Thresholds in the life cycle of the spruce bark beetle under climate change

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Abstract

Using a simple temperature-driven multistage threshold developmental model, we analyse the impact of climate change on the life cycle dynamics of the spruce bark beetle *Ips typographus*. The completion of a full reproductive second generation within a single year (bivoltinism) might increase the risk of devastating bark beetle outbreaks. A network of more than 300 climate stations, comprising time series of air temperatures both observed as well as simulated using regional climate models, is exploited on the country scale. It is shown that current conditions strongly favor univoltine behavior, whereas climate scenarios predict almost strictly bivoltine behavior for southern Norway in 2071-2100. The dynamics of this threshold phenomenon is investigated in detail. Using a logistic regression, the impact of regional warming can be described as a northward movement of bivoltinism by some 600 kilometres. Thus, the risk for Norway spruce infestations in Scandinavia may be drastically increased over the next decades.

1. Introduction

Climate rules natural as well as managed ecosystems. For instance, even a small increase in mean yearly temperature may have severe consequences for agriculture and forestry through effects on pathogens and insect pests. Insects are physiologically sensitive to temperature, have short life cycles and great mobility, and their

developmental rate and geographical distribution are therefore highly responsive to changes in temperatures.

One important aspect of insect development is their *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 that can be completed is limited by the length of the growing season. For a given species, 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, 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, where it has killed more than 50 million m^3 of Norway spruce (*Picea abies*) in large-scale outbreaks since the 1940's (Christiansen and Bakke 1988; Führer 1996; Worrell 1983). 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; Trägårdh and Butovitsch 1935) and southern Norway (Austaraa et al. 1977). Closer 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 temperature threshold, and increase 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 and also reproduces the few observations of bivoltinism from southern Norway. 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. Bark beetle developmental model

The current model was developed based on experimental data from Wermelinger and Seifert (1998). This is the most recent study that provides all the necessary parameters to model development, and their values agree reasonably well with other studies (e.g. Annila 1969, Netherer and Pennerstorfer 2001). Data on initiation of beetle flight in the spring are taken from Annila (1969). 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

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

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).

The initiation of mass-flight in spring requires a certain maximum daily temperature, since flight of *I. typographus* mainly takes place at temperatures above 19.5 ºC (Annila 1969). If available, measured daily maximum temperatures (T_{max}) were used; if not the mean difference between mean and maximum temperature from other stations were used to increase the daily mean values a few degrees (typically 4-5 ºC during summer). In addition to T_{max}, mass-flight is controlled by the accumulation of degree-days (D^o) above a threshold temperature of 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 The bivoltine potential

When the first generation (spring generation) has completed its development, a second summer generation is initiated when temperatures are favourable 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.

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

Stadium α	T$^\alpha$ (°C)	D°($K\cdot$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

3   Temperature data used in the model

Ease of availability demands the use of measured air temperatures at 2 m height for the developmental model. Microclimatic measurements of inner bark temperatures may be more relevant for calculation of developmental rates; however, although the temperature in the inner bark is always higher than in the air, Netherer et al. (2004) and others showed that the difference was much smaller on trees inside a stand than on edge trees, and was negligible inside stands and during overcast days. Our model results based on air temperatures may thus be regarded as conservative but not too pessimistic estimates of the true developmental rates, and are representative for bark beetles developing in trees inside a forest stand.

