

Shifting altitudinal distribution of outbreak zones of winter moth *Operophtera brumata* in sub-arctic birch forest: a response to recent climate warming?

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Climatic change is expected to affect the extent and severity of geometrid moth outbreaks, a major disturbance factor in sub-arctic birch forests. Previous studies have reported that the two geometrid species involved, autumnal moth and winter moth, differ in their temperature requirements and, consequently, in their altitudinal and latitudinal distribution patterns. In this study, we document the altitudinal distribution of winter moth outbreaks in a large coastal area in northern Norway. We show that, in the present winter moth outbreak, defoliated birch stands were seen as distinct zones with a rather constant width in the uppermost part of the forest and where the upper limit coincided with the forest line. The outbreak zone closely followed the spatially variable forest line as an undulating belt, although some of the variation in outbreak zone width was also related to variation in topographical variables, such as distance from the coast, forest line altitude, and slope of the terrain. A distinct outbreak zone at the altitudinal forest line is the typical picture that has been depicted in more qualitative historical records on previous outbreaks of autumnal moth rather than winter moth. We suggest that the recent documented climate warming in this region may have induced a shift in distribution of the winter moth both relative to topography and geography. Further investigation is, however, required to substantiate these suspicions.

In northern Fennoscandia, in a narrow biogeographic zone between the coniferous boreal forest and the mountain tundra, mountain birch *Betula pubescens czerepanovii* usually sets the northern and alpine forest limit (Wielgolaski 2001). Periodic insect defoliation is the principal natural disturbance factor in these sub-arctic birch forests (Neuvonen et al. 2005). Especially important insect herbivores are the two geometrid moth species winter moth *Operophtera brumata* and autumnal moth *Epirrita autumnata*. Both of them show cyclic outbreak dynamics with a period of ca 10 yr in this ecosystem (Tenow 1972). Outbreaks happen synchronously in both species (Tenow 1972), except that winter moth sometimes lags 1–2 yr behind autumnal moth (Tenow et al. 2007). The outbreaks usually have dramatic effects, with complete defoliation and, occasionally, death of the forest over hundreds or thousands of km² (Tenow 1972, Tenow and Bylund 2000,

Karlsson and Weih 2003, Karlsson et al. 2004). The phenomenon is a key example of population cycles and outbreaks in northern and mountainous regions in the ecological literature (Berryman 1996, 2002, Ruohomäki et al. 2000, Turchin et al. 2003).

Concern has repeatedly been raised regarding the potential impact of climate and climate change on the outbreak dynamics of the two geometrids, and therefore on the relative extent of broad-leaved versus coniferous forests in northern Fennoscandia (Bylund 1999, Neuvonen et al. 1999, 2005). However, the climate-outbreak relationship is not clear, which is partly because it is difficult to assess the relative importance of direct (e.g. effect of increased winter temperature on egg survival) vs indirect effects (e.g. effect of increased temperature on plant resistance or natural enemies; (Virtanen and Neuvonen 1999, Niemela et al. 2001)). Indeed, in a climatic context, a distinct differentiation

in species-specific outbreak areas in relation to altitude has been reported for these insects. While autumnal moth has been reported to predominate close to the forest limit, winter moth has been reported to occur primarily at lower altitudes (Hågvar 1972, Tenow 1972). Climate is often inferred to be the underlying cause for such altitudinal distribution patterns in insects (Hodkinson 2005). Similarly, egg mortality caused by the accumulation of cold air at low altitudes in winter (temperature inversion) is often considered the most parsimonious explanation for the observed altitudinal distribution of autumnal moth (Bylund 1999, Neuvonen et al. 1999). However, since winter moth eggs are only slightly less cold tolerant (ca 2°C) than autumnal moth eggs (Macphee 1967, Niemela 1979, Tenow and Nilssen 1990), differential egg mortality caused by temperature inversion is unlikely to account for the observed altitudinal segregation of the two species. Air temperatures drop predictably by 0.5–0.65°C 100 m⁻¹ elevation under normal atmospheric pressure (Tveito et al. 2000), which should translate into a difference of 350–400 altitude meters. Thus, assuming that it may help directing future climate-related research on the mechanism underlying cycles and outbreaks, more detailed investigations of the altitudinal distribution of outbreak zones in these insects, including estimates of how the outbreak zones vary in shape and size in relation to relevant environmental variables, is warranted.

