaks and place recent outbreaks into a historical context. Tree rings permit a longer record of moth outbreaks than is available through the short-term population monitoring used in previous studies of moth-climate relations in Fennoscandia. Tree rings do not record moth populations, of course, but, rather, the occurrence of moth outbreaks. It is the outbreaks that are of primary interest in understanding birch forest dynamics. Because of the length of the tree-ring chronology, we can identify several outbreaks that allow us to analyze outbreak-climate relationships at the valley and regional scale.

We consider four hypotheses. First, because the balance of evidence indicates that a positive relationship should exist between

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winter temperatures and moth outbreaks, we hypothesize that this same relationship will hold at the broader, yet still local, spatial scale of a single valley within northern Sweden. Second, we examine the relationship of outbreaks with spring and summer temperatures, although expectations are unclear because of the conflicting results found in previous studies. We will test the hypothesis that lower spring and summer temperatures produce greater outbreak severity possibly due to larval parasitism (Neuvonen et al., 1999; Virtanen and Neuvonen, 1999). Third, we hypothesize that region-scale relationships between moth outbreaks and climate resemble the relationships found at the single-valley scale. Ecological synchrony at broad spatial scales is a distinguishing signature of climatic effects on ecosystems (Swetnam et al., 1999). Global phenomena such as the North Atlantic Oscillation (NAO) have been shown to predict several insect pest populations in the northern hemisphere (Klemola et al., 2003; Westgarth-Smith et al., 2007; Lima et al., 2008; Aluja et al., 2012; Ducic et al., 2012; Hodar et al., 2012). Because the NAO exerts a positive influence on temperature and precipitation across northern Sweden (Hurrell, 1995) and has been used as an index of winter temperature in previous research on geometrid moth populations (Klemola et al., 2003), we look for relationships between outbreak severity and NAO to evaluate our third hypothesis. Our fourth hypothesis is that spatial synchrony should be evident at relatively local spatial scales, but not over the whole region. Although climate can impose regionwide synchrony of disturbance events, animal populations are known to exhibit asynchronous population fluctuations (Shaw et al., 2010) and traveling waves (Palacio et al., 2008) at broad scales because of biotic mechanisms intrinsic to the populations (Beck et al., 2011). These kinds of spatial dynamics have been illustrated for a wide variety of taxa, including both mammals (Coop and Givnish, 2008; Palacio et al., 2008; Shaw et al., 2010) and insects (Price et al., 2006; Loffler et al., 2011). Insect populations have been shown to exhibit different patterns of spatial synchrony at different scales. For example, synchrony has been documented in larch bud moth populations at the valley scale, whereas traveling waves have been identified at broader spatial scales (Price et al., 2006). If nonclimatic outbreak dynamics occur among geometrid moths in northern Sweden, then spatial synchrony should be evident at relatively local spatial scales but not over the whole region.

Methods

STUDY AREA AND FIELD METHODS

The study sites are located at treeline on the east side of the Scandes Mountains in northern Sweden, above the Arctic Circle (Fig. 1). Annual mean summer temperature is 8 °C (Tuomenvirta et al., 2001), and mean annual precipitation is 300 mm, though there

