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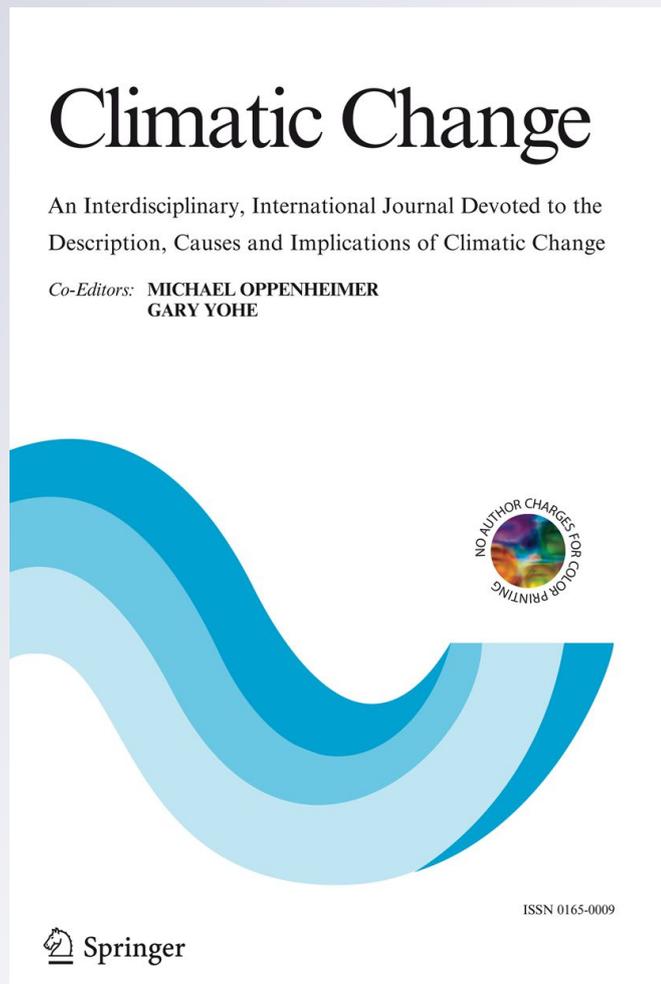
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Modelling the potential impact of global warming on *Ips typographus* voltinism and reproductive diapause

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Abstract The Eurasian spruce bark beetle, *Ips typographus*, is one of the major forest insect pests in Europe, capable of mass-attacking and killing mature Norway spruce trees. The initiation and development of a new generation are strongly controlled by temperature and a warmer climate may affect the number of generations that is produced per year and hence the outbreak dynamics. Experimental knowledge regarding reproductive diapause adaptations is, however, too sparse for large-scale assessments of future trends. We developed a model description of diapause induction, and used gridded observational temperature data to evaluate multiple combinations of day length and temperature thresholds to find the model parameterisation most coherent with *I. typographus* monitoring data from Scandinavia. The selected model parameterisation is supported by European literature data, though further experimental studies are required to analyse population specific adaptations and capacity for adjustments to changing climate conditions. Implementing the

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model description of reproductive diapause in a temperature driven model of bark beetle phenology (swarming activity and development from egg to mature bark beetle), enabled us to assess the length of the late summer swarming period that is a critical determinant of the risk of forest damage. By using regional climate model data we show that higher temperatures can result in increased frequency and length of late summer swarming events, producing a second generation in southern Scandinavia and a third generation in lowland parts of central Europe. Reproductive diapause will not prevent the occurrence of an additional generation per year, but the day length cues may restrict the length of the late summer swarming period.

1 Introduction

Climate models driven by different scenarios for future emission of greenhouse gases project a likely global temperature increase between 1.1 and 6.4°C by the end of this century (IPCC 2007). This can have profound ecosystem effects by inducing phenological changes and northward shifts in the distribution of both plant and animal species (Parry et al. 2007), including major pest species that can have dramatic effects on forest ecosystems (Carroll et al. 2003; Hagen et al. 2007; Kurz et al. 2008; Vanhanen et al. 2007). For several species, ongoing changes have already been indicated (Kurz et al. 2008; Menzel et al. 2006; Parmesan 2006). In addition, climate extremes may become more common due to increased climatic variability (Schär et al. 2004; Good et al. 2006; IPCC 2007), and extreme events such as prolonged summer drought, extended water logging, wind storms and spring frost episodes may damage trees. Subsequent damage from secondary organisms, such as bark beetles, may be even more substantial than the triggering climatic events and can lead to extensive tree mortality (Nihlgård 1997; Rouault et al. 2006).

The Eurasian spruce bark beetle *Ips typographus* L. (Coleoptera, Curculionidae) is one of the most important pests of mature Norway spruce (*Picea abies* L. Karst.; Christiansen and Bakke 1988; Schelhaas et al. 2003). Like other insects, *I. typographus* is sensitive to temperature (e.g. Bakke 1992), which strongly influences the number of generations that can be initiated per year. The onset of spring swarming is affected by two temperature dependent factors: emergence from winter hibernation and a temperature threshold for flight activity (Annala 1969; Wermelinger and Seifert 1998; Wermelinger 2004). Temperature also controls the developmental time from egg to mature bark beetle (Annala 1969; Harding and Ravn 1985; Wermelinger and Seifert 1998; Netherer and Pennerstorfer 2003). The life stage to which temperature allows the offspring to develop before winter is of particular interest, as only adult beetles are well adapted to survive the winter, whereas eggs, larvae and pupae are facing high winter mortality (Annala 1969; Faccoli 2002; Baier et al. 2007).

Today, *I. typographus* generally has one generation per year in Sweden, Norway and Finland (Eidmann 1965; Annala 1969; Bakke 1983), but attacks by a second generation have been observed both in southern Norway and Sweden (Austarå et al. 1977 and references therein). Two generations per year are common in Denmark (Harding and Ravn 1985) and central Europe below 600 m altitude (Seitner 1923–24; Bender 1948; Kuhn 1949; Merker 1952; Wild 1953), but not at higher elevations (Schimitschek 1931; Wermelinger and Seifert 1999). In lowland parts of central Europe, favourable temperature conditions may even support the initiation of a

third generation (Merker 1952; Wild 1953; Netherer 2003; Netherer and Nopp-Mayr 2005). Modelling studies indicate that summer swarming with development of a second generation may occur frequently at the end of the 21st century in both Norway (Lange et al. 2006, 2009) and Sweden (Jönsson et al. 2007, 2009) as an effect of climate change. However, the occurrence of reproductive diapause in the adult stage creates uncertainties in modelling the potential for two *I. typographus* generations per year in Scandinavia (Jönsson et al. 2007), as the factors inhibiting summer swarming are not well documented (Wermelinger 2004).

A study of five Scandinavian populations indicated latitudinal differences in the fraction of diapausing individuals (Forsse 1991). Dolezal and Sehnal (2007) showed that the onset of diapause was affected by a combination of day length and temperature conditions, as high or low temperatures could delay respectively advance diapause. Further, they discussed a possible impact of short days during spring on the timing of emergence from hibernation sites. Faccoli (2009) found no evidence of a third generation in the southeastern Alps, as only mature beetles that had completed their entire development at photoperiods above 15 h were able to initiate a new generation. Even though these studies report effects of temperature and day length for some local populations, the large-scale geographic patterns for inducing diapause in *I. typographus* remain unknown.

Species-specific phenological models driven by data from climate models are useful tools for assessing the impact of climate change on insect life cycles. The quality of such impact assessments is, however, influenced by model uncertainties

Table 1 Summary of the different steps in this study and the rationale for taking them

	Step	Rationale
1	Swarming threshold calibration	To reduce impact from biases associated with climate model data by comparison between simulated temperature dependent swarming activity and monitoring data.
2	Diapause model development	To reduce uncertainties associated with model calculation of bark beetle voltinism, and to be able to assess the length of the summer swarming period.
3	Diapause model parameterisation	Evaluate multiple combinations of day length and temperature thresholds to find the diapause model parameterisation that is most coherent with monitoring data.
4	Assessment of model performance	Compare bark beetle model calculations with and without the diapause extension to evaluate if the selected diapause model parameterisation represents a likely adaptation. Analysis of model sensitivity.
5	Impact of global warming on <i>I. typographus</i>	Run the extended bark beetle model with climate scenario data to simulate the number of generations and length of summer swarming period.