We carried out an aerial survey in a coastal area in northern Norway, in the core of the sympatric outbreak zone of the two geometrids, to determine the outbreak-altitude relationship in winter moth on a large spatial scale. We took advantage of a situation where severe and wide spread winter moth outbreaks were present concurrently with virtual absence of the autumnal moth. Our primary goal was to evaluate the assumption that severe winter moth outbreaks primarily occur at relatively low altitudes in the forest, rather than at the forest line, as seems to be the case for the autumnal moth. Another goal was to provide quantitative estimates of the width of the outbreak zones of winter moth and to establish whether the width was dependent on environmental variables, such as the altitude of the forest limit, the distance from the coast, slope, and aspect. A few small scale studies have documented altitudinal abundance gradients in sympatric populations of the two birch forest geometrids (Hågvar 1972, Ruohomäki et al. 1997, Mjaaseth et al. 2005). However, we are not aware of previous large scale studies providing a quantitative approach to estimating the altitudinal extent of geometrid outbreak zones in sub-arctic birch forest and their environmental correlates. We think such large scale, pattern oriented analyses may be an important compliment to the conventional small scale studies (Hågvar 1972, Mjaaseth et al. 2005) aimed

to uncover causal mechanism underlying outbreak events.

Methods

The aerial survey of severe winter moth outbreaks was conducted in 2006 in the northern part of Troms County in northern Norway (69°45'N, 21°0'E, Fig. 1). The climate in this region is typically oceanic with cool summers and relatively mild winters (Tveito et al. 2000). The region has experienced a marked increase in mean temperatures in recent years (Fig. 2). The natural forest is dominated by mountain birch and forms a reasonably homogenous belt from sea level to the forest line at ca 350–400 m elevation. The survey was designed to cover the coast line and larger valleys in an area where winter moth outbreaks, leading to defoliation of birch forest stands, had been confirmed by field surveys earlier the same year (results not shown here). The abundance of the autumnal moth in this area was extremely low (i.e. hardly detectable) as it was in previous outbreaks in coastal birch forest in the same geographic region (Ims et al. 2004). Moreover, in 2006, there were large geometrid outbreaks all over northern Norway. Based on pictures in newspapers, television news reports, personal visits to outbreak zones in various other parts of the region as well as personal communication with other researchers and locals, it was concluded that most (if not all) outbreaks were by winter moth. Thus, we had an ideal situation at hand where the altitudinal distribution of winter moth outbreaks could be investigated from the air on a large spatial scale within the sympatric outbreak zone while maintaining a high certainty of the species identity.

The survey transect was covered twice. The first survey (29 July, transect line 457 km, mean altitude 388 m) was done to obtain detailed digital photographs of all mountain sides along the transect. In most of these pictures, the level of detail was sufficient to distinguish individual trees or small groups of trees. The second survey (5 August transect line 364 km, mean altitude 739 m) was done to obtain high altitude overview photographs of the outbreak zones identified during the first survey. Forest areas that were completely or almost completely defoliated by winter moth gave a clear brownish-black contrast to areas with moderate or no damage and were easily recognized from the air. The survey was done in a fixed-wing aircraft (Cessna 172) by 2 observers. The exact time stamp of each digital photograph was recorded and later synchronized to the GPS track log using the software GPS-Photo Link (GeoSpatial Experts LLC). The digital photographs were projected onto a wall canvas and sketch maps of outbreak zones

