To be or twice to be? The life cycle development of the spruce bark beetle under climate change

Holger Lange, Bjørn Økland and Paal Krokene
Norwegian Forest and Landscape Institute
Høgskoleveien 8, N-1432 Ås, Norway
holger.lange@skogoglandskap.no

Abstract

We analyze the impact of climate change on the life cycle of the spruce bark beetle *Ips typographus* by means of a temperature-driven threshold model and temperature data from a network of more than 300 climate stations in Scandinavia. Using observed temperatures as well as climate model simulations, our model results exhibit univoltine behavior under current conditions, but predicts almost strictly bivoltine behavior for southern Norway in 2071-2100. The dynamics of this threshold phenomenon is investigated in detail. By logistic regression, the impact of regional warming can be described as a northward movement of bivoltinism by some 600 kilometers. Extension to two generations per year (bivoltinism) might increase the risk of devastating bark beetle outbreaks, although the impact of photoperiod-induced diapause in late summer and the ratio of soil or under-bark hibernations should be taken into account.

1. Introduction

Insects are physiologically sensitive to temperature, have short life cycles and great mobility, and their developmental rates and geographical distributions are therefore highly responsive to changes in temperatures. Even a small increase in mean yearly temperature may have severe consequences for agriculture and forestry through insect pests (Logan et al. 2003).

One important aspect of insect development is *voltinism* (the number of generations per year), which varies both between species and geographically within one species. In temperate regions, where winters are too cold for development to proceed, the number of generations is limited by the length of the growing season. There is usually only a certain developmental stage that is able to survive the winter, and the insects need to synchronize their development with the phenology (Logan and Bentz 1999), e.g. by completing either one or two generations per year (*uni-* or *bivoltinism*). Studies e.g. from North America have indicated that changes in voltinism can have profound effects on the outbreak dynamics of tree-killing bark beetles, and thus have severe consequences for tree mortality (Hansen and Bentz 2003). On the other hand, the role of a second generation may be less important for the frequency of outbreaks when resource-depletion dynamics is a dominating factor (Økland and Bjørnstad 2006).

The Eurasian spruce bark beetle *Ips typographus* (L.) is one of the most destructive forest insects in Europe. In Norway, Sweden and Finland *I. typographus* normally has only one generation per year (Annila 1969), but in particularly warm summers a second generation has been initiated in southern Sweden (Butovitsch 1938) and southern Norway (Austaraa et al. 1977). Empirical studies under Norwegian conditions have indicated that the summer is too short to complete the second generation. Most individuals reach the pupal stage, which is less cold tolerant than the adult stage and does not survive the following winter (Austaraa et al. 1977). Bivoltinism is, however, common in Central Europe, and up to three generations of *I. typographus* have been assumed to develop in warm years (Harding and Ravn 1985). If global warming extends the growing season, a higher proportion of the second generation may reach the cold hardy adult stage and survive the winter. Future temperature increase may thus lead to a northward expansion of the areas experiencing two beetle generations per year. This work attempts to estimate the northward spread of *Ips typographus* bivoltinism using regional climate scenarios for Norway.

The development of bark beetles and other insects has often been modelled accurately on the basis of temperature alone (Logan and Powell 2001). Developmental rates are almost zero below a lower, developmental stage dependent temperature threshold, and increase more or less linearly with temperature over a restricted (but ecologically relevant) temperature range above this threshold. Here we present a phenologically detailed model that describes the seasonal development of the spruce bark beetle based on *degree-day sums*, which has been validated in a rearing cage experiment (Wermelinger and Seifert 1998) and also reproduces the few observations of bivoltinism from southern Norway well. We use a large set of historical temperature time series to explore the current geographical distribution of bivoltine development in Norway, and its possible future spread using regional climate scenarios.

2. The model of bark beetle development

The current model was developed based on experimental data from Wermelinger and Seifert (1998), as this study provides all necessary parameters to model development, and their values agree reasonably well with other studies (Annila 1969; Netherer and Pennerstorfer 2001). Our model calculates bark beetle development using daily mean (air) temperatures from a time series of several years as input data. For each of five developmental stages $\alpha(=1,2,3,4,5)$ (Table 1), the onset and closure Julian dates within a given year, d_1^{α} and d_2^{α}, are determined through the condition that

$$D^o\left(d_1^\alpha, d_2^\alpha\right) = \sum_{d=d_1^\alpha}^{d_2^\alpha} \left(T(d) - T^\alpha\right) \Theta\left(T(d) - T^\alpha\right) \qquad (1)$$

equals or just exceeds stage-specific degree day thresholds F^α. Here, d is the Julian day within a year, $T(d)$ is the daily mean temperature, T^α is the stage-specific threshold temperature for development, below which development stops, Θ is the Heaviside function ($\Theta(x) = 0$ for $x < 0$ and $\Theta(x) = 1$ for $x > 0$), and D^o is the degree days function. The model is used to represent the centre value of a beetle cohort that may be followed throughout the year, provided that its dispersion is sufficiently small (which seems to be a plausible assumption). In addition, initiation of mass-flight in spring requires a maximum daily temperature above 19.5 ºC (Annila 1969). Beetle development thus proceeds according to accumulated D^o above certain stage-specific developmental threshold temperatures (egg stage, larval stages, pupae, immature adults; Table 1).