Steps 1–4 are required to extend the existing model of *I. typographus* phenology (Jönsson et al. 2007) by including reproductive diapause initiated by photoperiodic and thermal cues, and step 5 is required to use the extended model to assess the impact of global warming on beetle voltinism

and limitations. The goal of this study is to improve modelling of voltinism in *I. typographus* by investigating potential mechanisms behind inhibition of summer swarming and onset of reproductive diapause. Our first aim is to extend an existing model of *I. typographus* phenology, based on temperature only (Jönsson et al. 2007), by including reproductive diapause initiated by photoperiodic and thermal cues. For this purpose, we developed a method for using pheromone trap monitoring data in combination with climate data to assess thresholds of day length requirement and temperature conditions promoting reproductive diapause. Implementing reproductive diapause in the *I. typographus* phenology model will enable us to assess the frequency and length of the late summer swarming period with the initiation of a second or third generation, which are important determinants of the risk of forest damage in a warmer climate. Our second aim is to use the extended model to assess the impact of global warming on voltinism in *I. typographus*. An overview of the different methods used to fulfil the aims of this study is presented in Table 1. Uncertainties associated with the quality of climate data are considered both during model development and model calibration, and uncertainties related to the choice of regional climate model projections are taken into account when interpreting the results of impact model runs.

2 Material and methods

2.1 Original model

Here we give a brief outline of the original bark beetle phenology model, for a detailed description see Jönsson et al. (2007). The model has been developed for simulating large-scale trends of swarming and development of *I. typographus*, using gridded climate data with low spatial resolution (50 × 50 km) as input data. It is therefore, by necessity, more generalized in some aspects than modelling concepts that have been developed to simulate local, stand-specific topoclimatic conditions (Netherer and Nopp-Mayr 2005; Baier et al. 2007). Thermal sums are expressed as degree-days (dd) above a developmental threshold set to +5°C for all developmental stages, according to Annala (1969). Stage-specific thresholds (Wermelinger and Seifert 1998) were not used, as these would have increased model sensitivity to biases in climate model data (Jönsson et al. 2009). Emergence from winter hibernation was set to 120 dd (Annala 1969). Swarming was modelled to occur when the daily maximum temperature exceeded a temperature threshold, calibrated to fit the climate data sets used in this study in order to reduce uncertainties associated with climate model biases (see Section 2.4). Egg development was modelled to start on the seventh day after swarming, accounting for a pre-oviposition period (Wermelinger and Seifert 1999) and sufficient time to oviposit 50% of the eggs (Anderbrant 1990). Variation in microclimate within forest stands, in particular caused by differences in sun exposure, creates a continuum of breeding conditions for the beetles. Beetles developing in shaded substrates need more time to obtain the temperature sum needed for complete development than individuals in exposed substrates. Because our air temperature data does not reflect this difference we introduced two different thermal thresholds for development. The lower limit (625 dd) corresponds to completed

development in sun-exposed trees and the upper limit (750 dd) to development in shaded trees (Harding and Ravn 1985; Jönsson et al. 2007).

In this study, we included calculations of development of a third generation to be able to evaluate the influence of day length and temperature on beetle development during late summer over its entire distribution area in Europe. Swarming of the second generation was modelled to start on the first day with a maximum temperature above the swarming threshold, given that the lower temperature sum for completed development was fulfilled and that reproductive diapause was not indicated by diapause model parameterisation. Egg and larval development was modelled as for the two earlier generations.

2.2 Climate data for model development and climate change impact assessment

Three different climate datasets were used in this study. European weather data for the period 1950–2006 was obtained from the gridded observational dataset (daily temporal resolution, 0.44 degree spatial resolution), available via the EU-FP6 project ENSEMBLES (Haylock et al. 2008). The gridded observational dataset was used for model calibration and evaluation purposes, as it is not subjected to biases induced by any regional climate model. Daily temperature data from the regional climate model RCA3 (Kjellström et al. 2005) was provided by the Swedish Rossby Centre. At the lateral boundaries, RCA3 was forced by ERA 40 (1961–2005) and driven by output from the ECHAM5/MPI-OM (Jungclaus et al. 2006), SRES A1B climate change scenario (1950–2100; Nakićenović and Swart 2000). In this run, the RCA3 output data has a spatial resolution (grid cell size) of 0.44 degrees. The data was split into 30-year periods that were compared with each other. For our analysis, we used three periods: 1961–1990 (reference period), 2011–2040 and 2071–2100. Biases induced by the regional climate model were quantified by comparing bark beetle model runs using data from the gridded observational data set and RCA3 ERA40, as the boundary conditions of the RCA3 ERA40 run are related to observed weather data. Data from RCA3 ECHAM5/MPI-OM for the period of 1950–2005 is related to observed greenhouse gas forcing but not to observed weather conditions, and can therefore not be used in chronological comparisons. Data from RCA3 ECHAM5/MPI-OM scenario A1B was thus only used for analysis of climate change impacts. The projected annual temperature increase by the end of this century is approximately 2.5°C in the south part and 4°C in the north part of the *I. typographus* distribution area.

2.3 Monitoring data for model development

Monitoring data from Sweden, Norway and Denmark (Table 2) was used for model calibration and evaluation. The trapping period in which at least 10% of the annual catch occurred was used as a criterion for evaluating swarming temperature threshold parameterisation, and the period in which at least 90% of the annual catch was recorded was used as a criterion for evaluating diapause model parameterisation. The 10% threshold was selected to account for uncertainties associated with low temporal resolution of monitoring data, and for model calculations of swarming activity being based on gridded temperature data. Some flight activity is expected to have occurred before the calculated date in spring and after the calculated date in late summer, due to site-specific temperature conditions deviating from the gridcell

Table 2 Pheromone trap monitoring data of *I. typographus* from Sweden, Norway and Denmark used in model calibration and evaluation

Country	Years	No. of sites	Trap records
Sweden	1995–2007	4 sites in south and mid Sweden	Week 21, 24, 28, 33
	Started in 2005	30 sites in south and mid Sweden	Week 21, 24, 28, 33
	Started in 2006	2 sites in mid and north Sweden	Mid April–September every week
Norway	1979–1986	On average 130 traps per year, in more than 100 different sites in south and mid Norway	Week 21, 24, 28, 33 one week later in 1979 and for some sites during 1980 and 1981
Denmark	1993–1996	7–11 sites covering Denmark (1993 n = 9, 1994 n = 7, 1995 n = 11, 1996 n = 10).	May–September, every second week

average. The national datasets differ somewhat in quantity and quality, and the analysis was designed to make the best use of available information.

The Swedish pheromone trap data covers 12 years with records from groups of three traps in 4 to 36 sites per year, mainly in south and mid Sweden. Norwegian pheromone trap data covers eight years with records from groups of four traps in about 130 sites in south and mid Norway (128–139 sites per year). Swedish and Norwegian traps were set out May 1st and emptied four times during summer, and the model performance was evaluated based on whether or not the calculated date of spring swarming and last date of summer swarming were within the time interval given by the monitoring data.

The Danish pheromone trap data covers four years and a maximum of eleven sites with two-week trapping periods from May to September. The data series were not complete for every site and year, but datasets with incomplete spring records were included in the analysis when providing reliable information about late summer swarming. For this dataset, having a higher temporal resolution than the two other datasets, the swarming threshold parameterisation was evaluated by comparison between modelled timing and timing of the first period with trapped *I. typographus*. The diapause model parameterisation was evaluated by calculating the number of days between the date when accumulated trap catches exceeded 90% of the annual catch (i.e. the last 10%), and the modelled date for diapause induction. A value close to zero indicates a good correspondence between model and observation.

2.4 Swarming threshold calibration

Mass flight for reproduction is in general initiated when the daily maximum temperature exceeds 20°C (Annala 1969; Wermelinger 2004). However, daily maximum temperatures simulated by the RCA3 model output have been found to be approximately 4°C lower than temperature records from weather observations for the spring and summer season (March to August), whereas daily mean temperatures are closer to observations, mainly within the range of $\pm 1^\circ\text{C}$ for most parts of Europe (Kjellström et al. 2005). The biases are related to modelling of cloud water content, downward longwave radiation, and clear-sky downward shortwave radiation (Persson et al. 2007). Since it is not possible to correct the modelled daily maximum temperature, the correspondence between observed flight activity and the established temperature threshold is expected to be weak. The temperature threshold

parameterisation for swarming was therefore calibrated and validated both for the observational dataset and for RCA3-ERA40 data, using pheromone trap monitoring data. Swedish data was used for model calibration, testing the temperature thresholds of 16, 18, and 20°C. Data from Norway and Denmark were used for validation.

