Predicting spatial and temporal patterns of bud-burst and spring frost risk in north-west Europe: the implications of local adaptation to climate

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Abstract

The timing of spring bud-burst and leaf development in temperate, boreal and Arctic trees and shrubs fluctuates from year to year, depending on meteorological conditions. Over several generations, the sensitivity of bud-burst to meteorological conditions is subject to selection pressure. The timing of spring bud-burst is considered to be under opposing evolutionary pressures; earlier bud-burst increases the available growing season (capacity adaptation) but later bud-burst decreases the risk of frost damage to actively growing parts (survival adaptation). The optimum trade-off between these two forms of adaptation may be considered an evolutionarily stable strategy that maximizes the long-term ecological fitness of a phenotype under a given climate. Rapid changes in climate, as predicted for this century, are likely to exceed the rate at which trees and shrubs can adapt through evolution or migration. Therefore the response of spring phenology will depend not only on future climatic conditions but also on the limits imposed by adaptation to current and historical climate. Using a dataset of bud-burst dates from twenty-nine sites in Finland for downy birch (*Betula pubescens* Ehrh.), we parameterize a simple thermal time bud-burst model in which the critical temperature threshold for bud-burst is a function of recent historical climatic conditions and reflects a trade-off between capacity and survival adaptation. We validate this approach with independent data from eight independent sites outside Finland, and use the parameterized model to predict the response of bud-burst to future climate scenarios in north-west Europe. Current strategies for budburst are predicted to be suboptimal for future climates, with bud-burst generally occurring earlier than the optimal strategy. Nevertheless, exposure to frost risk is predicted to decrease slightly and the growing season is predicted to increase considerably across most of the region. However, in high-altitude maritime regions exposure to frost risk following bud-burst is predicted to increase.

Keywords: Betula pubescens, bud-burst, climate change, downy birch, Fennoscandia, Finland, frost risk, growing degree days, growing season, phenology

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Introduction

Several studies have detected the effect of recent anthropogenic climate change on the phenology of spring bud-burst. An extended growing season has been observed from satellite data in northern high latitudes (Myneni

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et al., 1997; Slayback *et al.*, 2003; Karlsen *et al.*, 2007, 2008) and from ground-based phenological observations (Menzel, 2000; Menzel *et al.*, 2001, 2006; Ahas *et al.*, 2002; Badeck *et al.*, 2004; Schwartz *et al.*, 2006; Doi & Katano, 2008; Nordli *et al.*, 2008). Along with the timing of autumn leaf senescence, the timing of spring bud-burst determines the effective length of the growing season utilized by deciduous plants. An earlier bud-burst has implications for the carbon balance of regions (Tanja *et al.*, 2003; Picard *et al.*, 2005), physiological processes including the potential for frost damage (Cannell &

Smith, 1986; Hänninen, 1991; Howe et al., 2003; Prozherina et al., 2003; Rigby & Porporato, 2008), changes in altitudinal and latitudinal tree lines (Dalen & Hofgaard, 2005), boundaries between deciduous and evergreen forests (Givnish, 2002) and shrub expansion in tundra (Tape et al., 2006). Furthermore, predictive models of vegetation leaf phenology are a critical component of the soil–vegetation–atmosphere transfer schemes and dynamic global vegetation models utilized by global climate models (Potter & Klooster, 1999; Cox, 2001; Picard et al., 2005; Kucharik et al., 2006).

The nature of the biochemical mechanisms associated with the triggering of bud-burst in spring remains poorly known. However, a large body of data has shown temperature to be the primary meteorological factor that triggers bud-burst in most species, with other factors, including soil moisture, solar radiation, photoperiod and rate of change of photoperiod, found to play a secondary role (Chuine, 2000; Heide, 2003; Linkosalo & Lechowicz, 2006; Wesolowski & Rowinski, 2006). Leaf phenology of a number of tree species under field, laboratory and common garden conditions has been modelled successfully using accumulated forcing units (often accumulated degree days above a threshold temperature), with or without the additional constraint of a chilling requirement (usually accumulated days below a threshold temperature) running consecutively or concurrently (Cannell & Smith, 1986; Murray, 1989; Hunter & Lechowicz, 1992; Myking & Heide, 1995; Linkosalo et al., 2008). Chuine (2000) has attempted to unify varying models under a common framework. The simplest form of these models, the simple thermal time (STT) model, has three parameters: the day of the year after which temperature sums are accumulated; the base temperature threshold, above which temperature sums are calculated; and the critical thermal sum threshold, which represents the accumulated temperature sum at which bud-burst is triggered. Recent work (Linkosalo et al., 2006, 2008) suggests that, although complex models may produce closer fits to parameterization data, when tested against independent data STT models perform better, suggesting that more complex model forms may suffer from over parameterization.