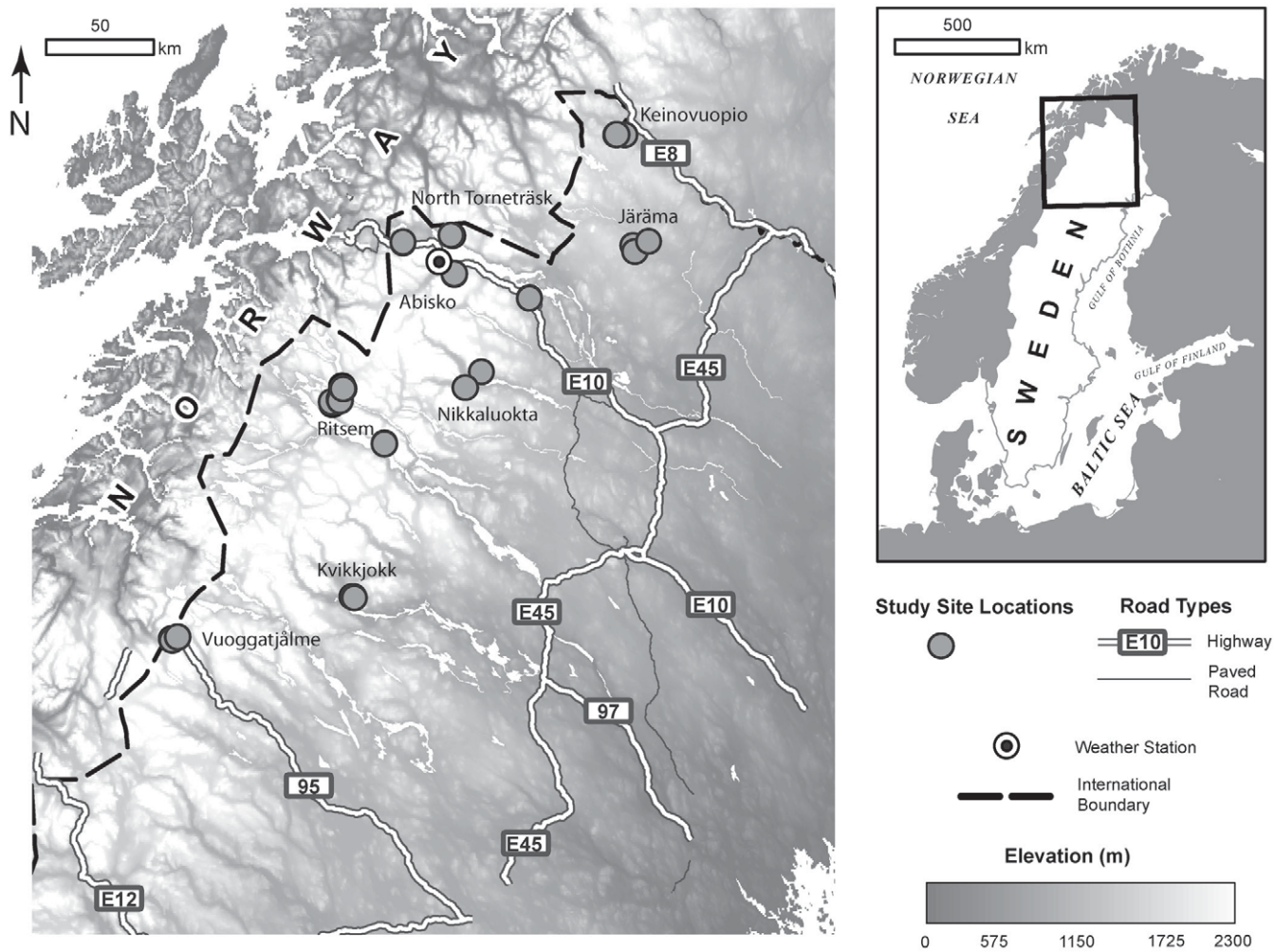


FIGURE 1. Sampled locations in northern Sweden.

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is variation within the region with location relative to the spine of the Scandes (Wielgolaski, 2005). Mountain birch dominates the landscape from valley bottoms up to treeline at approximately 600–800 m a.s.l. Scots pine is locally dominant but is typically found 200 m below the treeline.

We sampled 25 mountain birch stands in eight valleys within the study area (Fig. 1). All mountain birch cores were collected from patches of trees within the treeline ecotone. We also cored Scots pine trees (*Pinus sylvestris* L.) in each valley to generate nonhost chronologies that reveal climatic influences on tree growth without the effect of moth herbivory, as explained below. Scots pine is a suitable nonhost species because its dendroclimatic relations are similar to those of mountain birch, with both species responding positively to July temperature of the current growing season (Young et al., 2011). Pines were absent from or inaccessible in three valleys; we paired the birch chronologies for those valleys with the pine chronologies from the nearest available valley. At each stand, 20 adult trees were cored, except at Ritsem, where only 8 pines were cored, and at Vuoggatjålme, where 40 birch trees were cored (Table 1). We collected two cores from each tree. Trees were

TABLE 1

Summary statistics for the mountain birch tree-ring chronologies.