2.1 Bivoltine potential and bivoltine fraction

When the first generation (spring generation) has completed its development, a second summer generation is initiated when temperatures are favorable for flight. If development of the second generation could not be completed before the temperature drops below zero in the autumn, the model recorded the fraction of completion of the pupal stage (as number of stage-specific D° reached, divided by total D° required for completion of pupation). This fraction is termed *bivoltine potential* (BP), a real-valued variable to be correlated with site and climatic properties in the next section. If the second generation can be completed to the adult stage, the BP of the site in the given year is one.

The spatial distribution of bivoltinism in Norway is investigated by dividing, for each station, the number of years where the second generation actually has been completed (BP=1) with the observation length (usually 30 years). This ratio is the *bivoltine fraction* (BF) of a location. Since an immature second generation is not expected to survive the next winter, BF is a better impression of the long-term spatial spread of bivoltinism compared to BP.

Table 1. Standard parameter values for stage specific developmental threshold (T^α) temperatures and heat sum requirements (D°) for *Ips typographus* (from Annila 1969 and Wermelinger and Seifert 1998).

Stadium α	T^α (°C)	D°($K \cdot \text{days}$)
Flight of 1st generation	5	110
Egg	10.6	51.8
Larvae	8.2	204.4
Pupae	9.9	57.7
Immature adult	3.2	238.5

2.2 Diapause and photoperiod

It is well known that certain environmental conditions can trigger the onset of diapause, i.e. a physiological state of dormancy, in insects, which is considered to be a risk-avoiding behaviour. An example for such a trigger is light availability, determined by the photoperiod or daylength for a given calendar date and location, combined with unfavorable temperature conditions. However, the mechanisms behind the onset of diapause and the inhibition of development and late-summer swarming are poorly understood, making a model assessment difficult (Jönsson et al. 2007). A detailed phenological model (Baier et al. 2007) concluded that 14.5 hours is to be considered as the critical daylength were bark beetle in the Austrian Alps start diapausing, whereas rearing cage studies indicate a photoperiod between 16 and 18 hours for Scandinavian and central European populations (Dolezal and Sehnal 2007). This phenotypic plasticity renders the effect of photoperiod limitation uncertain. We shortly comment on its importance in our context in the results section.

3   Temperature data used in the model

3.1 Measured temperature data

The historical data used were based on 337 meteorological stations covering conterminous Norway (Skaugen and Tveito 2004). Daily means and, if available, daily maxima were used. In accordance to standards in climate research, the 30 years reference period 1961 to 1990 has been selected as « presence ». To further explore the geographical distribution of bivoltine development in Europe, the developmental model was also run with 16 historical mean daily temperature data from selected localities along a latitudinal gradient through Sweden, Denmark and Germany.

3.2 Regional climate scenarios

We ran the developmental model with three dynamically downscaled temperature scenarios for Norway from two different climate models (Hadley AGCM model with the A2 and B2 emission scenarios and the ECHAM4 model with the B2 scenario). The scenario period was 2071-2100. Using the REGClim approach (Skaugen and Tveito 2004), the downscaling procedure yields gap-free daily mean temperatures for the full 30-year scenario period for each of the 337 Norwegian stations.

4   Exploring the developmental model

4.1 Sensitivity analysis for the model

Each of the 10 parameters given in Tab. 1 was subjected to changes to investigate the crucial factors determining BP, using a site with a medium value (BP=0.3) for the standard set and measured temperatures. Apart from the immature adult threshold and heat sum requirement, all parameters strongly influence BP; e.g., a 20% decrease of the heat sum parameter for the larvae stage increases BP from 0.3 to 0.7. Thus, the parameters of the model are relatively well-defined.

For the location Ås, where a longer uninterrupted temperature series (1952–2005) was available, the impact of mean values in temperature for individual months was calculated by simply shifting daily values by constant amounts. This impact turned out to be rather strong; particularly decisive were August and September values, where a shift of less than +1° C changes the BP from 0.1 to 1. Swarming start dates for the first generation of the year always lay between July 18th and September 10th, which is in good agreement with this result.