The sensitivity of bud-burst timing to meteorology is known to vary along climatic gradients (Doi & Takahashi, 2008; Pudas et al., 2008), reflecting variation in optimal strategy under different climatic conditions. Genotypes with different geographical origins typically have different critical thermal sum thresholds, and therefore require different model parameterizations or forms (Thompson & Clark, 2006; Pudas et al., 2008). Several studies have shown that provenances from higher latitudes have lower critical thermal sum thresholds for bud-burst than do those originating further south; when grown together in a common garden, those from higher-latitude origins thus leaf-out first (Lockhart, 1983; Myking & Heide, 1995; Hänninen & Hari, 1996; Leinonen & Hänninen, 2002). This result may appear paradoxical, because it implies that northern phenotypes therefore either withstand greater frost damage or invest more resources in minimizing frost damage than southern phenotypes would at the same latitude, presumably at a physiological cost to fitness. Among others, Lockhart (1983) and Leinonen & Hänninen (2002) have concluded that a trade-off principle fits the observations, where selection pressure to minimize frost risk (survival adaptation) is balanced by pressure to maximize the growing season (capacity adaptation). Lockhart (1983) expresses this fitness trade-off purely in terms of the carbon balance, in that both the production gained during the growing season and the production lost due to frost damage may be considered as gains and losses in carbohydrates.

The spatial variation in bud-burst strategy that the survival/capacity trade-off implies clearly becomes problematic if we wish to apply a bud-burst model across regions, and even across species, as is required for climate or carbon balance modelling. If future changes in climate exceed the rate at which vegetation can adapt through evolution or migration, the response of spring phenology in natural or seminatural vegetation to anthropogenic climate change will depend not only on future climatic conditions but also on the local strategy of the vegetation, which is a function of both the current and historical climate of the location.

To address the problem of spatially varying strategies, Thompson & Clark (2006) developed spatio-temporal models of phenology which allow observations across climatic gradients to be analysed simultaneously by allowing the parameters of a model to vary linearly with latitude. This approach implicitly incorporates the effect of geographical (climatic) provenance on bud-burst thresholds. We aimed to constrain this approach of allowing model parameters to vary spatially using the survival/capacity trade-off hypothesis stated by Lockhart (1983) and Leinonen & Hänninen (2002). Our goal was to parameterize a model of bud-burst in which the critical temperature sum threshold for bud-burst represents the optimal compromise between capacity and survival adaptation under the climatic conditions at the natural growing sites of the provenance. This would allow the effect of regional genotypic variation to be incorporated into predictive models of bud-burst phenology.

Here we present a SST model fitted to observations of bud-burst for Betula pubescens Ehrh. (Downy Birch) in Finland from the Finnish Forest Research Institute (METLA). The novelty of our approach is that, rather than derive a single parameterization for the data set as

a whole, or parameterize the critical sum threshold separately for each observation site to obtain the best fit, we assume that the critical sum threshold at any point in space is that which will produce the optimum trade-off between survival and capacity adaptation under the long term average climate at that site. This is obtained by using the observations to establish a linear relationship between the expected number of spring frosts and the length and magnitude of the growing season following bud-burst, and assuming that this observed relationship is close to the optimal survival/capacity trade-off. This relationship allows us to predict: (a) expected critical sum thresholds in locations or for genotypes where observations do not currently exist, allowing predictive mapping of budburst strategy; and (b) the response of budburst timing, and the associated postbudburst spring frost risk, to future climate scenarios, when strategies may be suboptimal for those climates. We assess the applicability of this approach by using long-term gridded climate data sets to predict the long-term average bud-burst days recorded in the literature from sites in Norway, Sweden and Russia (Karlsson *et al.*, 2003; Wielgolaski, 2003; Shutova *et al.*, 2006); the results demonstrate that our predictions can with confidence be extended to a wider geographical area encompassing Scandinavia, Finland and north-west Russia.