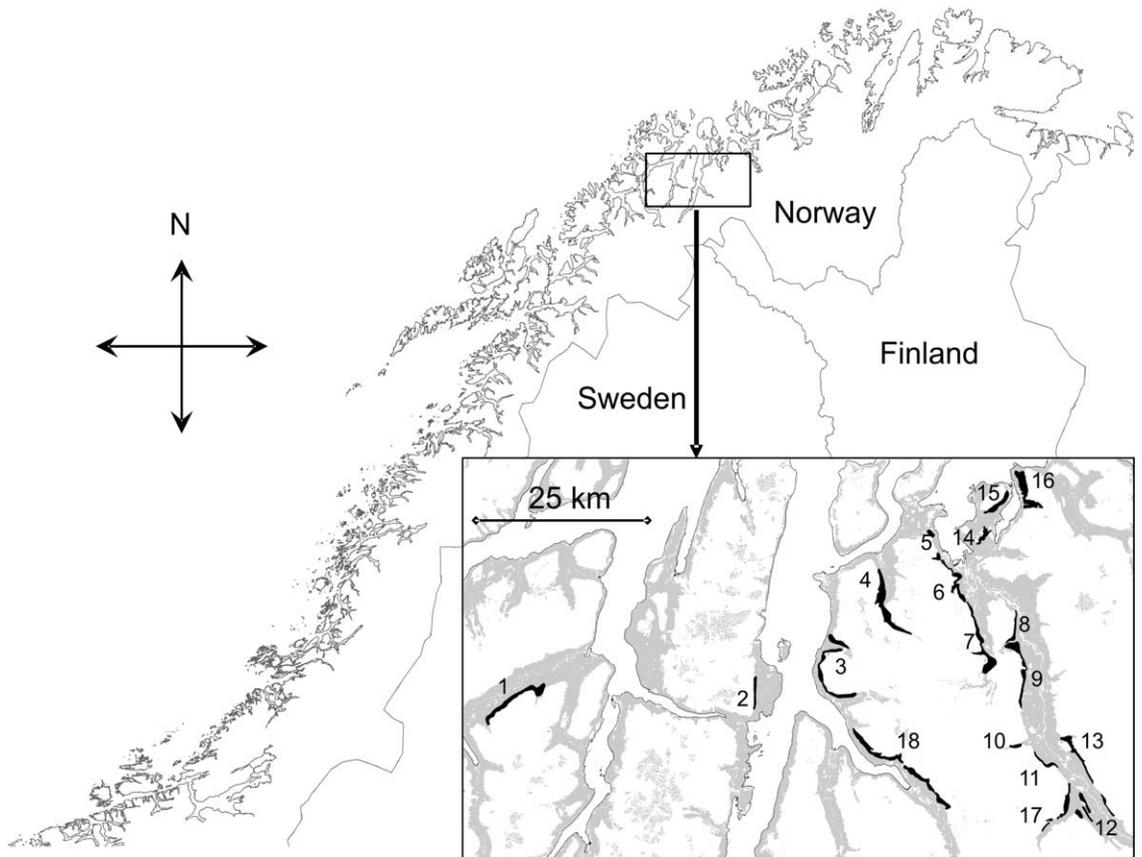


Fig. 1. The study region in Troms County in northern Norway. Grey shaded areas are forest, primarily mountain birch. Black areas indicate the 18 outbreak zones with complete or almost complete defoliation.

with complete or almost complete defoliation were hand drawn on high resolution topographic maps. No attempt was made to delineate areas with moderate or low damage. Sketch maps were subsequently digitized to a GIS. A total of 18 continuous or discontinuous outbreak zones were identified for which the boundaries could be clearly delineated from the photographs (Fig. 1, insert). Each zone was characterized using a number of altitudinal transects placed perpendicular to the slope with a minimum distance of 1 km between transects (yielding a total of 128 altitudinal transects). For each transect we extracted the maximum and minimum altitude of the intersecting outbreak zone (Fig. 3, “Min” and “Max”). The coast line or the valley floor was taken as a base line altitude for transects located along the coast or in valleys respectively (Fig. 3, “Base”). Our original intention of locating the forest line as well as the maximum altitude of the outbreak zone from the photographs was abandoned, since the maximum outbreak altitude always appeared to be at or very close to the forest line. The terrain variables, slope (0° – 90°) and aspect

(0° – 360°), were calculated from a digital elevation model (DEM) with 25 m pixel size (Statens Kartverk). Slope, aspect and the distance from the coast are given as length weighted mean values along the part of the transect line located within the outbreak zone (e.g. from minimum to maximum outbreak altitude).