Site	Earliest year	Average age	Cores (*n*)	Trees (*n*)	Interseries correlation	Mean sensitivity	Autocorrelation
Keinovuopio							
KND	1886	78	20	11	0.609	0.527	0.576
KNB	1907	65	16	11	0.53	0.514	0.581
KNA	1858	88	13	9	0.576	0.493	0.622
Järäma							
JAB	1895	73	17	10	0.524	0.48	0.305
JAA	1923	53	25	16	0.69	0.475	0.441
PUA	1822	83	19	13	0.615	0.576	0.558
North Torneträsk							
NTA	1889	68	21	14	0.577	0.531	0.544
NTB	1887	50	29	15	0.585	0.532	0.531
Abisko							
ABD	1935	60	21	13	0.71	0.481	0.475
ABA	1865	83	28	11	0.611	0.516	0.592
ABB	1899	66	20	14	0.568	0.56	0.6
Nikkaluokta							
NID	1878	50	23	14	0.586	0.594	0.467
NIE	1882	66	29	17	0.668	0.53	0.52
Ritsem							
GAH	1927	33	20	13	0.629	0.453	0.547
GAR	1944	42	21	16	0.641	0.389	0.616
GAL	1931	64	20	12	0.66	0.496	0.419
RIT1	1917	67	15	13	0.63	0.462	0.573
RIT3	1944	39	15	9	0.541	0.499	0.44
RIT2	1935	36	28	13	0.671	0.467	0.493
VAK	1930	48	14	10	0.687	0.503	0.436
Kvikkjokk							
SJN	1940	42	27	16	0.685	0.556	0.305
KVI	1935	44	25	15	0.611	0.597	0.583
Vuoggatjålme							
MAD	1915	78	9	7	0.506	0.542	0.373
JUA	1876	92	22	17	0.636	0.536	0.503
STR	1900	80	12	11	0.517	0.546	0.503

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cored across the slope at breast height (137 cm) for pines and at the base (10 cm) for the birches.

The data set used here represents the largest single dendroecological data set for mountain birch available. The international tree-ring data bank (ITRDB) contains only one tree-ring series for the species. There are other series for mountain birch that have not been submitted to the ITRDB, but nearly all of these are either based on relatively few trees (e.g. <50) and/or are for relatively small geographical areas (Eckstein et al., 1991; Hoogesteger and Karlsson, 1992; Kirchhefer, 1996; Aune et al., 2011; Van Bogaert et al., 2011). The inclusion of 327 trees from 25 stands in eight regions represents a significant increase in dendroecological data on mountain birch.

LABORATORY METHODS

Cores were mounted to grooved blocks and sanded to a polish using progressively finer sanding paper (60–400 grit). Birch cores were dyed with phloroglucinol to detect faint ring boundaries (Patterson, 1957). Cores were visually crossdated (Stokes and Smiley, 1968) and then measured using a Velmex measuring system (0.001 mm). We used the COFECHA program (Holmes, 1986; Grissino-Mayer, 2001) to crossdate the series statistically (Table 1) and omitted from further analysis any series that we could not crossdate. We used the ARSTAN program (Cook and Holmes, 1986) to generate a standardized chronology for each tree-ring series, with age-related growth trends removed through double-detrending (negative exponential curve and 20 yr cubic spline; Speer et al., 2001). We also used ARSTAN to combine the individual chronologies into an average pine chronology for each valley. These average pine chronologies were used as the nonhost chronologies.

GEOMETRID MOTH OUTBREAK DETECTION

Outbreaks of the autumnal moth were detected using the program OUTBREAK (Holmes and Swetnam, 1996), which was developed to analyze insect outbreaks by identifying periods of suppressed radial growth associated with outbreaks (Swetnam et al., 1988). Tree growth is a complex phenomenon related to multiple factors besides insect herbivory; to minimize the risk of misinterpreting periods of growth suppression, OUTBREAK removes the common climate signal from each host series by subtracting the average standardized chronology of the nonhost species from it. This procedure has been used extensively to infer the impacts of insects in cases where dendrochronological records provide a window into the deeper past than do direct records of insect populations (Speer et al., 2001; Esper et al., 2007; Buentgen et al., 2009). It does, however, have limitations because host and nonhost species do not have the exact same responses to climate (Speer et al., 2001; Humbert and Kneeshaw, 2011). We chose to use Scots pine (*Pinus sylvestris*) as the nonhost species because it is the other dominant tree species in northern Fennoscandia and it has a broadly similar climate response to mountain birch (Young et al., 2011). OUTBREAK applies two criteria to the resultant "climate-free" host chronology to identify insect outbreaks: maximum growth reduction and outbreak length. Maximum growth reduction is defined as the standard deviation (–1.24) that encapsulates the smallest 10% of the corrected ring index for all chronologies (Swetnam et al., 1988). We used an outbreak length of 2–4 years (Tenow, 1972). A period of low growth must fulfill both these criteria to be considered an outbreak. We reconstructed the outbreak history for each plot by identifying years when at least 20% of the birch series signaled an outbreak. We chose the 20% filter because, based on a visual assessment, it best reproduced the defoliation events reported in historical records (Tenow, 1972; Tenow et al., 2007).