3.1 Measured temperature data

The historical data used were obtained at a set of 337 meteorological stations covering conterminous Norway. They form the backbone of routine monitoring of temperature by the Norwegian Meteorological Institute (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, which is a standard choice. 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
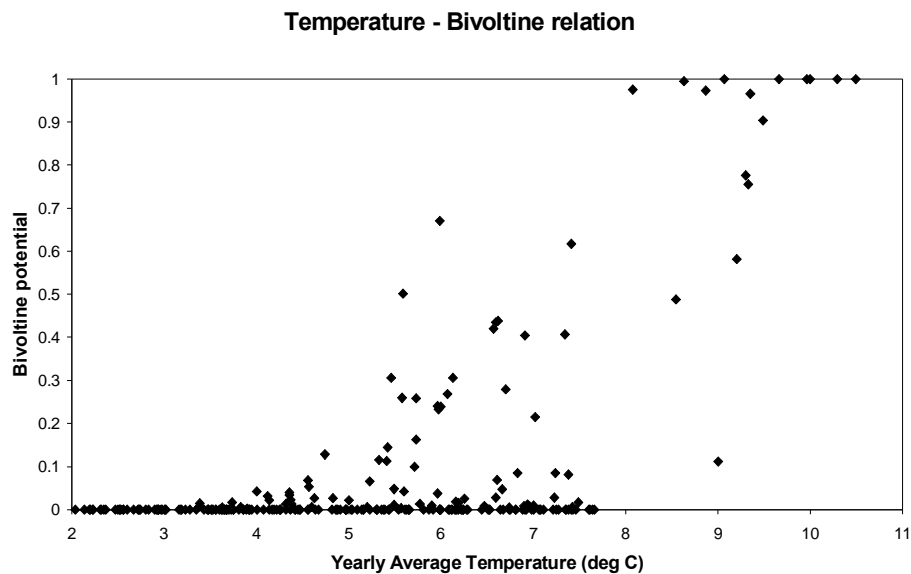
Figure 1. The relation between annual mean temperatures and bivoltine potential for 353 stations.

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.

In a second step, we tried to determine the part of the year for which the temperature history is most decisive for the development. To that end, D° values were calculated for a time window starting at a given day of the year and with a certain length (in days), and correlate these sums with the BP again for Ås (1952-2005). The resulting correlation landscape is shown in Fig. 2. The optimal correlation (r=0.8) is achieved for a window running from May 12th (day 133) to September 13th (period length 124 days). This maximum is relatively well-defined, but extending the period in both directions still leads to high correlations; e.g., including the whole year-D° leads to r=0.68 (lower right corner of the graph). For the optimal 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 $K \cdot days$.

In order to test the universality of this optimal temporal window, it was used to correlate D° with BP for all the other stations. It turned out that for a major fraction of the Norwegian sites, BP was highly correlated to the windowed D° ($r > 0.5$), whereas further south some of the BP series were non-significantly, or even negatively, correlated to it. Early spring (prior to budburst in Norway) temperatures might as well be important at these locations.

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. 3, 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. 3 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; however, there is a huge spatial variability, with e.g. much higher increases in mountainous ranges of southern Norway, and a few percent of the sites showing even a negative trend). 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 unfavourable for a second generation.
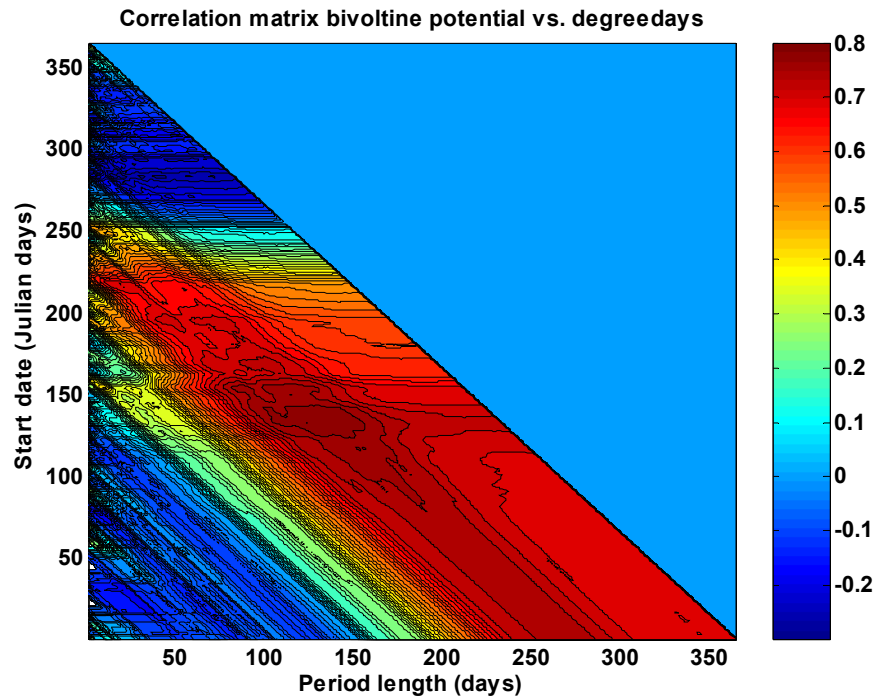
Figure 2. Correlation landscape for Ås temperatures, 1952-2005. Shown is the color-coded correlation coefficient *r* between bivoltine potential and degree days sums (threshold 5° C), varying start date as well as period length for calculation of the sums. (The upper right triangle corresponds to meaningless combinations of start date and period length.)
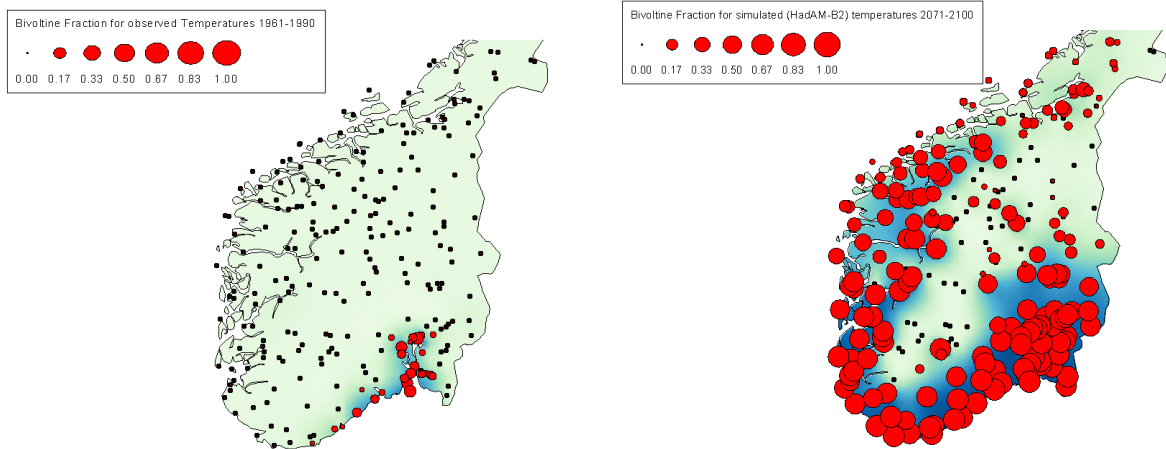