The strength of the temperature – bivoltinism relation was studied in a first step in a highly aggregated manner by using annual average temperatures for all 353 sites on one hand, and 30-year average of BP on the other (Fig. 1).
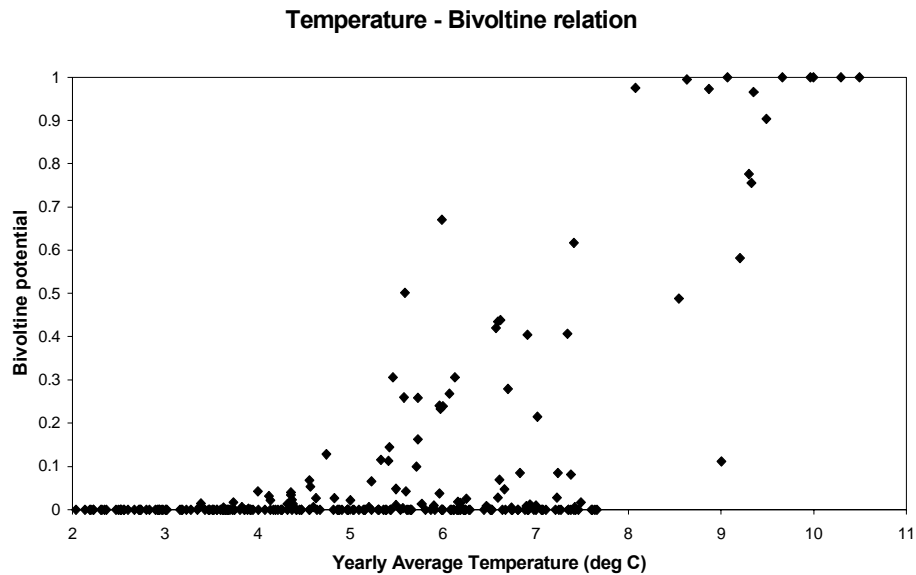
Temperature - Bivoltine relation

Figure 1. The relation between annual mean temperatures and bivoltine potential for 353 stations.

It is obvious that this relationship is double-sided thresholded, with approximate limit temperatures of resp. 4 and 9.5° C. The relation between these limits is not particularly strong but clearly nonlinear (S-shaped). Although the chosen independent variable is extremely aggregated and simple, the correlation is significant. We also tried to determine the part of the year for which the temperature history is most decisive for the development. D° values were calculated for a time window starting at a given day of the year and with a certain length, and these sums were correlated with the BP again for Ås (1952-2005). The optimal correlation (r=0.8) is achieved for a window running from May 12th to September 13th. For this window, a steep ramp-like connection between D° and BP exists, switching from BP=0 at 1200 $K \cdot days$ to BP=1 at 1300 $K \cdot days$.

Our developmental model so far corresponds to a critical daylength (CD) of 0 hours. The effect of diapausing was investigated by simply varying CD between 0 and 18 hours. When actual daylength falls below this threshold, the development of the second generation ceases independent of temperature. The BP remains stable up to approx. 12-13 hours and then starts to drop. For observed temperatures in Ås, BP is halved at 14.5 hours, the estimate of (Baier et al. 2007), and vanishes for 17 hours and

more, the latter representing an implausible value given the maximum daylength of 18.5 hours for this location. The photoperiod limitation requires further investigation.

4.2 Bivoltinism under current and future climatic conditions

Under current (1961-1990) climate conditions, a nonvanishing BP is restricted to the region around the Oslofjord in SE Norway, confirming empirical observations (Fig. 2, left panel). North of 65 degrees latitude, not even a completed first generation could be found by the model. The picture changes dramatically when using the climate scenarios (2071-2100). The right panel of Fig. 2 shows the results for the Hadley B2 scenario, which is the mildest among the three investigated in terms of spatiotemporal average temperature increase predicted (2.5º C from 1961-1990 to 2071-2100). According to these temperature predictions, the occurrence of bivoltinism is very common at least for large parts of southern Norway. Several locations show two generations in every single year within the 30 year period; a few sites at higher elevations continue to be unfavorable for a second generation.

4.3 Climate Change as shift in latitude for *Ips typographus*

A phenomenological description of the bivoltinism – latitude relationship was performed in the following way. We seek a parametrization of the bivoltine fraction which interpolates between a value of 100% south of a threshold latitude, as indicated by the temperature series from Central Europe, and zero in regions far north unsuitable for spruce trees, and which is S- shaped between these two extremes. The following (logistic) function fulfils these requirements:

$$BP = \frac{1}{1 + \exp\left(\alpha \log\left((\phi - \phi_s)/(\phi_{90} - \phi)\right) - \gamma\right)} \tag{2}$$
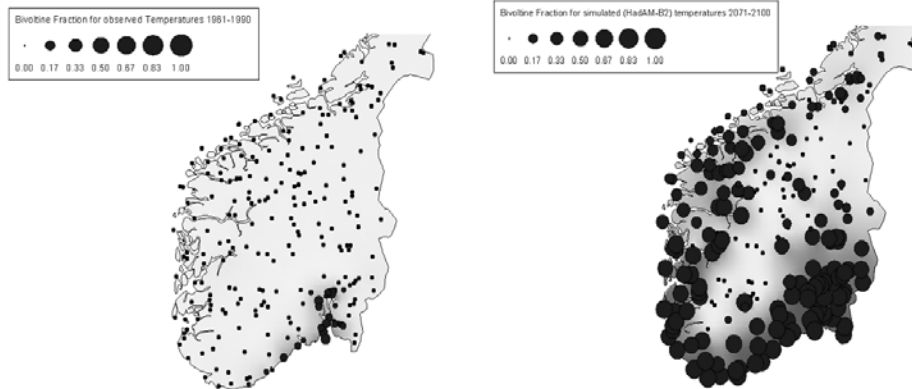

Figure 2. Bivoltine Potential (BP) according to our model (eq. (1)) for southern Norway. Seven classes for the 30-years average BP have been built. Left panel: using observed temperatures from 1961 to 1990 ; right panel: Hadley model B2 scenario for 2071 to 2100.
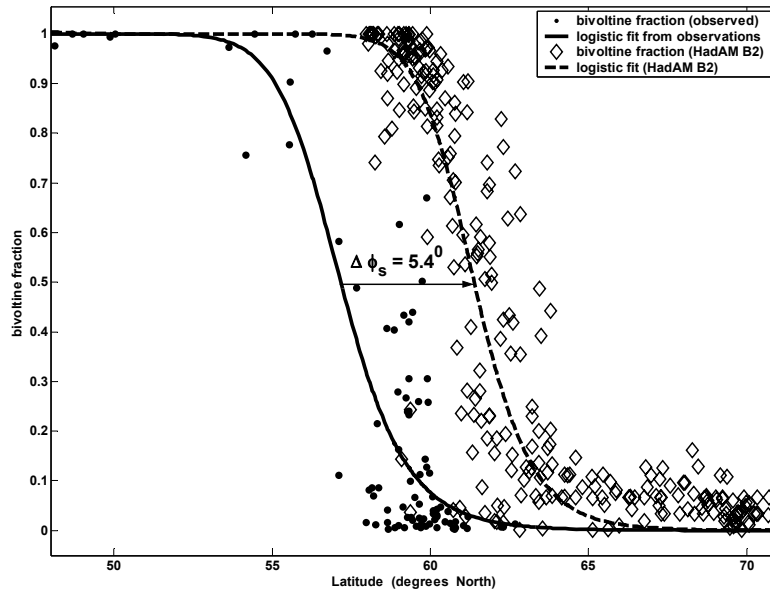
Figure 3. Bivoltine fractions calculated from observed temperature series (1961-1990) and the HadAM B2 scenario for 2071-2100, and respective fits using a logistic function with three parameters. The resulting northward shift is indicated by the arrow.

where ϕ is geographical latitude; for simplicity, we require the bivoltine fraction to be vanishing only at the North Pole (ϕ_{90}); ϕ_s is the southern threshold latitude, and α and γ are empirical shape parameters of the function. For observed temperature series, this approach leads to a satisfying fit shown in Fig. 3 ($R^2 = 0.75, RMSE = 0.17$; both α and γ estimates were highly significant different from zero). The optimal value for the latitude threshold was found to be $\phi_s(obs) = 48^0$. Assuming that this empirical relationship holds unchanged in structure as well for the climate scenarios, we fixed the values for α and γ obtained and readjusted the threshold latitude. Fig. 3 shows the result for the HadAM B2 climate scenario. The optimal value found was $\phi_s(HadAMB2) = 53.4^0$, and the performance of the fit was even slightly better ($R^2 = 0.80, RMSE = 0.16$). Thus, for this climate scenario, a northward movement of the change in reproduction cycle of $\Delta\phi_s = 5.4^0$, or 600 km with a standard deviation of only 10 km, is predicted. Other scenarios give qualitatively similar results.

5. Summary

We developed a simple model that makes use of easily available data, which can be run with relatively well-defined parameters, and which agrees with field observations. Using this model on historical as well as climate scenario temperature series, Norway seems to be in a highly transient situation where the life cycle of *Ips typographus* changes from univoltine to bivoltine. This shift has potentially profound effects on the

spruce forest ecosystem and on forestry. With two generations per year, there will also be two attack periods on spruce annually, one in the spring and one in July/August. It worsens the situation that Norway spruce is probably more susceptible to beetle attacks later in the summer than during the current flight period in mid-May. The current study does not analyze the role of adaptation strategies of Norway spruce and *Ips typographus* for life cycle development and outbreak dynamics under future conditions.

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