2.5 Diapause model development and parameterisation

The adaptive value of reproductive diapause in *I. typographus* can be illustrated by calculating the frequency of unsuccessful initiations of a second or third generation given the null hypothesis that *I. typographus* is unable to recognize any environmental cues that trigger reproductive diapause. A model of diapause induction including a day length requirement (H_x) and a subsequent temperature requirement (T_y) was then developed based on the assumption that *I. typographus* has adapted to arrest reproduction when these environmental cues indicate that the remaining thermal sum will be insufficient to complete a new generation before winter. The day length requirement makes the onset of diapause robust against temporary cold-spells during summer, and the temperature requirement prevents restrictions by day length thresholds during late summer periods with high temperatures (Dolezal and Sehnal 2007).

We used climate data for the reference period 1961–1990 to find the day length of the day during late summer when the thermal sum for the rest of the year was just sufficient for development of the new generation up to the stage able to survive winter. This calculation, carried out for each gridcell and two thresholds for winter survival (P_z), was done to test hypotheses about the impact of historical climate variations on the survival of *I. typographus* with different day length requirements for induction of diapause (H_x). Three assumptions about the strength of the selective pressure were analysed: H_1) strong impact from years with cold autumn temperatures, i.e. a day length requirement corresponding to the earliest date during the 30-year reference period, H_2) intermediate impact from cold autumns, i.e. a day length requirement corresponding to the average date during the reference period minus one standard deviation, H_3) weak impact from cold autumns, i.e. a day length requirement corresponding to the average date during the reference period. Day length, not including civil twilight, was calculated for each Julian day using the software Pgraph v1.3 (Jansson and Claréus 1996).

The model descriptions of day length requirement were tested alone and in combination with different temperature thresholds (T_y). Following an initial screening procedure to find temperatures with a potential to act as threshold cues, mean temperatures of 14°C, 15°C and 16°C and minimum temperatures of 10°C and 12°C were chosen for further analysis. The mean temperature threshold of 12°C and the minimum temperature thresholds of 5°C and 7.5°C were selected for additional comparisons, in order to cover the range of reported development thresholds (Annala 1969; Wermelinger and Seifert 1998).

I. typographus is not likely to survive winter under the bark of spruce trees unless it has completed the preimaginal development (Faccoli 2002), corresponding to 60% of the thermal sum required for total development (Baier et al. 2007). However, only completely developed beetles leave the brood trees in response to cold spells for hibernation in forest litter (Annala 1969). Hibernation below an insulating snow cover increases the chances for survival during cold winters, frequently occurring in

northern Europe. In this study, the combined effect of cues from day length and temperature was therefore evaluated for model calculations using two thresholds (P_z) expressed as percentages of completed development, 60% and 100% corresponding to 375 dd and 625 dd, respectively. The calculations were carried out for the temperature sum required to complete development in sun-exposed trees, as *I. typographus* generally prefers sun-exposed brood trees (Christiansen and Bakke 1988).

Temperature data from the gridded observational dataset was used for evaluating the multiple combinations of day length and temperature thresholds in order to find the diapause model parameterisation that is most coherent with monitoring data. The timing of summer swarming was calculated for the null hypothesis that *I. typographus* does not enter diapause ($H_0 T_0 P_{(60/100)}$). This was also calculated for the alternative hypotheses with three alternative day length thresholds in combinations with the daily mean temperature thresholds of 12, 14, 15 and 16°C ($H_{(1-3)} T_{\text{mean}(1-4)} P_{(60/100)}$), daily minimum temperature thresholds of 5, 7.5, 10 and 12°C ($H_{(1-3)} T_{\text{min}(1-4)} P_{(60/100)}$) and without temperature influence ($H_{(1-3)} T_0 P_{(60/100)}$). In total 54 combinations ($H_x = 3$, $T_y = 9$, $P_z = 2$) were used for calculating the latest day of swarming, and monitoring data was used to evaluate the performance of the different model parameterisations.

2.6 Assessment of model performance

A comparison between bark beetle phenology model calculations with and without the diapause extension was carried out to evaluate if the selected diapause model represents a likely adaptation. We evaluated model sensitivity to temperature threshold parameterisation by calculating the relative model performance (see below), with a deviation of $\pm 1^\circ\text{C}$ from the selected best model fit. In addition, the possibility of using a simple diapause model dependent on cues from temperature alone ($H_0 T_y P_{100}$) was evaluated using the same method.

The performance of the alternative hypothesis, defined by the $H_x T_y P_z$ diapause model parameterisation, was compared with the performance of the null hypothesis $H_0 T_0 P_z$ by calculating a ratio (R_{xyz}). The ratio was based on model simulations covering the reference period 1961–1990 and included the initiation of both a second and a third generation. First the difference between the number of years (yrs) with summer swarming (S) and the number of years when the developmental stage for winter survival (P_z) was reached was calculated for the null hypothesis as $H_0 T_0 S_{\text{yrs}} - H_0 T_0 P_{z-\text{yrs}}$; i.e. the number of years with suboptimal performance of the null hypothesis. Then the number of successful swarming events not detected by the alternative hypothesis ($H_0 T_0 P_{z-\text{yrs}} - H_x T_y P_{z-\text{yrs}}$; i.e. weaker performance of the alternative hypothesis), and the number of unsuccessful swarming events not eliminated by the alternative hypothesis ($H_x T_y S_{\text{yrs}} - H_x T_y P_{z-\text{yrs}}$; i.e. no improved performance by the alternative hypothesis) was subtracted. Finally, the performance of the alternative hypothesis was expressed as a ratio by dividing the obtained number with the total number of years: $R_{xyz} = ((H_0 T_0 S_{\text{yrs}} - H_0 T_0 P_{z-\text{yrs}}) - (H_0 T_0 P_{z-\text{yrs}} - H_x T_y P_{z-\text{yrs}}) - (H_x T_y S_{\text{yrs}} - H_x T_y P_{z-\text{yrs}}))/30$. This ratio varies between -1 and 1 . A positive ratio indicates that the parameterisation of the diapause model reduced the number of potentially unsuccessful late summer swarming events, whereas a negative ratio indicates that the diapause model reduced the number of potentially successful summer swarming events.

2.7 Impact of global warming on *I. typographus*

Based on evaluation with monitoring data, the diapause model parameterisation $H_1 T_{\text{mean}15} P_{100}$ was selected for analysing the impact of climate change on *I. typographus* voltinism. For both the second and the third generation, the length of the potential swarming period was calculated as the interval between the first swarming event after completion of the parental generation and modelled onset of diapause. Early and late swarming was calculated based on the lower and upper temperature sum for completed development of the parental generation (625 and 750 dd, see Section 2.1). The calculations were based on the model assumption that the day length requirement of *I. typographus* will not change in response to climate change. In addition, the potential change in day length requirement was calculated for the two climate periods 2011–2040 and 2071–2100 according to the H_1 assumption of selective pressure. The potential length of the swarming period was then calculated for 2071–2100, the modelling period when the effect of global warming is most pronounced. The increase in length of swarming period was expressed as the additional number of days, given the assumption that *I. typographus* will be in equilibrium with the new climate conditions.

We also calculated the day length for the earliest date in each time period when the swarming threshold was exceeded, to consider the possibility that day length requirement may postpone spring swarming in years when the temperature requirements for swarming are fulfilled at an early date. All model calculations were performed in MATLAB (7.0.4, The MathWorks Inc.).

3 Results

3.1 Swarming threshold calibration

Modelled date of spring swarming was compared with Swedish pheromone trap monitoring data, and a swarming threshold of 16°C daily maximum temperature was found to be optimal for model runs both with the gridded observational dataset and with RCA ERA-40 (Fig. 1). Using temperature thresholds of 16, 18, and 20°C, 75%, 60% and 53% of the modelled onset of spring swarmings fell within the observed onset period, respectively. Varying the swarming threshold between 16–20°C resulted in a larger span in modelled timing of spring swarming for RCA ERA-40 than for the gridded observational dataset, indicating an effect of RCA3 model biases. Model calculations using RCA ERA-40 data and a threshold of 16°C could identify the onset of spring swarming at 59% of the sites and years, whereas only 35% and 26% of the swarming events were recognized within the correct time period using the thresholds of 18°C and 20°C, respectively.