OUTBREAK–CLIMATE RELATIONSHIPS

To evaluate climatic influences on moth outbreaks in the Abisko Valley (our first and second hypotheses), we created an outbreak severity variable by calculating the percent of trees signaling outbreak in all five Abisko birch stands during each year. We included only the years represented by at least 10 trees. We then correlated this yearly outbreak severity variable with climate variables for the Abisko scientific research station. Specifically, we used monthly average temperature and monthly total precipitation data for January–September of the outbreak year and all months of the previous calendar year. Abisko is the only valley in our study area with a long climate record suitable for such an analysis.

We included the climate variables that were correlated with outbreak severity in a stepwise regression model to determine the contributions of each month's conditions to the outbreak severity and to reduce redundancy among the variables. We also evaluated the impact of seasonally aggregated temperatures on outbreak occurrence using linear regression (Autumn = September, October, and November of the previous calendar year; Winter = December of the previous calendar year, January and February of the year of the outbreak; Spring = March, April, and May; and Summer = June, July, and August).

To look for climatic influences on moth outbreaks across the entire region (our third hypothesis), we calculated a regional outbreak severity variable and correlated it against winter NAO and the annual NAO index. We used the Jones et al. (1997) NAO index updated to 2007. Winter NAO index was calculated as the mean NAO value for the months of December, January, February, and March (cf. Klemola et al., 2003).

SPATIAL SYNCHRONY OF OUTBREAKS

We used semivariogram analysis to investigate the degree of spatial synchrony apparent in the derived outbreak chronologies (our fourth hypothesis) (cf. Schlesinger et al., 1996; Foster et al., 2013). Semivariogram analysis allows the determination of the scale over which spatial autocorrelation is evident in a data set. We used this technique to evaluate the degree to which outbreaks (measured as the percentage of trees showing indication of an outbreak) at both individual sites and the regions were correlated. Stand locations were measured in the field using a GPS. The location of regions was calculated as the geographic center of the sites that were included within each region. In both site-level and regional analyses there is a time-series of data. Semivariance (γ) is calculated for pairs of points separated by distance (h) using Equation 1, where $N(h)$ is the number of distinct pairs at distance h, and z is the percentage of trees showing evidence of an outbreak at a specific point (either a stand or a region). Because our data are multitemporal, we have modified the standard semivariance equation (Matheron, 1963) to include multiple observations over many years by including a temporal term in the equation (t) that represents the year. T is the number of time periods (years). We fit a Gaussian

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model to the semivariograms using Splus to determine the range of the semivariograms.

$$\gamma(h) = \frac{1}{2\left|N(h)\right| * \left|T\right|} \sum_{N(H)} \sum_{t} (z_{it} - z_{jt})^2 \qquad (1)$$

Results

OUTBREAKS

We identified between 4 and 17 outbreaks in each stand (Fig. 2). The outbreaks averaged 3.4 years in length and occurred at intervals of 7.1 years, on average (Table 2).

OUTBREAK CLIMATE—RELATIONSHIPS

Outbreak severity in the Abisko Valley was significantly ($\alpha < 0.05$), though weakly, correlated with temperatures in February ($r = 0.24$), April ($r = 0.21$), July ($r = 0.23$), and August ($r = 0.23$) of the outbreak year, and with temperatures in May ($r = 0.22$) and November ($r = 0.23$) of the previous year. In all cases, the temperatures were positively related to outbreak severity, indicating that warmer conditions in those months promote the occurrence of an outbreak. Precipitation in no month was significantly correlated with the outbreak data.

Stepwise linear regression produced a model with four explanatory variables (February and July temperatures of the outbreak year, and May and November temperatures of the previous year). The model fit is significant ($F = 5.624$ on 4 and 89 degrees of freedom, p-value < 0.001), but the overall predictive ability of the model is low (adjusted-$R^2 = 0.166$). All coefficients in the model are positive with the exception of the intercept. For the seasonally aggregated temperature values, only the autumn temperatures were significantly related to outbreak severity. The predictive ability of the model is low (adjusted-$R^2 = 0.0458$) but statistically significant ($F = 5.464$ on 1 and 2 degrees of freedom, p-value $= 0.022$). The winter and annual NAO indices were not significantly correlated with outbreak severity at the regional scale.