Figure 3. Bivoltine Potential (BP) according to our model (eq. (1)) for southern Norway. Seven classes for the 30-years average BP have been built. Left panel: using observed temperatures from 1961 to 1990 ; right panel: Hadley model B2 scenario for 2071 to 2100.

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 comprising three adjustable parameters fulfills these requirements:

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

where ϕ is geographical latitude ; for simplicity, we require the bivoltine fraction to be vanishing only at the North Pole, with geographical latitude ϕ_{90} ; ϕ_s is the southern threshold latitude, and α and γ are empirical shape parameters of the function.
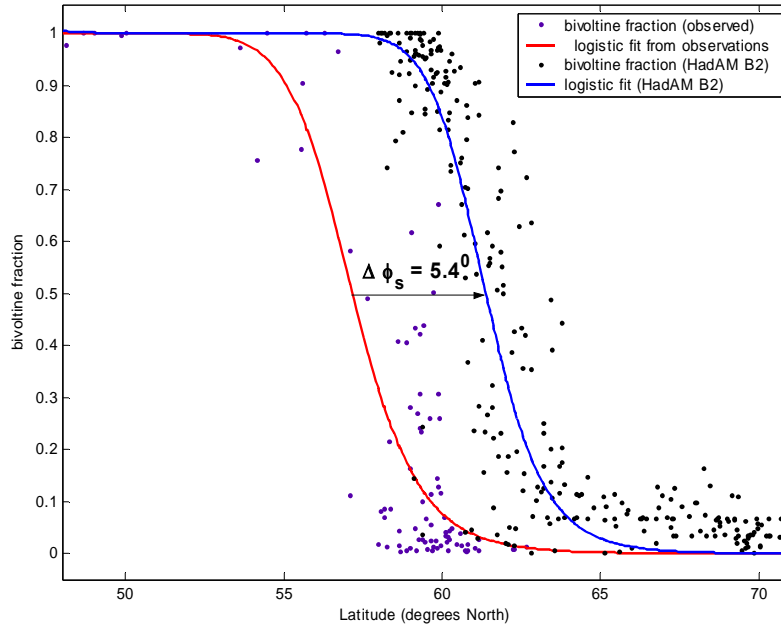
Figure 4. Bivoltine fractions calculated from observed temperature series (1961-1990) and the HadAM B2 scenario for 2071-2100, and respective fits using a logistic function with three parameters. The resulting northward shift is indicated by the arrow.