Monitoring data from Norway and Denmark were used to validate model calculations with a swarming threshold of 16°C. Using the gridded observational dataset, 71% of the spring swarmings in Norway were modelled to occur within the correct monitoring period, and 84% was modelled to occur no later than the following week. The correspondence with monitoring data was somewhat lower for calculations with RCA-ERA40 data (50% and 74% respectively). In the mountainous regions of Norway, most of the gridded temperature data used for model calculations were representative of a colder climate at higher altitudes than the corresponding

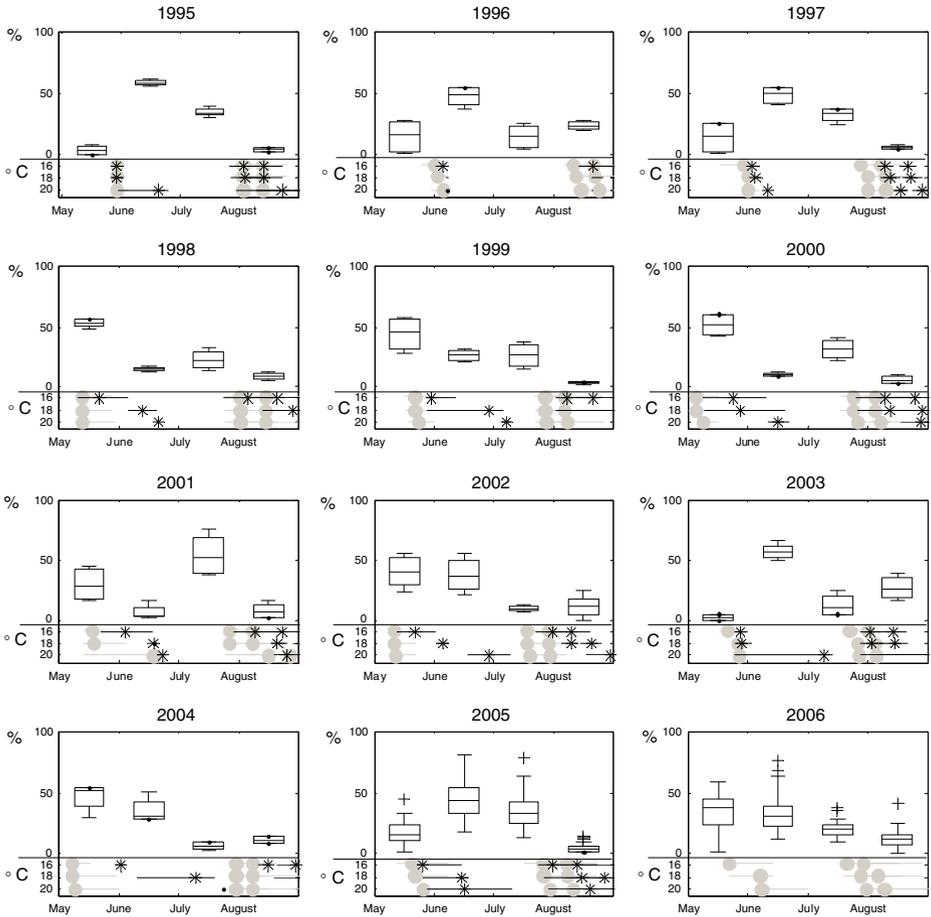


Fig. 1 Boxplots showing the percent of annual pheromone trap catches of *I. typographus* in May, June, July and August at monitoring sites in Sweden during the period 1996–2006 (Table 2). The boxes show the interval that corresponds to the 25 and 75 percentiles of the catches. The lines within the boxes show the 50 percentile, the bars the 10 and 90 percentiles, and + indicate outliers. The lower part of each subplot contains information about timing of spring swarming, early and late completed development of the first generation, calculated for the corresponding gridcells using three swarming temperature thresholds (16°C, 18°C and 20°C). Model calculations were carried out using climate data from the gridded observational dataset (results shown in grey) and RCA ERA-40 (results shown in black, data missing for 2006). The grey and black lines indicate the range of dates for swarming and completed development for each temperature threshold (sometimes there is an overlap in calculated dates for early and late completed development). The grey dots and black asterisks indicate the mean dates for spring swarming, early and late completed development with potential summer swarming

monitoring sites (Fig. 6d), causing a later than observed bias in modelled timing of swarming. For the Danish dataset, the timing of spring swarming calculated with the gridded observational dataset corresponded to the first 14-day trapping period, whereas the timing calculated with temperature data from RCA-ERA40 corresponded to the second trapping period (Fig. 2). The pheromone trap records for the 11 sites and 4 years showed an almost continuous flight activity throughout

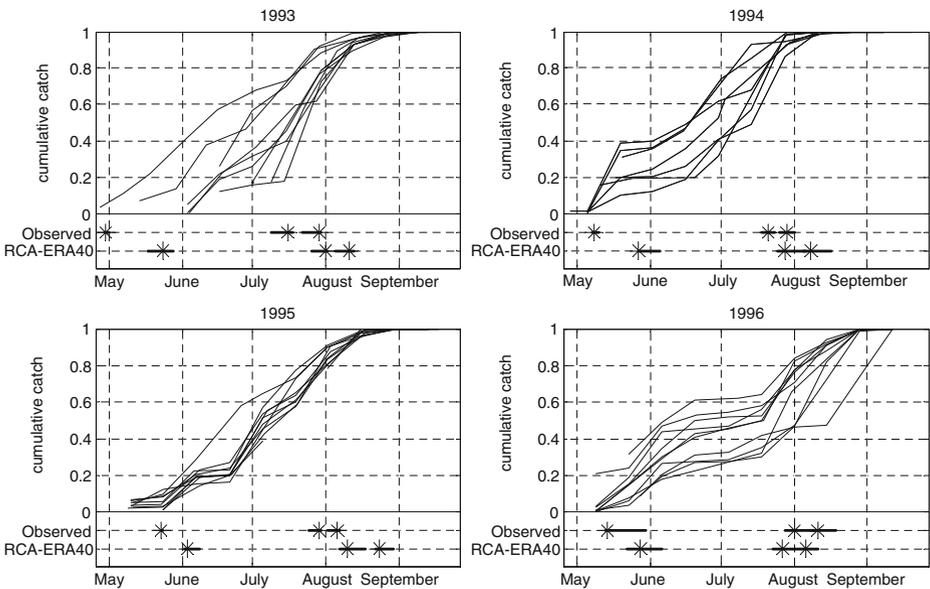


Fig. 2 Monitoring data from Denmark, showing the cumulative catch of *I. typographus* in pheromone traps for the period of 1993–1996 (Table 2). Spring swarming and completed development of the first generation were calculated for the corresponding gridcells using a swarming temperature threshold of 16°C. Lines in the lower part of each subplot indicate the interval of swarming dates for the different sites calculated using climate data from the gridded observational dataset and RCA ERA-40. Asterisks indicate the mean date for spring swarming, as well as early and late timing of summer swarming

the summer. This includes both initiations of sister broods, produced by the parental generation, and a second generation, occurring later in season after maturation of the first generation.