Materials and methods

Phenological and meteorological data

Phenological observations of bud-burst in *B. pubescens* were obtained from 29 research stations of the Finnish Forest Research Institute (METLA) for the years 1999–2005. Climatic data (mean and minimum daily temperature) were obtained for 31 stations from the Finnish Meteorological Institute. The phenological stations were matched with the nearest meteorological station and temperatures were adjusted for differences in altitude between meteorological and phenological stations using a fixed lapse rate of $6\,°C\,km^{-1}$. The average number of degree days above a series of low-temperature thresholds between -5 and $10\,°C$, accumulated before the recorded bud-burst date, was fitted through a least-squares procedure for each phenological station. The best model fits to the observations (overall RMSE <3.5 days) were achieved at a range of low temperature thresholds between 0 and $3.5\,°C$. A constant $3\,°C$ threshold was selected for consistency with the minimum threshold of growth for *B. pubescens* identified by Skre (1993); this is within the range of threshold values fitted to bud-burst data for *B. pubescens* in previous studies (Karlsson *et al.*, 2003).

In order to test the ability of the model to predict bud-burst dates using coarse-scale gridded climate data outside of the region in which it was parameterized, we used average bud-burst dates recorded in published studies from eight additional locations in Norway, Sweden and Russia. Only multiyear averages reported in published papers were available from these sites for this study, and the period and length of data collection varied considerably, so these sites were not used in parameterizing the model but were intended as a check on the ability of the models to predict the approximate date of bud-burst at localities in which they have not been parameterized. We used average dates reported from a 4-year period from two sites ('oceanic', near sea-level and 'high-level', near the tree line) at Sognfjord, Norway reported in Wielgolaski (2003); from 1956 to 2000 at a high-latitude site close to the altitudinal treeline in Abisko, Sweden (Karlsson *et al.*, 2003); and five high-latitude sites, Pasvik Reserve and Svanhovd (data reported 1994–2003), and Lapland Reserve, Kandalaksha and Kirovsk (1964–2003) in Russia (Shutova *et al.*, 2006). These locations, along with the Finnish phenological and meteorological network sites, are shown in Fig. 1.

Gridded climate data

To obtain gridded spatial climatic data across the region we used the monthly $0.5°$ resolution grids from the Climate Research Unit CRU TS 2.0 data set (Mitchell *et al.*, 2004) for the period 1961–1990 across the study area. To interpolate average daily mean and minimum temperatures, we assumed that seasonal average temperatures approximate a sine-curve. The *seasonal average* course of daily mean temperature, $T(t)$ is then given by:

$$T(t) = \bar{T} - A\cos\left(\frac{2\pi(t-a)}{365.25}\right) \qquad (1)$$

and of daily minimum temperature $T_{\min}(t)$ by:

$$T_{\min}(t) = \bar{T}_{\min} - A_{\min}\cos\left(\frac{2\pi(t-a)}{365.25}\right), \qquad (2)$$

where t is the Julian day of the year (i.e. 1st January = 1); a is the coldest day of the year; 365.25 is the average number of days in a year; $\bar{T}$ and $\bar{T}_{\min}$ are the annual means of daily mean and daily minimum temperature; and A and $A_{\min}$ are the amplitude of the respective sine-curves, representing half the annual range in daily mean/minimum temperature.

Fitting curves to the daily meteorological station data revealed that values of a varied by only 3 days between stations, with an average of 20; this value is used in subsequent analyses. The seasonal average course of temperature climate can therefore be summarized by

Fig. 1 Location of Finnish phenological stations (open circles), meteorological stations (filled circles) and locations where average bud-burst dates recorded in the literature (Karlsson *et al.*, 2003; Wielgolaski, 2003; Shutova *et al.*, 2006) were used for validation in this study (squares).

the variables $\bar{T}$ and $\bar{T}_{min}$, that represent gradients in annual average temperature, such as latitudinal or altitudinal gradients, and A and A_{min}, that represent the degree of seasonality of the climate, such as gradients in continentality.