Statistical analysis

The width (i.e. the altitude range) of the outbreak zone, measured in elevation meters, was the focal response variable to be estimated and analyzed with respect to the environmental covariates. Sources of variation in outbreak zone width within and among the 18 outbreak zones, using the 128 altitudinal transects (observational unit), were analyzed using linear mixed-effects models. This was done to specify correctly the replicates (i.e. the 18 outbreak zones, which were used as random factor in the model) while simultaneously taking into account the level of within-replicate variation (i.e. variation in outbreak zone width between the various altitudinal

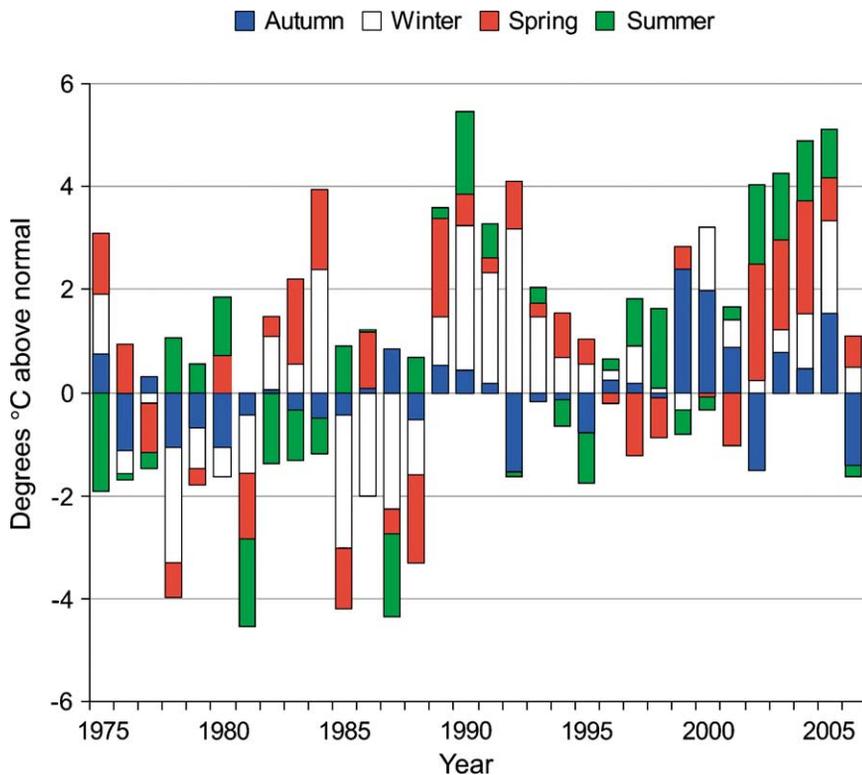


Fig. 2. Temperature statistics for the study region (Tromsø airport, 69°40'N, 18°40'E). The graph show mean temperatures compared to normal (1961–1990) for winter (Dec.–Feb.), spring (March–May), summer (June–Aug.) and autumn (Sept.–Nov.). A pronounced increase in mean temperatures is evident in all seasons. Source: Norwegian Meteorological Inst., <www.met.no>.

transects within each of the 18 outbreak zones). In all of the analyses, the main explanatory (environmental) variable was forest limit altitude. We also included five co-variables that we suspected might influence the results. These were distance from the coast in kilometers, slope of the terrain in degrees, squared and cubed values of slope as well as aspect (8 levels, S, SE, E, NE, N, NW, W, SW; aspect was treated as a factor

variable). To find the best possible statistical model for the observed data, given the candidate set of models, we used model selection based on the two Information Criteria AIC and BIC (Burnham and Anderson 1998, Miller 2002), BIC penalizing model complexity more than AIC (see Link and Barker (2006) for a recent discussion). These model selection criteria strike the balance between variance (too many parameters) and