3.2 Diapause model development

Simulations according to the null hypothesis ($H_0T_0P_{(60/100)}$) indicated that *I. typographus* is subjected to diapause restrictions under current climate conditions. That is, without diapause restriction swarming activity in late summer would occur more frequently than observed, as daily maximum temperatures in late summer generally are high enough to encourage continued swarming and unsuccessful reproduction attempts (Fig. 3). Daily mean or minimum temperature alone provides sufficient information for model tuning of diapause onset in large parts of Scandinavia (Fig. 4). In this region, the ratio of relative model performance indicated that the model improvement was closely related to the frequency of unsuccessful early swarming events with initiations of a second generation (Fig. 3), being higher at latitudes between 60–65°N than further north or south. There were no major differences between mean temperature thresholds of 14°C to 16°C, and minimum temperature thresholds of 10°C and 12°C (Fig. 4). The potential for reducing unsuccessful late summer swarming events was significantly lower for the mean temperature threshold of 12°C and minimum temperature thresholds of 5°C and 7.5°C. However, diapause model

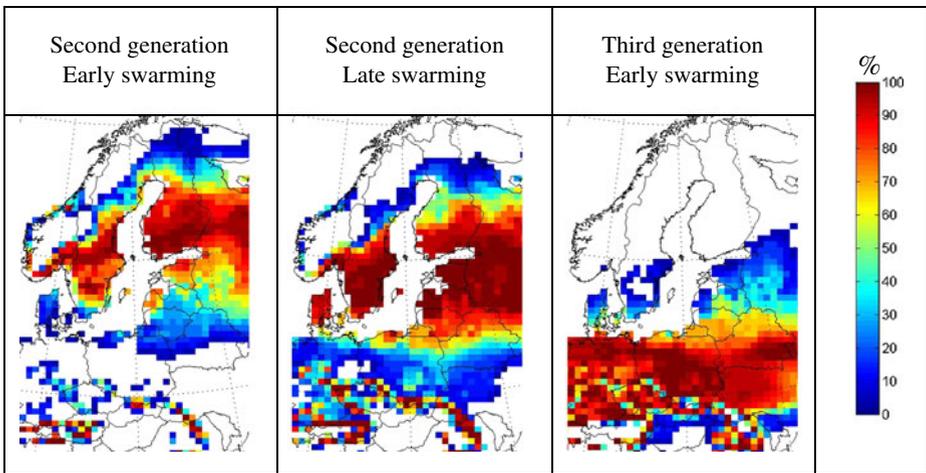


Fig. 3 Simulated frequency of unsuccessful initiations of a second and a third generation, given the assumption of the null hypothesis that *I. typographus* is unable to recognize any environmental cues for triggering diapause. The early and late swarming was calculated based on a temperature sum interval for development of the parental generation, accounting for natural variation in microclimate and light exposure. Early swarming corresponds to development in sun-exposed trees and late swarming to development in shaded trees. Model calculations were carried out with temperature data from the gridded observational dataset

parameterisation requires additional information on day length conditions, as the modelling of a second generation otherwise would be overly restricted by temporary cold-spells during summer at latitudes below 55°N (indicated by a negative ratio of relative model performance).

The day length of the earliest day during the reference period 1961–1990 when the temperature during the rest of the year was sufficient to complete development (625 dd) followed a latitudinal gradient with 15–16 hours in central Europe (occurring in August) and above 20 h in northern Scandinavia (occurring close to mid summer; Fig. 5b). The potential influence of day length and temperature on diapause in *I. typographus* was tested using the 54 different model parameterisations ($H_xT_yP_z$), and model calculations of the latest date of swarming were evaluated with monitoring data (Fig. 6a, c). Calculations based on 60% completed development did in general generate a later than expected date for diapause onset, whereas calculations based on 100% completed development agreed better with monitoring data. Due to inter-annual variations in temperature conditions, it was not sufficient to only optimise the day length requirement. Model calculations using day length in combination with temperature performed better than calculations based on day length alone, and mean temperature thresholds performed better than minimum temperature thresholds. Two model parameterisations, $H_1T_{\text{mean}15}P_{100}$ and $H_1T_{\text{mean}16}P_{100}$, performed equally good when compared to Swedish monitoring data (Fig. 6a). In about 70% of the cases the modelled onset of diapause occurred within a week of the monitoring period in which the last 10% of swarming bark beetles were caught. These parameterisations were also among the best for monitoring data from Norway, but here several other parameterisations performed equally well (Fig. 6b). Due to the mismatch

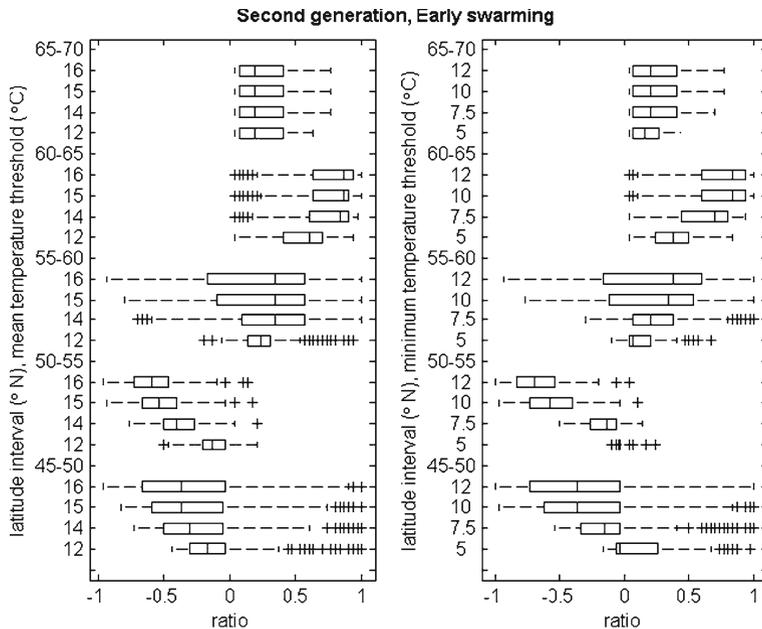


Fig. 4 Diapause model parameterisation using different temperature thresholds, without any influence from day length, compared with the null hypothesis that there are no diapause restrictions. The relative performance of model calculations, using the gridded observational dataset, was expressed as a ratio ranging from -1 to 1 . The *boxes* show the 25 and 75 percentiles of the ratio for gridcells between latitude $45\text{--}70^\circ\text{N}$, within 5° interval. The *lines within the boxes* show the 50 percentile, the *bars* the 10 and 90 percentiles, and *+* indicate outliers. A positive ratio indicates that the parameterisation of the diapause model reduced the frequency of unsuccessful late summer swarming events, whereas a negative ratio indicates that the diapause model parameterisation resulted in a reduction of the calculated potentially successful summer swarming events

between temperature data and monitoring conditions in Norway (Fig. 6d), model parameterisations influenced by day length alone produced the same results as $H_1T_{\text{mean}15}P_{100}$ and $H_{1-3}T_{\text{mean}16}P_{100}$. The parameterisation $H_1T_{\text{mean}15}P_{100}$ performed better than the alternatives for Danish monitoring data (Fig. 6c).

Model parameterisation including day length requirement (Fig. 7) did not perform worse than the null hypothesis in any geographical region as opposed to model parameterisation using only temperature requirements (Fig. 4). A sensitivity analysis indicated that the model output was little affected by temperature threshold parameterisation within the range of $14\text{--}16^\circ\text{C}$ (Fig. 7). The $H_1T_{\text{mean}15}P_{100}$ model parameterisation, which was selected for climate change impact assessments, filtered out unsuccessful swarming events without removing successful swarming events. The ratio of relative model performance thus had a close to zero impact on model performance in areas with low frequency of unsuccessful initiations (Fig. 3). For early and late swarming with initiations of a second generation the ratio was highest at latitudes $60\text{--}65^\circ\text{N}$ and $55\text{--}60^\circ\text{N}$, respectively. For early swarming with initiations of a third generation, the ratio was highest at latitudes $50\text{--}55^\circ\text{N}$. At latitudes $45\text{--}50^\circ\text{N}$, the ratio was highly influenced by altitudinal variation that can differ considerably between adjacent gridcells due to the low spatial resolution.