These variables may be derived directly from the CRU monthly mean climatic data by fitting a curve of the form:

$$T_{monthly}(m) = \bar{T} - A\left(\sin\left(\frac{2\pi(m - a/30.44)}{12}\right) - \sin\left(\frac{2\pi(m - 1 - a/30.44)}{12}\right)\right), \quad (3)$$

where $T_{monthy}(m)$ is the monthly mean temperature; m is the month of the year (from 1 to 12); 12 is the number of months in a year; and 30.44 is the average number of days in a month.

Predicting the probability of frost events

The sine-curves described in Eqns (1) and (2) are an approximation of the expected daily minimum and mean temperature at any given time of year. However, unseasonably warm or cold temperatures may occur and rare and extreme events (particularly in this case late spring frosts) may be critical in determining the balance between capacity and survival adaptation (Rigby & Porporato, 2008). For this reason we adopt a probabilistic model of frost occurrence, dependent on the seasonal expected minimum temperature and

parameterized by the relative frequency of frost events in the Finnish meteorological data. Frost is considered to be a random binary event (*i.e.* frost or no frost) with a probability that depends on the expected (seasonal average) minimum temperature for that day of the year. We use logistic regression (Zar, 1996) to predict the probability of a frost event. For a given seasonal average minimum temperature, the probability of a frost event (defined here as the temperature falling below a temperature α) occurring may be estimated by the logistic relationship:

$$F(T_{min}) = \frac{e^{\alpha - \beta T_{min}}}{\left(1 - e^{\alpha - \beta T_{min}}\right)}, \quad (4)$$

where $F(T_{min})$ is the probability of a frost event given an expected seasonal minimum temperature T_{min}; α is the temperature in °C defining a frost event; and β is a fitted constant.

Fitting this equation to data from all meteorological stations, and using a threshold value $\alpha = 0\,°C$, an average value of $\beta = 0.321$ was derived, and is used in subsequent analyses. No relationship was found between values of β derived from individual stations and either latitude or longitude.

Determining a trade off between frost risk and growing season temperature sum

If mean temperature follows the sine-curve of Eqn (1), the expected total number of degree days G_{total} above a
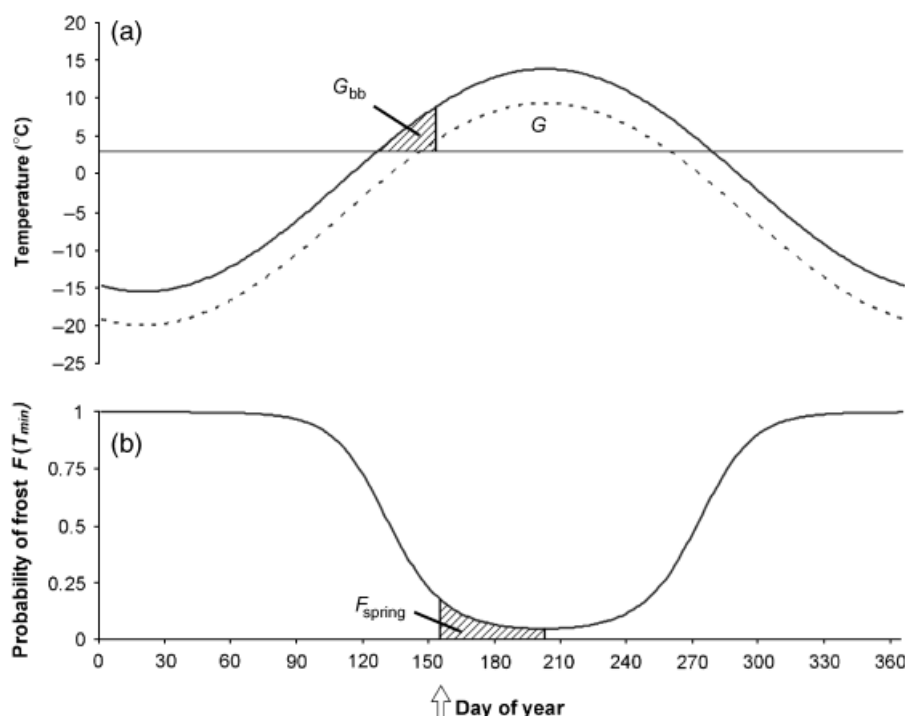
Fig. 2 Schematic diagram illustrating: (a) mean daily temperature (solid line) and average minimum daily temperature (dashed line) of a hypothetical climate; (b) calculated daily probability of frost using the logistic relationship. If bud-burst is recorded at the point marked by an arrow, area G_{bb} represents the cumulative degree days before bud-burst, G represents the total potential degree days following bud-burst and F_{spring} represents the expected number of frost days after bud-burst.