For observed temperature series, this approach leads to a satisfying fit shown in Fig. 4 ($R^2 = 0.75, RMSE = 0.17$; both α and γ estimates were highly significant different from zero). The optimal value for the latitude threshold was found to be $\phi_s(obs) = 48^0$ (which is, e.g., the southernmost part of Germany, a few kilometres north of the Alps).

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. 4 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 conceptually simple model which makes use of data often easily available, can be run with relatively well-defined parameters, reproduces rearing cage experiments and confirms qualitative observations in the field. 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 may possibly have profound effects on the spruce forest ecosystem and on forestry. With two generations per year, there will also be two attack periods on spruce, 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. It is self-evident that these statements hold under the current climate; we cannot exclude the possibility of adaptation strategies of Norway spruce under future conditions.

References

Annila, E, 1969, Influence of temperature upon the development and voltinism of *Ips typographus* L. (Coleoptera, Scolytidae). *Ann. Zool. Fennici* **6**, 161-208.

Austaraa, Ø., Pettersen, H. and Bakke, A. 1977. Bivoltism in Ips typographus in Norway, and winter mortality in second generation. *Medd. Nor. Inst. Skogforsk* **33**, 272-281.

Butovitsch, V., 1938, Om granbarkborrens massförökning i södra Dalarne. *Norrlands Skogsvårdsforbunds Tidskrift* **1938,** 91-126.

Christiansen, E. and Bakke, A. 1988, The spruce bark beetle of Eurasia. In: Berryman, A.A. (Ed), Dynamics of forest insect populations. *Population ecology: theory and application*. Plenum Press, New York, 479-503.

Führer, E., 1996, Entomologische Aspekte der Umwandlung montaner Fichtenforste. *Entomologia Generalis* **21** (1-2), 1-15.

Hansen, E.M. and Bentz, B.J., 2003, Comparison of reproductive capacity among univoltine, semivoltine, and re-emerged parent spruce beetles (Coeloptera: Scolytidae). *The Canadian*

Entomologist **135**, 697-712.

Harding, S. and Ravn, H., 1985, Seasonal activity of Ips typographus in Denmark. *Z. Angew. Ent.* **99**, 123–131.

Logan, J.A. and Powell, J.A., 2001, Ghost Forests, Global Warming, and the Mountain Pine Beetle (Coleoptera: Scolytidae). *Amer. Entom.* **47 (3)**, 160-172.

Netherer, S. and Pennerstorfer, J., 2001, Parameters Relevant for Modelling the Potential Development of *Ips typographus* (Coleoptera: Scolytidae). *Integrated Pest Management Reviews* **6 (3 - 4)**, 177-184.

Netherer, S., Pennerstorfer, J., Baier, P., Schopf, A., Führer, E., 2004, Modellierung der Entwicklung des Fichtenborkenkäfers, Ips typographus L., als Grundlage einer umfassenden Risikoanalyse. *Mitt. Deut. Gesell. Allg. Ang. Ent.* **14**, 277–282.

Økland, B. and Bjørnstad, O.N., 2006, A resource depletion model for forest insect outbreaks. *Ecology* **87(2)**, 283-290.

Skaugen, T.E. and Tveito, O.E., 2004, Growing-season and degree-day scenario in Norway for 2021-2050. *Climate Research* **26 (3)**, 221-232.

Trägårdh, I. and Butovitsch, V, 1935, Redogjörelse för barkborrekampanjen efter stormhärjningarna 1931-1932. *Medd. Statens Skogsforörsöksanstalt* **28**, 1-268.

Wermelinger and Seifert, 1998, Analysis of the temperature dependent development of the spruce bark beetle *Ips typographus* (L.) (Col., Scolytidae). *J. Appl. Ent.* **122**, 185-191.

Worrell, R., 1983, Damage by the spruce bark beetle in south Norway 1970-80: a survey, and factors affecting its occurrence. *Medd. Nor. Inst. Skogforsk.* **38** (6), 1-34.