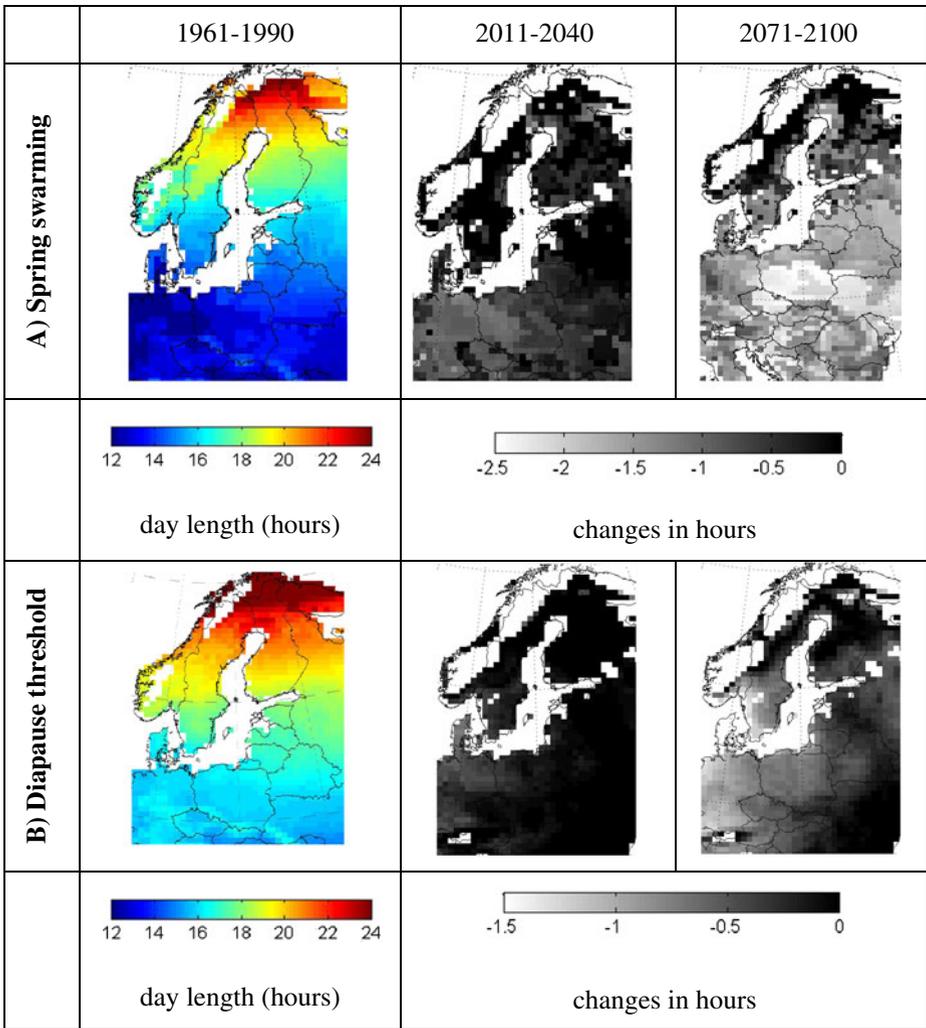


Fig. 5 **a** Day length at the first day in each gridcell when the spring swarming threshold was fulfilled, and changes in day length for the period 2011–2040 and 2071–2100 in comparison with the reference period 1961–1990. **b** Day length of the first day during the reference period 1961–1990 when the temperature sum for the rest of the year was just enough to fulfil the lowest temperature requirement (625 dd) for completed development of *I. typographus*, according to model calculation using the gridded observational climate dataset. Changes in day length, compared with the reference period 1961–1990, for the first day in each gridcell when the temperature sum during the rest of the year was ≥ 625 dd. *White areas* on the maps represent mountainous regions that do not support the development of even one beetle generation. Calculations were performed with data from RCA ECHAM5/MPI-OM, scenario A1B

3.3 Impact of global warming on *I. typographus*

The impact model driven by climate data from RCA ECHAM5/MPI-OM, scenario A1B, indicated a shift in the phenology of *I. typographus* from mainly univoltine

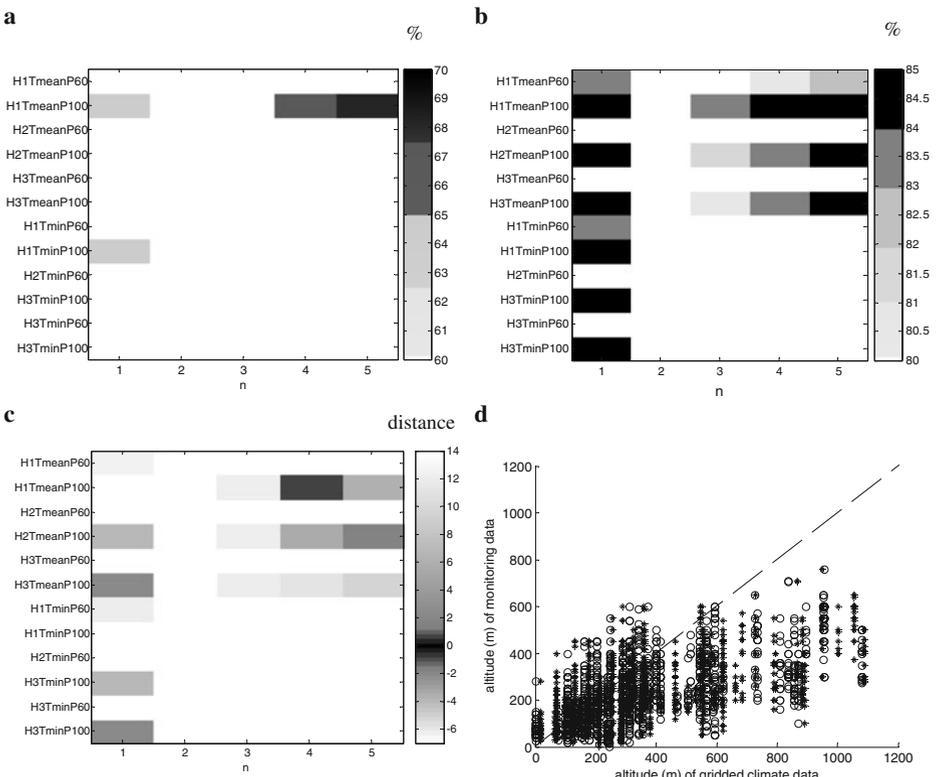


Fig. 6 Evaluation of diapause model parameterisation using monitoring data. Three hypotheses of day length requirement (H1–H3) were tested separately (n1) and in eight combinations with a temperature requirement, based on Tmean (n2–n5: 12, 14, 15 and 16°C) and Tmin (n2–n5: 5, 7.5, 10 and 12°C). The day length and temperature requirements were tested for two thresholds of winter survival, 60 and 100% of completed development (P60 and P100). A higher percentage indicates a better correspondence between model parameterisation and monitoring data from **a** Sweden and **b** Norway. **c** A value close to zero indicates a good correspondence between model parameterisation and Danish monitoring data. **d** Altitude of the gridcells in the gridded observational dataset [*] and the RCA-ERA40 dataset [*] vs. the actual altitude of the monitoring plots in Norway. The *dashed line* indicates the 1:1 relationship

to predominantly bivoltine by the end of this century in a zone covering Denmark, southern Sweden, the Baltic countries and southernmost Finland (Fig. 8). South of this zone, in the central parts of Europe, the initiation of a third generation was projected to increase in frequency and be common by the end of this century. The model also projected an increase in the length of the summer swarming period, which was calculated to increase by approximately one month in central Europe, southern Scandinavia and the Baltic countries and less further north (Fig. 9). However, these calculations assume that the day length requirement for onset of reproductive diapause in *I. typographus* is not adapted to the new climate conditions. Given the assumption that the day length requirement of *I. typographus* will adjust to the climate conditions in 2071–2100, there is an additional increase in the length of swarming period of the first generation by an average of nine days in western parts of