threshold T_{th} during the season is:

$$G_{total} = 2 \sum_{t=t_{th}-a}^{182.125+a} T(t) - T_{th}, \qquad (5)$$

where t_{th} is the first day on which the temperature exceeds T_{th}, and is:

$$t_{th} = \frac{365.25}{2\pi} \cos^{-1}\left(\frac{T_m - T_{th}}{T_a}\right) + a \qquad (6)$$

G, the total number of degree days available following bud-burst, is then:

$$G = G_{total} - G_{bb}, \qquad (7)$$

where G_{bb} is the recorded number of degree days before bud-burst.

Similarly, if average minimum temperatures follow the sine-wave of Eqn (2), and the probability of a frost event for a given seasonal average minimum temperature follows Eqn (4), the average expected number of spring frost days after bud-burst but before the statistically warmest day of the year, F_{spring}, can be calculated as:

$$F_{spring} = 2 \sum_{t=t_{bb}-a}^{182.125+a} F(T_{min}) \qquad (8)$$

A schematic diagram illustrating fitted sine-curves for mean and minimum temperatures, and daily frost risk, is shown in Fig. 2.

Calculating G_{total} using the CRU TS 2.0 climate data and Eqns (3) and (5), and G_{bb} derived from the Finnish phenological observations and meteorological data, G and F_{spring} were calculated using Eqns (4), (7) and (8). For the eight locations outside Finland, estimated values of G_{bb}, G and F_{spring} were calculated using the average published bud-burst dates and the CRU TS 2.0 climate data, adjusted for altitude. The relationship between spring frost days after bud-burst (F_{spring}) and degree days after bud-burst (G) is close to linear (Fig. 3); a least-squares linear regression (to the Finnish data only) produced a fit of the form:

$$F_{spring} = 7.38 - 0.00258G(R^2 = 0.5201, P < 0.001) \quad (9)$$

Combining Eqns (7) and (9)

$$G_{bb} = G_{total} - \frac{7.38 - F_{spring}}{0.0258} \qquad (10)$$

G_{total}, the total growing season temperature sum, is constant under a given climate and frost risk F_{spring} decreases with time as the thermal sum G_{bb} increases throughout the spring. The optimum thermal sum threshold for budburst is predicted at the value that satisfies Eqn (10).
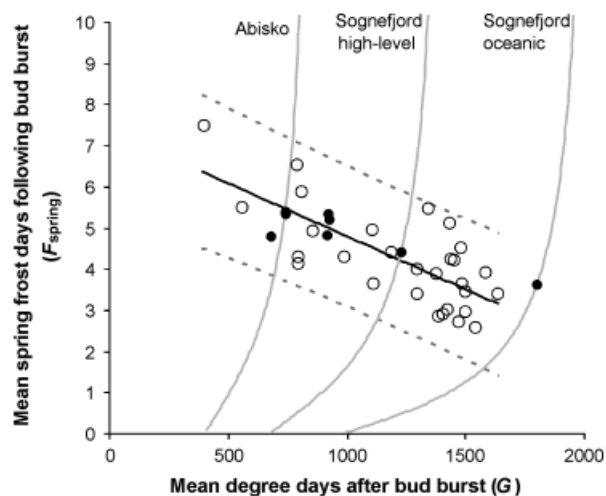
Fig. 3 Plot showing the relationship between predicted spring frost days following bud-burst (F_{spring}) and degree days after bud-burst (G) derived from Eqns (1)–(8) using observed degree day requirements for bud-burst from annual observations from the Finnish phenological stations (open circles) and multiyear averages from the literature (filled circles). Solid line shows linear fit ($R^2 = 0.520$, $P < 0.001$), dashed line shows 95% confidence intervals. Grey curves show the range of climatically possible values for sites from the literature, Abisko, Sognefjord High Level and Sognefjord Oceanic.