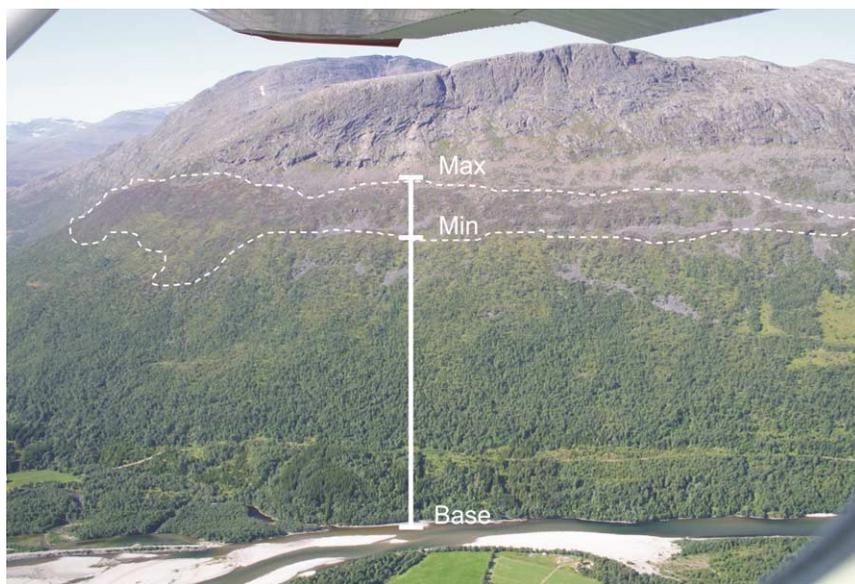


Fig. 3. An overview photograph of a typical outbreak zone to illustrate how maximum, minimum and base line altitudes were identified.

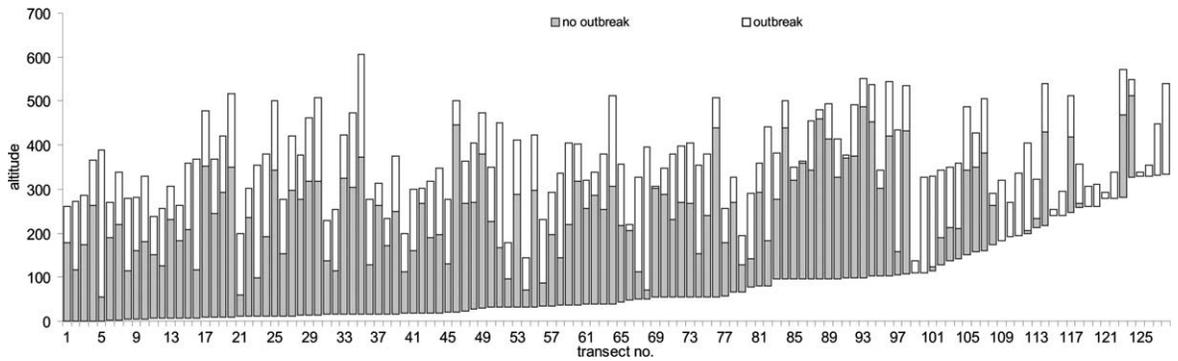


Fig. 4. The altitudinal distribution of outbreak and non-outbreak zones in each of the 128 altitudinal transects sorted according to base line altitude (non-shaded area along x-axis). White bars indicate areas of complete defoliation (“outbreak”), while grey bars indicate areas with no clearly visible defoliation (“no outbreak”). E.g. in transect 1 there was no outbreak from sea level up till ca 180 m, whereas between 180 and 270 m the forest was completely or almost completely defoliated. The maximum outbreak altitude always appeared to be at or very close to the forest line.

bias (to few parameters) when selecting predictor variables to be included in the statistical models, i.e. the model with the lowest AIC- and BIC-values is selected. All analyses were carried out using the statistical software R (Anon. 2005).

Results

A graphical depiction of the altitudinal extent of the 128 transects, including the sections with complete defoliation by winter moth (Fig. 4), showed that the outbreak areas were distributed as an uninterrupted altitude zone, extending from a mean altitude of 251 m (95% CI = 233–269 m, max = 512 m, min = 54 m, n = 128) more or less to the forest limit at a mean altitude of 367 m, (95% CI = 350–384 m, max = 606 m, min = 137 m, n = 128). There was a clear association between the forest line altitude (and the upper limit of the outbreak zone) and the lower limit of the zone (Fig. 5). This means that the outbreak zone had a relatively constant width, i.e. it followed the forest line as an undulating “belt” (Fig. 4). The mean width of the outbreak zone was 116 elevation meters (95% CI = 105–128 m, min = 5 m, max = 335 m, n = 18). In the vertical dimension, the average outbreak zone extended over 3.19 km² (95% CI = 2.13–4.24 km², min = 0.51 km², max = 7.71 km², n = 18).