SPATIAL SYNCHRONY OF OUTBREAKS

The range value for the semivariograms for the regional and individual site analyses were very similar (102.63 km for the regions and 123.7 km for the individual stands). The range statistic for a semivariogram indicates the distance over which spatial autocorrelation is evident in the data. In this case, stands or region centroids that are nearer than about 100 km (Fig. 3) exhibit spatial autocorrelation, meaning that they are more likely to have similar characteristics in the outbreak data than are more distant locations. We interpret these results to mean that outbreak conditions at a site likely do not influence outbreak conditions beyond about 100 km from the site. Although there are relatively few pairs of points at short distances from each other, the pattern of spatially autocorrelated results at short distances holds true for both

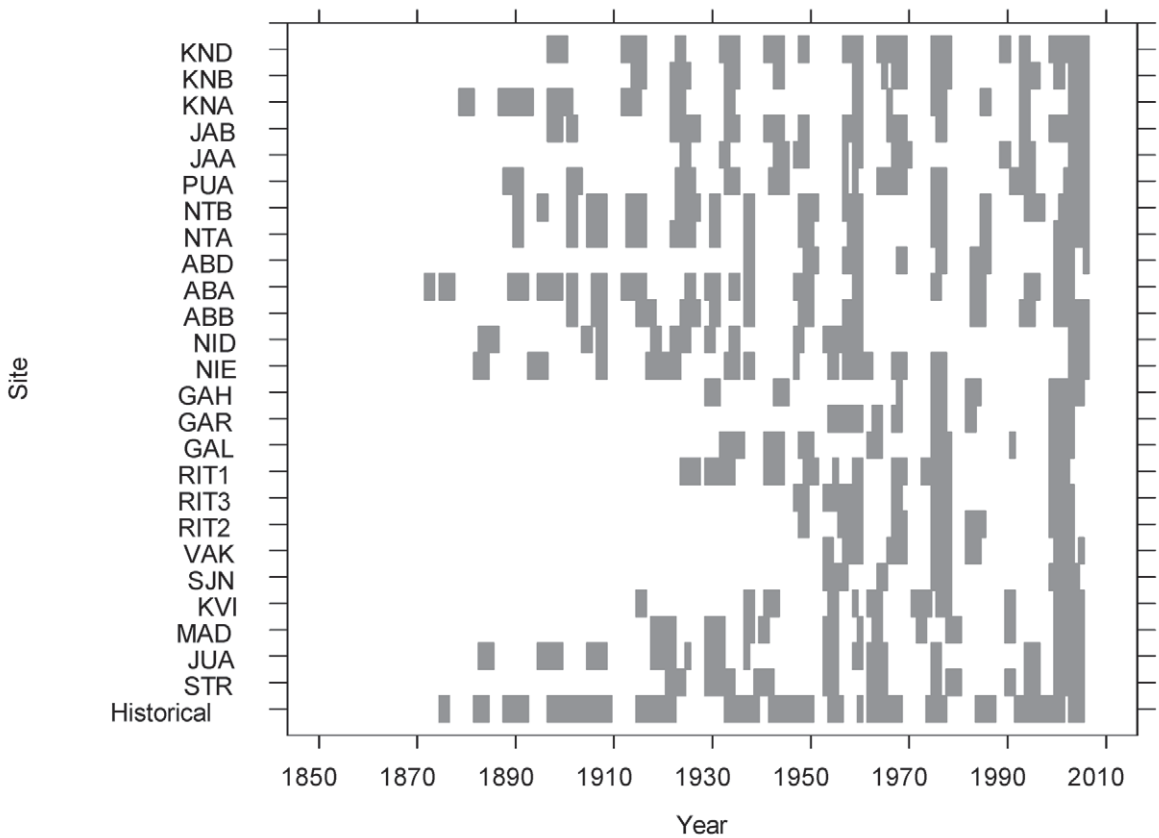


FIGURE 2. Tree-ring-derived outbreak periods for sites in northern Sweden.

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Table 2

Characteristics of outbreaks identified using the OUTBREAK model from the tree-ring series for mountain birch. Individual sites are grouped by valleys.