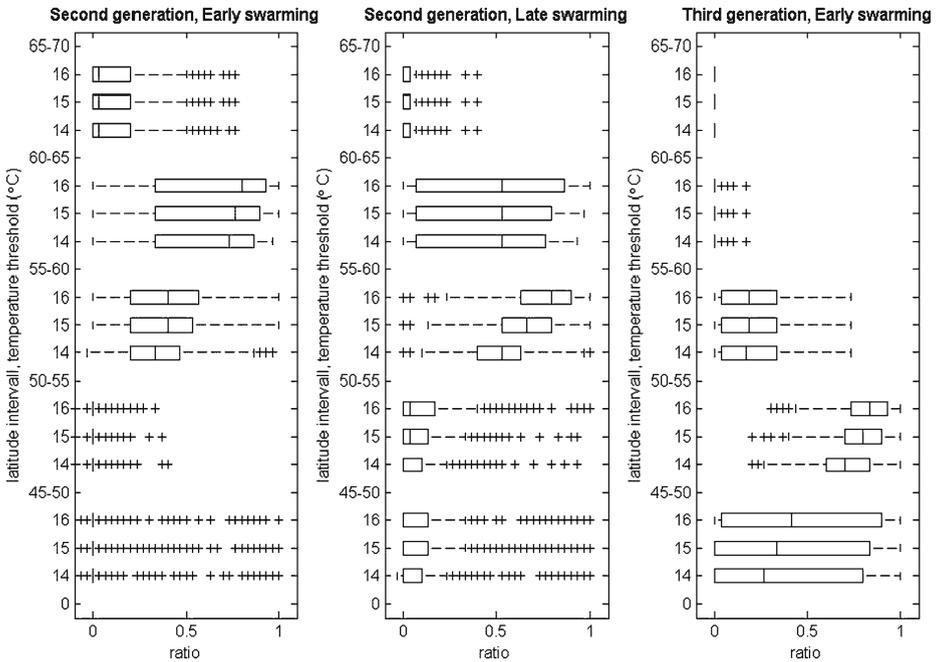


Fig. 7 Sensitivity analysis of the diapause model parameterisation $H_1T_{\text{mean}15}P_{100}$, selected as optimal according to monitoring data, varying the temperature threshold within the range of $\pm 1^\circ\text{C}$. The relative performance of model calculations was expressed as a ratio (R_{xyz} , see Section 2.6 for details). A positive ratio indicates that the parameterisation of the diapause model reduced the number of unsuccessful late summer swarming events. The boxes show the 25 and 75 percentiles of the ratio for gridcells between latitude 45–70°N. The lines within the boxes show the 50 percentile, the bars the 10 and 90 percentiles, and + indicate outliers

central Europe. The additional increase is less than one week for the first generation in eastern parts of central Europe and Scandinavia, and for the second generation in central Europe.

For the period 2071–2100, the calculated day length for optimal diapause induction was up to 1.5 hours shorter than for 1961–1990 (Fig. 5b). The projected climate change impact was most pronounced in western parts of central Europe and southern Scandinavia, and less evident further northwards and eastwards. In a warmer climate, the temperature requirement for swarming is reached earlier in spring, at a correspondingly shorter day length (Fig. 5a).

4 Discussion

The implementation of reproductive diapause in a temperature driven model of bark beetle phenology enabled us to assess the length of the late summer swarming period, which is an important determinant of the risk of forest damage by *I. typographus* in a warmer climate. Our modelling study showed that higher temperatures can result in increased frequency and length of late summer swarming events, with the

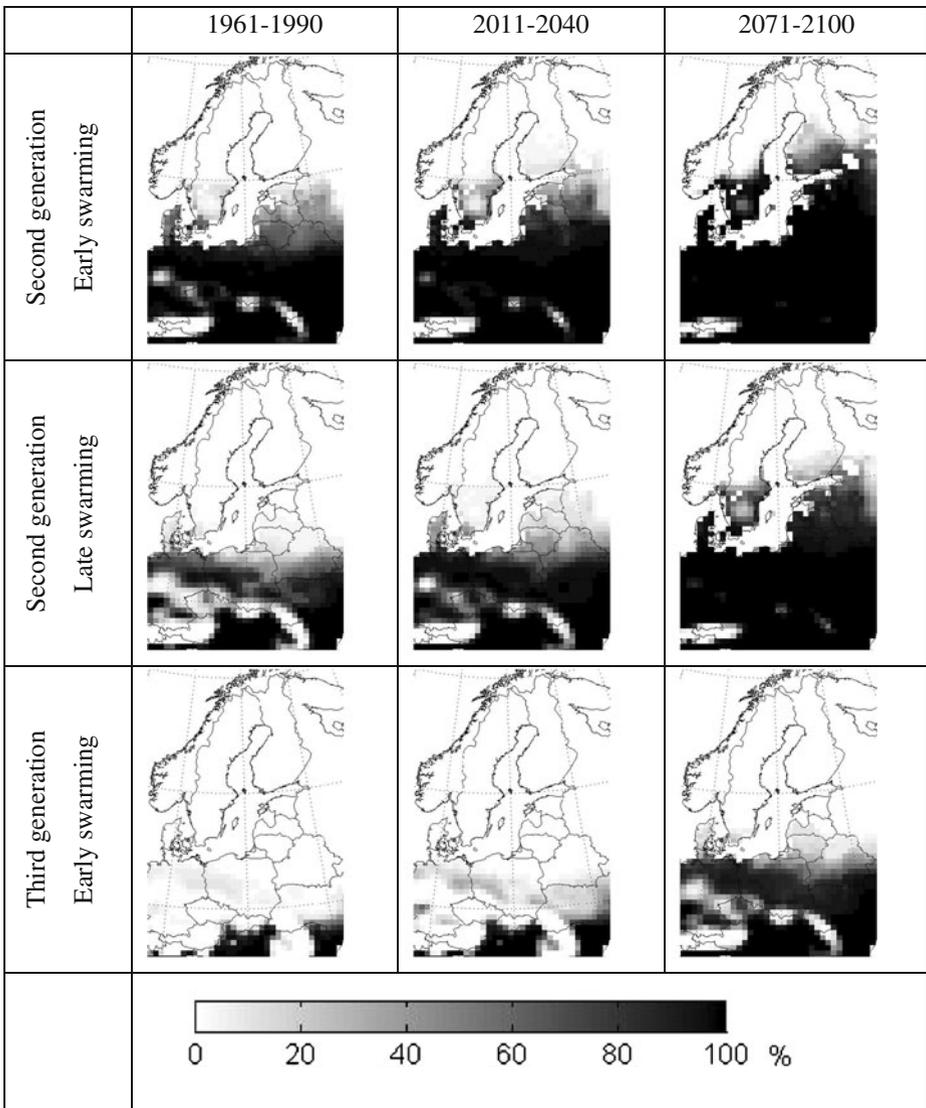


Fig. 8 Percentage of years with initiation of a second and a third generation of *I. typographus*. Early swarming corresponds to development in sun-exposed trees and late swarming to development in shaded trees (based on a temperature sum interval for development). Calculations were performed using the diapause model parameterisation $H_1T_{\text{mean}15}P_{100}$ and climate data from RCA ECHAM5/MPI-OM, scenario A1B

production of a second generation in southern Scandinavia and a third generation in lowland parts of central Europe. This result is in line with the general expectations that global warming will induce changes in phenology, voltinism and geographical distribution for a wide range of insect taxa (Ayres and Lombardero 2000; Volney and Fleming 2000), and that more than three generations of *I. typographus* will not occur