Although the width of the outbreak zones were fairly constant, general mixed modeling focusing on the variation in zone width yielded a best model including the variables forest line altitude, slope of terrain and distance from coast (Fig. 6, Table 1). The parameter estimates from this model showed that the width of the outbreak zones increased both with increasing forest line altitude ($b = 36.6 \text{ m } 100 \text{ m}^{-1}$, 95% CI = 24.0–49.3) and with increasing slope of the terrain

($b = 1.81 \text{ m}/^\circ$, 95% CI = 0.693–2.93) and decreased with increasing distance from the coast ($b = -5.15 \text{ km}^{-1}$, 95% CI = -6.96–-3.34). There was a tendency for the effect of slope to flatten for slopes $> 20^\circ$ (Fig. 6, Table 1), but this effect was not very strong as BIC favoured a simpler model with only a linear effect of slope. The aspect of the terrain (north, south, east, and west) had, according to the model selection criteria, no explanatory power. There was a substantial variation (as estimated using the two standard deviations of the random effect zone and the residual term) in outbreak width both within zone ($\sigma_{WZ} = 47.3$) and among zones ($\sigma_{AZ} = 25.0$).

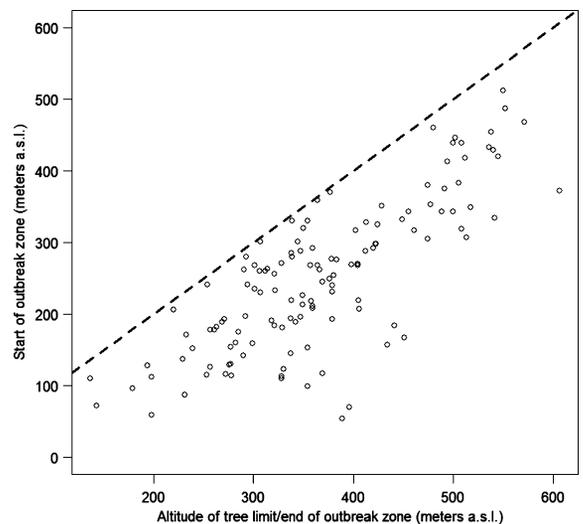


Fig. 5. The relationship between the altitude (m a.s.l.) of the forest limit (i.e. the upper limit of the outbreak zone) and the altitude of the lower limit of the outbreak zone. Since the upper limit of the outbreak zone by definition is higher than the lower limit, values are constrained below the dashed line (slope 1 through the origin).