Site	Duration (yr)	Growth reduction	Interval between outbreaks (yr)	Number of outbreaks recorded
Keinovuopio				
KND	3.14	94.5%	5.73	12
KNB	2.93	94.5%	6.1	11
KNA	3.08	93.2%	8.18	12
Järäma				
JAB	3.04	92.9%	7	11
JAA	2.84	89.1%	6.33	10
PUA	3.35	94.3%	8	11
North Torneträsk				
NTA	2.97	88.3%	7.09	12
NTB	3.13	92.7%	5.46	14
Abisko				
ABD	2.85	89.9%	6.86	8
ABA	2.87	90.6%	5.06	17
ABB	3.16	94.8%	6.9	11
Nikkaluokta				
NID	3.28	96.8%	10.22	10
NIE	3.04	89.7%	7.73	12
Ritsem				
GAH	2.95	77.3%	11.4	6
GAR	2.92	73.6%	5.8	6
GAL	3.26	91.3%	7.83	7
RIT1	3.3	87.9%	3.71	8
RIT3	3.18	88.4%	8.75	5
RIT2	3.56	84.1%	6.6	6
VAK	3.15	88.3%	5.17	7
Kvikkjokk				
SJN	3.08	93.2%	11.67	4
KVI	3.18	97.6%	7	10
Vuoggatjålme				
MAD	2.8	98.0%	5.6	11
JUA	2.77	89.6%	6.67	13
STR	2.95	91.7%	5.33	10

the regional and individual stand treatments of the data. The fact that the autocorrelation is not evident at larger distances emphasizes that there is little evidence of synchrony of outbreaks for points that are separated by more than 100 km.

Discussion

OUTBREAK RECONSTRUCTIONS

This study complements the historical outbreak accounts by generating a spatially extensive, environmentally recorded time series.

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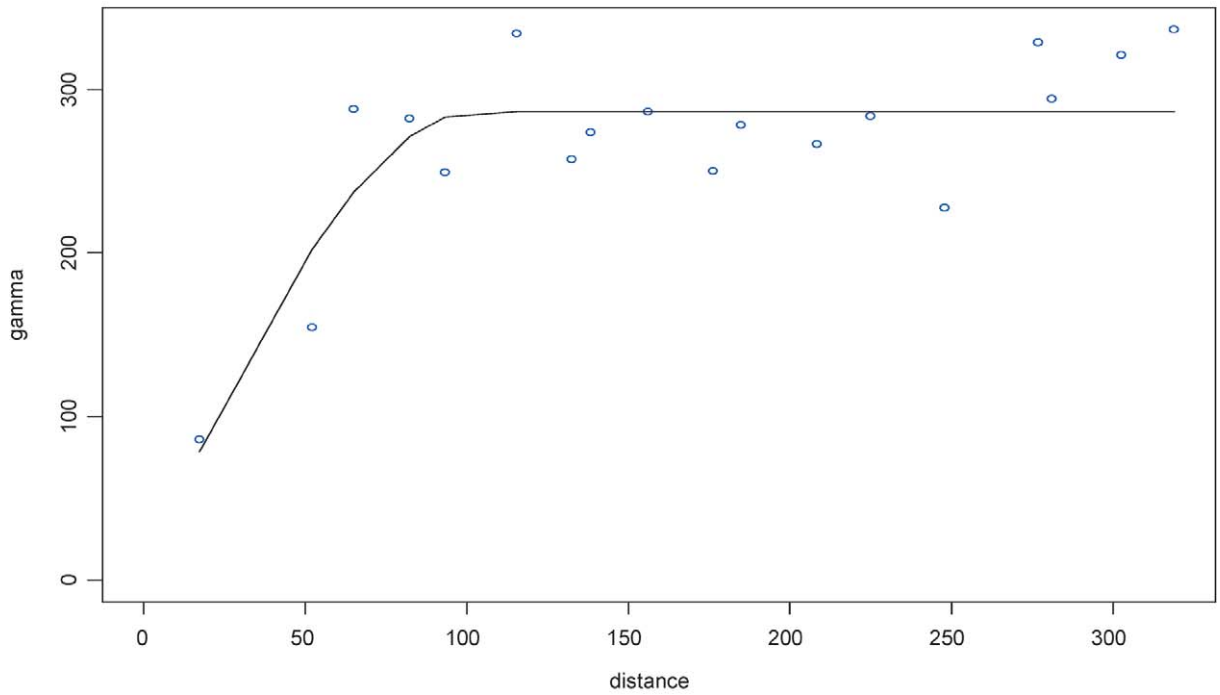


FIGURE 3. Semi-variogram for outbreak severity at sites in northern Sweden. Data are based on regionally aggregated sites. The range of the variogram is 102.6 km, the sill is 277.44, and the nugget is 8.65.