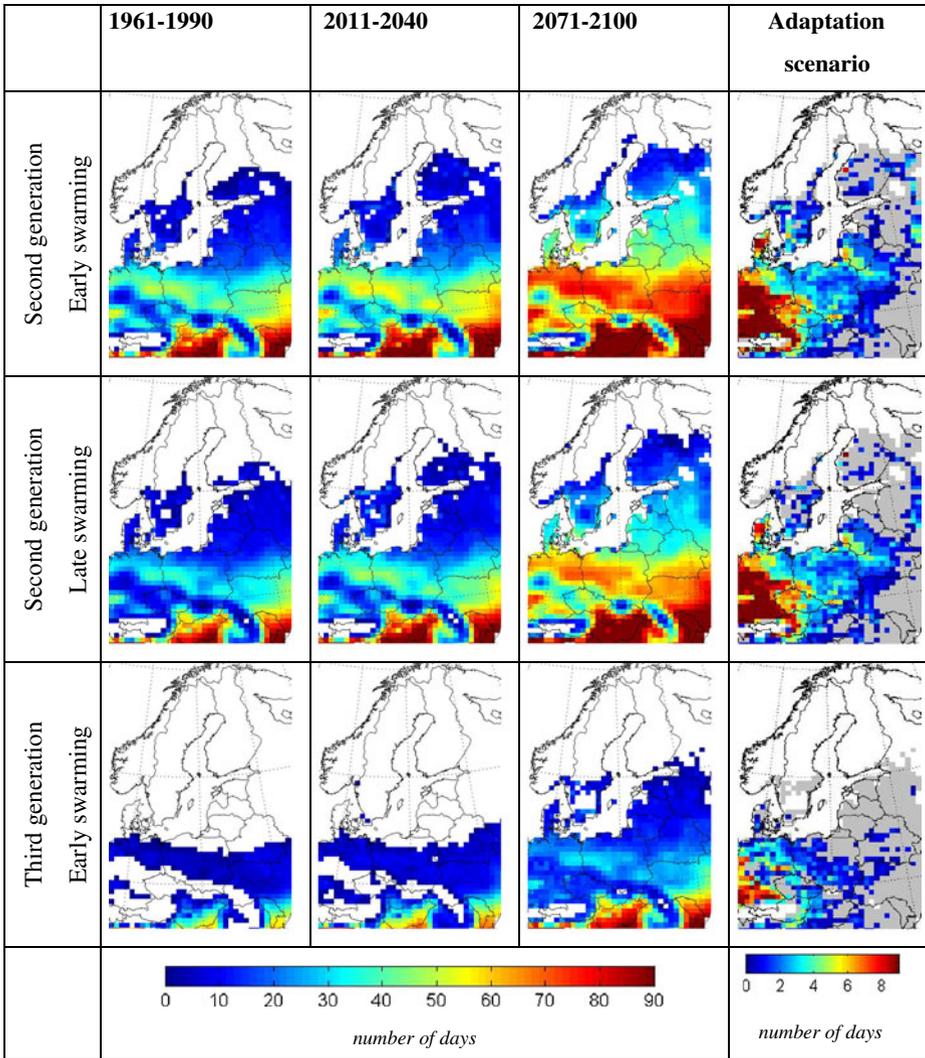


Fig. 9 Length of potential swarming period in late summer with initiation of a second or third generation of *I. typographus*. Swarming period is measured as the number of days between first swarming event after full development of the parental generation and modelled onset of diapause, according to the diapause model parameterisation $H_1T_{mean15}P_{100}$ and climate data from RCA ECHAM5/MPI-OM, scenario A1B. Early swarming corresponds to development in sun-exposed trees and late swarming to development in shaded trees (based on a temperature sum interval for development). The additional increase in swarming period, given the assumption that the day length requirement is in equilibrium with the new climate conditions, was calculated for the period 2071–2100

in the spruce forests of central Europe (Hlásny and Turčáni 2009). Diapause plays a fundamental role in life cycle synchronization in many insect species (Tauber and Tauber 1976; Denlinger 2002; Gomez-Zurita and Galian 2005), and incorporating

descriptions of species-specific diapause regulation into phenological models can be crucial for predicting the response to driving climate variables (Gray et al. 2001; Steinbauer et al. 2004; Tobin et al. 2008). Our study indicated that diapause may determine how far bi- and trivoltinism in *I. typographus* will expand in a warmer climate, as day length cues could restrict the length of the late summer swarming period unless adaptation occurs. Natural selection and migration of *I. typographus* from central Europe could potentially offset this limitation in southern Scandinavia, whereas genetic adaptation is required in the southern distribution area. Indeed, field data indicate that day length cues are currently restricting *I. typographus* from developing a third generation in the southeastern Alps (Faccoli 2009). The capacity for genetic adaptation depends on available genetic variation and fitness consequences (van Asch et al. 2007; Tobin et al. 2008) and may proceed rapidly.

Temperature and day length requirements may also restrict diapause termination in the spring, though the experimental support for this is rather rudimentary. Dolezal and Sehnal (2007) described that *I. typographus* is sensitive to day length below 17 h unless exposed to low temperatures (i.e. +5°C) for at least two months. However, already today the swarming temperature threshold is crossed at shorter days in the spring. Furthermore, the climate scenario data used in this study indicated an even earlier spring swarming in the future, along with an increased frequency of years when large parts of central Europe and southern Scandinavia will experience daily mean temperatures below 5°C for less than two months (more than 50% of the years by the end of this century, data not shown). *I. typographus* may thus be unable to respond to temperature conditions optimal for swarming in years with an early onset of spring, and climate change may thus be expected to induce a selection pressure also for this feature.

We have used impact modelling with observed climate data to determine large-scale day length and temperature conditions at the time of the year when *I. typographus* enters into reproductive diapause. Model evaluation using pheromone trap monitoring data suggested that daily mean temperature had higher predictive power than daily minimum temperature. However, the minimum temperature may be an equally good predictor (Fig. 4), and our results cannot be used to discriminate between the impact of minimum and mean temperature. In general, daily mean and minimum temperatures are highly correlated, but there are larger uncertainties associated with chronological comparisons between point observations and gridded minimum temperature than between observations and gridded mean temperature (Kjellström et al. 2005). This means that even if diapause manifestation is controlled by exposure to low temperatures, we are more likely to find a higher correlation with gridded daily mean temperatures. A rationale for using daily mean temperature is that it represents a measure of daily energy input that influences bark beetle activity, and for modelling purposes this could be a useful approximation.

In earlier versions of the impact model, diapause induction was calculated to occur when the daily mean temperature falls below 15°C in late summer (Jönsson et al. 2007, 2009). This simplified assumption is sufficient for describing *I. typographus* development under current climate conditions in most of Sweden (Fig. 3), as the ambient day length is shorter than the critical day length for diapause induction at the time when the first generation has completed development, but it is not adequate further south in Europe. The model for diapause induction selected in this study by comparison with monitoring data ($H_1 T_{\text{mean}15} P_{100}$), has a day length parameterisation

that corresponds to the longest day at which no beetles enter into diapause at optimal temperatures reported by Dolezal and Sehnal (2007). Further experimental studies with beetles from geographical regions with contrasting climates are required to test the model of how photoperiod and temperature influence diapause induction. One concern is that selection pressures may vary between geographical regions and that different cues thus may be operating in different parts of the distribution area of the species. Even though *I. typographus* has a high dispersal capacity and low genetic diversity, effects of isolation by distance has been detected in genetic studies (Stauffer et al. 1999; Sallé et al. 2007). Latitudinal diapause patterns, consisting of a mixture of individuals with different diapause adaptations, are created by long-distance migration in combination with regional climatic differences (Forsse 1991). The results of our study, using a model parameterisation based on the last 10% of the annual pheromone trap catches, give an insight into current adaptations, though they may not describe the typical population behaviour (e.g. only one generation per year in Norway and Sweden).

The climate data available for this study is not representative for the main distribution area of Norway spruce in Norway. The gridded temperature data generally represented regions above 600 m elevation, whereas Norway spruce, and thus *I. typographus*, are mainly present at lower altitudes. This influences the calculated timing of spring swarming and completed development, as shown by comparison with monitoring data. Thus, the impact of regional climate change on the voltinism of *I. typographus* in Norway was probably underestimated. Our model did not project any initiations of a second generation in response to a warmer climate in interior parts of southern Norway, whereas the frequency of bivoltinism increased in coastal areas of Norway and at corresponding latitudes in Sweden. In the modelling study by Lange et al. (2006, 2009) bivoltine development was predicted to occur over most of the distribution area of *I. typographus* in southern Norway by 2071–2100, and this conclusion is supported by the fact that the thermal sum in parts of southern Norway is almost sufficient for bivoltine development even under current climate conditions.

The future projection in this study is indicative of the A1B emission scenario. However, data from other scenarios, other combinations of global and regional climate models, and data from model runs realized with altered initial conditions will produce results with different magnitudes (Beaumont et al. 2007; Déqué et al. 2007; IPCC 2007). We have therefore presented our results in a generalised way, focusing on the large-scale trends in response to regional climate change and not looking into details about specific regions or absolute changes in number of days. The model description of reproductive diapause enabled us for the first time to assess how climate change may alter the length of the late summer swarming period. This is an important aspect of *I. typographus* phenology, as an extended swarming period may further increase the risk of forest damage. Damage levels may increase even in areas that currently have a high frequency of bivoltinism by involving individuals from the sister broods of the first generation, and by allowing initiation of sister broods of the second generation.

Climate change may call for altered forest management practice in order to reduce the future risk of attacks by *I. typographus*. The risk is ultimately dependent on the availability of brood material in the landscape (Økland and Bjørnstad 2006), and ecosystem analysis is required to assess the impact of climate change on the interaction between Norway spruce and *I. typographus*.

5 Conclusion

In this study, modelling of *I. typographus* response to climate change was improved by using pheromone trap data in combination with daily temperature data, analysing the effect of photoperiod and temperature on reproductive diapause. Further studies need to address the questions of (1) local adaptations of bark beetle populations and the capacity for adjustment to changing climate conditions, (2) the susceptibility of Norway spruce to *I. typographus* attacks in relation to weather extremes, and (3) future climate impact on *I. typographus* outbreaks in relation to uncertainties in climate model projections.

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