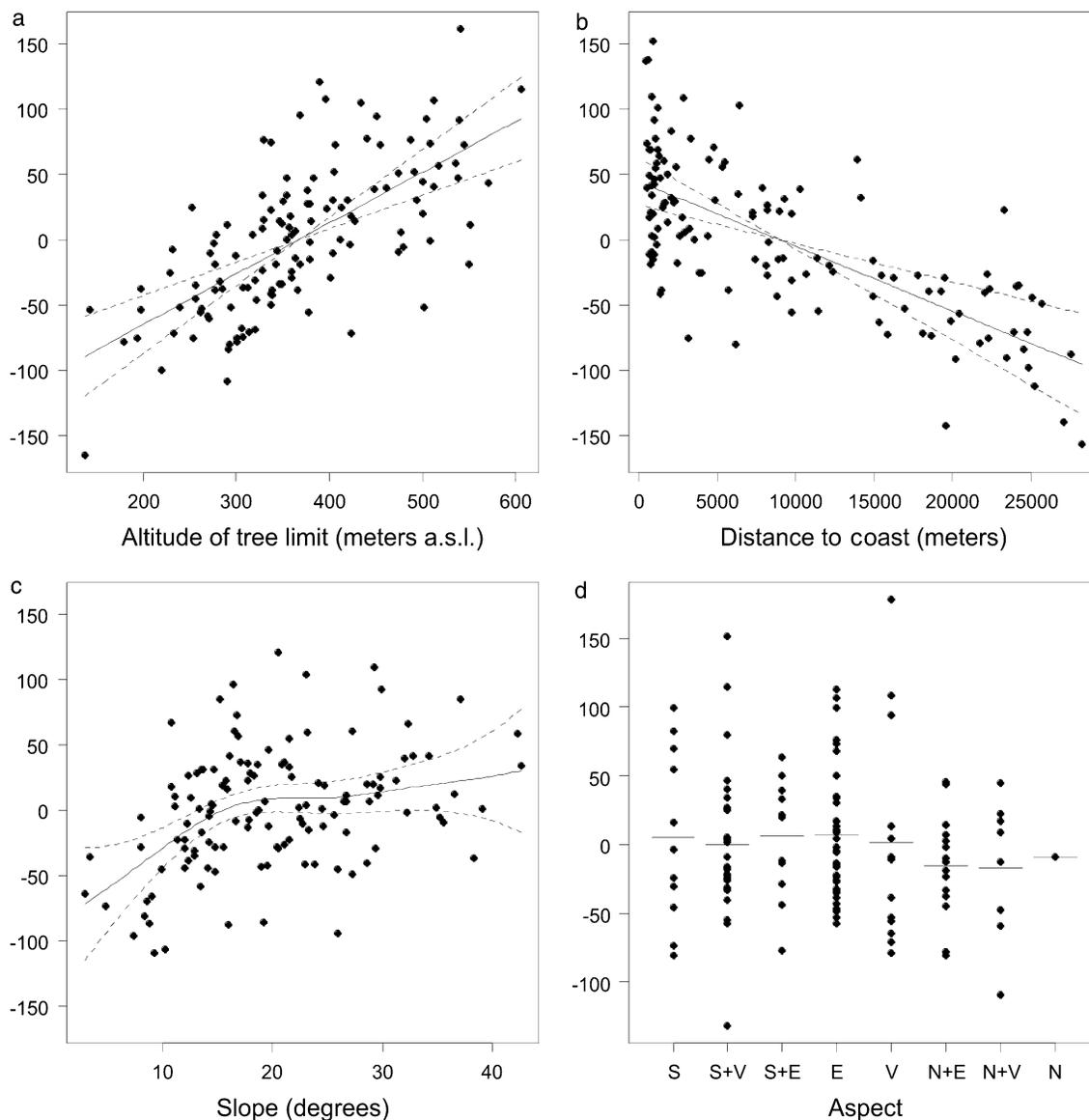


Fig. 6. Relationships between the width of the outbreak zones and the four predictor variables. The altitude of the forest limit (a), the distance from the coast (b) and the slope of the terrain (c), all had effects on the width of the outbreak zones, whereas aspect had no effect (d). All figures show partial residuals and estimated effects obtained using the generalized additive mixed model selected by AIC and BIC (Table 1).

Discussion

Distinct outbreak zones in the upper part of the mountain birch forest is the typical picture that has been depicted in more qualitative historical records on previous outbreaks of autumnal moth (Tenow 1972, 1996, Bylund 1999). In contrast, we are not aware of previous reports on severe winter moth outbreaks being restricted to the uppermost altitude zone and reaching the forest limit. Winter moth outbreaks have previously been reported to be most intense in the middle sections

of altitudinal forest slopes (Hågvar 1972, Tenow 1972). The different spatial distribution of outbreaks of the two dominant birch forest geometrids in northern Fennoscandia has been thought to have a climatic origin, with the winter moth presumed to take advantage of warmer climates along the coast and in the lower sections of the forest compared to the autumnal moth (Tenow 1972, Bylund 1999). For example, Tenow (1972) presumed that winter moth outbreaks were favored by a climatic “warm hang zone” in the middle of south facing slopes. This is at odds

Table 1. Model selection based on AIC and BIC weights of sources of variation in the width of winter moth outbreak zones in the 128 altitudinal transects. The best model (i.e. the one with the lowest AIC- and BIC-values) is highlighted in bold. All models include zone as a random factor, and the number of parameters (np) include only the fixed effects.