Previous studies have mapped the extent of individual outbreaks during the recent past (Babst et al., 2010), or have assembled historical records of observed outbreaks (Tenow, 1972). Some of our study sites have poor representation in Tenow's records, thus outbreaks in those regions had not been identified previously. Combining these two records paints a more comprehensive picture of the cyclical behavior of the geometrid moths over the landscape. This kind of analysis is not possible without an extensive and deep dendrochronological data set like the one that we have produced here.

The method used here to reconstruct geometrid moth outbreaks is not without limitations. The procedure relies on the use of reductions in growth of host species relative to nonhost species. One limitation of this procedure is that climate × herbivore interactions cannot be rejected based on this method. However, the procedure has been used extensively to infer insect outbreaks at other locations (Speer et al., 2001; Esper et al., 2007; Nishimura and Laroque, 2010) and has been shown to adequately identify insect outbreaks in dendrochronological records (Humbert and Kneeshaw, 2011). Nonetheless, it is not as definitive as insect population or tree defoliation surveys would be. We refer to reductions in birch growth relative to the nonhost pine species as outbreaks but recognize that there is some possibility that some of these are caused by factors other than insects. Our outbreak reconstructions do, however, appear to match the major outbreaks recorded in the historical records.

The most well-known outbreak to have occurred in Fennoscandia is the 1955 outbreak. It is particularly well documented for the Abisko Valley (Tenow, 1972; Van Bogaert et al., 2011), and we expected to identify the outbreak in the Abisko-Torneträsk series. Indeed, at three of the five stands in that valley, we observed a multiyear moth outbreak beginning in 1955. The outbreak appeared in the remaining two stands in 1956 and 1957, and it was also evident in the valleys north of Abisko. Tenow (1972) also documented the 1955 outbreak in the southern valleys (Nikkoloukta, Ritsem, Kvikkjokk, and Vuoggatjålme). Our reconstructions record an outbreak in the southern valleys during the mid-1950s, but it began during the early part of the decade and apparently was less synchronous than in the north.

In 1927, an extensive outbreak occurred in northern Finland, depressing treeline considerably in some areas (Nuorteva, 1963; Tenow, 1972; Kallio and Lehtonen, 1973; Lehtonen, 1987). This Finnish outbreak may correspond to the 1920s outbreak signals that we recorded in the northern valleys, although the reconstructed outbreak began during the early 1920s and appears to have terminated roughly at the time the Finnish outbreak peaked. The 1963–1966 outbreak was recorded throughout Fennoscandia (Tenow, 1972) and also seems evident in most of our series, albeit more coherent in the two northern valleys than elsewhere. Another widespread outbreak occurred in the early years of the 21st century (Nilssen et al., 2007; Tenow et al., 2007). This outbreak has been previously reported for northern Norway, where it began in 1999 and continued through 2006, with the peak occurring in 2002 and 2003 (Klemola et al., 2008). This outbreak was closely followed by an outbreak of winter moth (*Operophtera brumata*) in 2004 and 2005. The occurrence of the winter moth had not previously been recorded in this location. Our data indicate this recent autumnal/winter moth outbreak occurred throughout northern Sweden.

Our results show outbreaks occurring more frequently than previously reported (Haukioja et al., 1988; Tenow et al., 2007). The more frequent growth-reduction events that we observe are likely because our work is based on growth reductions in the tree-ring record, and not on observed massive defoliation events. Therefore, we may be observing smaller outbreaks that would not have been noticed using other observational methods. There is also some

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possibility that these growth reductions are caused by a process unrelated to insect outbreaks.

OUTBREAK-CLIMATE RELATIONSHIPS

Our results indicate that warmer winter temperatures are associated weakly with outbreak severity in the Abisko Valley, consistent with our first hypothesis. The positive relationship with winter (February/previous November) temperature is potentially explained on the basis of previous small-scale research, which suggests that mild winter temperatures should minimize wintertime egg mortality, enabling large moth populations and multiyear persistence of outbreaks. There are few days when temperatures in the Abisko Valley dip below critical temperatures for egg mortality, however (–35 °C: Tenow and Nilssen, 1990). Temperatures reached this threshold during only 3.1% of the years between 1913 and 2010. Therefore, wintertime egg mortality would not seem to exert a strong influence on outbreak initiation or termination, possibly explaining the weakness of the observed outbreak-climate relationships.