Altitude	Aspect	Slope	Distance from coast	Slope ²	Slope ³	np	ΔAIC	ΔBIC	AIC weights	BIC weights
X	x	x	x			11	7.93	26.67	0.01	0.00
X	x	x				10	31.51	47.40	0.00	0.00
X	x		x			10	16.54	32.42	0.00	0.00
X		x	x			4	1.23	0.00	0.22	0.64
	x	x	x			10	35.30	51.18	0.00	0.00
X	x					9	41.81	54.84	0.00	0.00
X		x				3	25.87	21.79	0.00	0.00
X			x			3	9.18	5.10	0.00	0.05
	x	x				9	45.21	58.24	0.00	0.00
	x		x			9	53.03	66.06	0.00	0.00
		x	x			3	27.68	23.60	0.00	0.00
X		x	x	x		5	0.27	1.89	0.36	0.25
X		x	x	x	x	6	0.00	4.48	0.41	0.07
						1	54.59	44.81	0.00	0.00

x: indicates that a variable is included in a model; the last line represents the constant model.

with our data both in terms of the vertical position of the outbreak zone and the lack of an effect of aspect on outbreak zone width.

Altitudinal variation in the performance of insect populations is thought to reflect spatial variation in climate, and indeed, altitudinal gradients are often invoked strategically to study the effect of climate (Hodkinson 2005). Thus there are good reasons to hypothesize that altitudinal climatic variation somehow underlies the position of geometrid moth outbreaks in coastal birch forest. However, the underlying causal mechanism remains unknown. A direct effect of winter climate in terms of differential egg survival is unlikely, since the minimum air winter temperatures in the coastal birch forest in northern Norway never approach lethal temperatures of -35 – -36° (Bylund 1999) for any of the two moth species. Mjaaseth et al. (2005) studied growth and development of larvae of both species in an altitudinal gradient from sea level to forest line just outside the present study region and failed to find any evidence for altitudinal effects on development rates. In that study, neither the development rates nor the spatial distribution in abundance of the two moth species could be explained by forest structure which varied considerably both within and among altitudes. Hansen (2006) has also shown in the same gradient that predation on pupae was unrelated to altitude. Considering other putative causal factors we think three in particular deserve more attention. First insect parasitoids are believed to be important determinants of the population dynamics in both winter moth (Roland and Embree 1995) and autumnal moth (Ruohomäki et al. 2000, Klemola et al. 2002). Thus the altitudinal pattern of parasitoid attack on both moth species, which may well be significant (Virtanen and Neuvonen 1999), needs to be explored. Second, the synchrony of

hatching of eggs and bud burst in host trees is regarded to be a very climate sensitive stage in the life cycle of folivorous Lepidoptera (Kerslake and Hartley 1997, Hunter and Elkinton 2000, Vanbergen et al. 2003, Tikkanen et al. 2006). It is yet unknown, however, whether this synchronicity varies according to moth species and spatial and temporal variation in climate along altitudinal gradients in coastal birch forests. Finally, the temporal timing of eclosion of adult moth from pupae relative to the onset of winter (i.e. snow fall) needs more attention. Winter moth eclose 2–3 weeks later than the autumnal moth in the fall and is thus more vulnerable to early snow falls, in particular near the forest line, than the autumnal moth (Peterson and Nilssen 1998). The altitudinal extents of early snow falls in the mountain birch forest may thus provide clues for climatic thresholds for winter moth survival. Indeed, the link between topographic/geographic climatic variation and responses in ecological systems may be non-linear and complex (Mysterud et al. 2001). For instance we are not yet able to explain why the width of the winter moth outbreak zone in this study decreased with distance from the coast or increased with the steepness of the slope. A first step towards an explanation of these sources of variation in outbreak zone width is to obtain knowledge about how altitudinal temperature gradients are molded by topographic factors.

In his seminal review of historical records of birch forest geometrid outbreaks, Tenow (1972) compiled information suggesting that the winter moth invaded our study area in Troms ca 100 yr ago and that outbreaks of this species by the end of 1960 had not been found in the most northeastern part of Fennoscandia (i.e. east of the river Tana) where only the autumnal moth then prevailed. The present (and still ongoing) large scale winter moth outbreak now extends

east of Tana (unpubl.) and as we have shown here prevails close to the forest limit in a “climatic outbreak niche” previously known to be occupied by the more northern and alpine autumnal moth. Naturally this suggests that the recent climate warming in this region (Anon. 2004) has allowed a shift in distribution of winter moth both relative to topography and geography. Only new studies and future targeted monitoring programs can substantiate such suspicions. We suggest that aerial surveys of the kind reported in this paper combined with small scale studies on the ground will be a valuable approach for elucidating the spatial dynamics of birch forest moth outbreaks in a changing climate.

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