The positive relationship of moth outbreak severity with spring (April) and summer (July/August) temperature in the Abisko Valley disagrees with our second hypothesis and with the findings of several previous studies (Niemela, 1980; Virtanen and Neuvonen, 1999; Selås et al., 2001) that found moth populations to be negatively related to spring and summer temperature. Our results are consistent with those of Klemola et al. (2003), however. The differences in response may reflect differences in the measured indicator of outbreak status. Previous work evaluated the effects of climate on moth populations directly, while our work investigates the secondary effect of those population numbers: the percentage of trees exhibiting significantly reduced growth. The proposed mechanism behind the negative relationships found previously (low temperatures reducing parasitoid and predator populations) does not seem to dominate at the spatial and temporal scales of our study. Rather, long-term patterns of moth outbreaks over an entire valley, as opposed to year-to-year variations in moth populations, appear to be influenced by climate in a different manner. High summer temperatures may facilitate an outbreak (as opposed to a small population change during non-outbreak years) by enabling rapid and widespread moth population growth at a rate that outstrips the parasitoid/predator populations (Tanhuanpää et al., 2001). Additionally, since parasitoids are most relevant for short-term, local population dynamics (Schott et al., 2010), their influence likely diminishes when outbreaks are viewed over an entire valley for several decades, while other influences become visible. For example, warm summer temperatures may improve forage quality (Kause et al., 1999; Lempa et al., 2004), resulting in the positive relationship we observed between outbreak severity and summer temperature. Warm summers also could promote moth fecundity (Haukioja and Neuvonen, 1985), resulting in outbreak persistence into subsequent years, an effect potentially signaled through the positive relationship with previous May temperature.

Regarding our third hypothesis, which was not supported, the discrepancy between our weak NAO relationships and the finding by Klemola et al. (2003) that moth populations were positively related to winter NAO likely reflects a difference in scale of the studies. Klemola et al. correlated moth populations based on 20 trees at Kevo, Finland, over a 12 year period and found a positive correlation. They interpreted this as cold dry winters associated with the negative phase of the NAO resulting in excessive winter kill of eggs. Our results are not surprising because we use regional-level chronologies that portray moth outbreaks rather than moth populations themselves. Moreover, our spatial analysis indicates that the moth outbreaks were synchronous over relatively short distances (approximately 100 km), a finding that agrees with our fourth hypothesis. The synchrony breaks down over longer distances. Given this spatial asynchrony at the regional scale, the weak correlation of moth outbreaks with a hemisphere-wide climatic index such as the NAO is unsurprising.

The observed patterns of spatial synchrony corroborate the findings of Klemola et al. (2006), which also show that outbreaks are spatially synchronous, although the distances across which synchrony is evident are lower than those shown by Klemola et al. (2006). Our results are more closely aligned with those of Tenow et al. (2007), who detected a limit of spatial synchrony at distances slightly shorter (60 km) than ours (~100 km). The presence of spatial autocorrelation at distances up to approximately 120 km is indicative of a "Moran effect" (sensu Ranta et al., 1999). The results of Klemola et al. (2006) were based on population data for the autumnal moth (larval counts and adult trap data), whereas our results represent the impacts of large populations of autumnal moth larvae on the landscape. They are, therefore, complementary.

Our three sets of analyses, combined with previous work on moth populations, climate, and spatial patterns, suggest that, indeed, moths are affected by climatic variations. Interannual differences in climate impinge directly on year-to-year population changes (cf. Klemola et al., 2003). Additionally, our results suggest that climatic variations establish the conditions that enable a transition to, and persistence of, outbreak conditions. The influence of climate on outbreaks is weak, however, because background climatic conditions alone cannot induce an outbreak. An outbreak would depend on both climatic and nonclimatic factors, such as tree age, which is influenced by time since previous severe outbreaks (Ruohomäki et al., 2000; Tenow et al., 2005), and the outbreak status of neighboring areas. A climatically linked outbreak could emerge synchronously across several valleys in one section of northern Fennoscandia and then ripple across the entire region over the next few years. Tenow et al. (2007, 2013) reported that outbreaks sometimes demonstrate such behavior, originating in a small area and progressing as a wave to encompass the region or even traveling over the entire continent. Valleys receiving an outbreak wave one or more years after its initiation elsewhere may show little evidence of a climatic linkage with the outbreak. At the regional scale and over the long term, therefore, we observe only weak outbreak-climate relationships.

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