Extending the trade-off model across north-west Europe

To assess the ability of a survival/capacity trade-off to parameterize the STT model Eqn (10) was applied to altitude-adjusted gridded climate data in order to predict the average bud-burst date for each of the eight validation locations from the literature. The predicted bud-burst dates using this parameterization were compared with those predicted using a constant value of $G_{bb} = 90.5$, the best fitted value for the entire parameterization data set (Fig. 4).

Equation (10) was used to predict the optimum critical temperature sum, number of frost days and expected day of bud-burst for each grid cell across the region under recent (1961–1990) climate. In order to predict the response of bud-burst to future climatic conditions, assuming no genetic migration or adaptation, expected bud-burst date and spring frost days were calculated applying these critical temperature sums to climate predictions from the UKMO-HadGEM1 general circulation model (Johns *et al.*, 2006) under the IPCC SRES A2 scenario (Nakicenovic & Swart, 2000) from the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 3 (CMIP3) multimodel dataset. Predicted climates were produced for the time periods 2010–2039, 2040–2069 and 2070–2099, using the CRU TS 2.0 data at half-degree
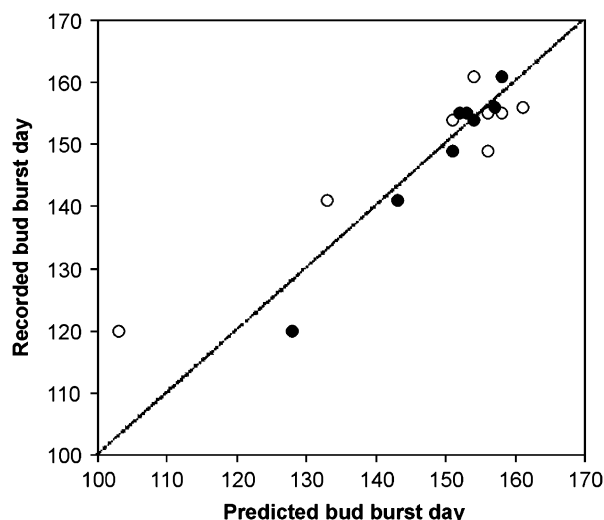
Fig. 4 Predicted vs. recorded bud-burst day for the eight validation sites using a Simple Thermal Time Model with the critical temperature sum (G_{dd}) parameterized by the trade-off model (filled circles) and set to a the mean value for the calibration sites (open circles).

resolution and modifying them with the simulated temperature change predicted for each time period by Had-GEM1 at 1° resolution. The A2 emissions scenario produces temperature predictions in the upper-middle range of scenarios in the region (Jylhä *et al.*, 2004).

Results

Using a single growing degree day threshold fitted to the Finnish parameterization data ($G_{bb} = 90.5$), the root mean squared error of the predictions of bud burst date from the eight locations outside Finland was 7.87 days. By using the survival/capacity trade-off to parameterize the threshold for each location depending on its climate, the RMSE was improved to 3.45 days (Fig. 4). When parameterized by the survival/capacity trade–off, average predicted bud-burst dates were within 3 days of those recorded in seven out of the eight test locations. At the oceanic site at Sognefjord, bud-burst was predicted 8 days later than recorded.

Here we describe the changes in bud-burst date and frost exposure predicted by applying the survival/adaptation trade-off parameterization of the STT model to the future climate scenarios. These 'predictions' are intended to be indicative of a possible warmer future climate only – the choice of climate model and emission scenario, along with uncertainties in model parameterization, create a large range of possible future climates, and assessing the full range of phenological responses and their likelihood is beyond the scope of this study. Warmer future climates are expected to increase the
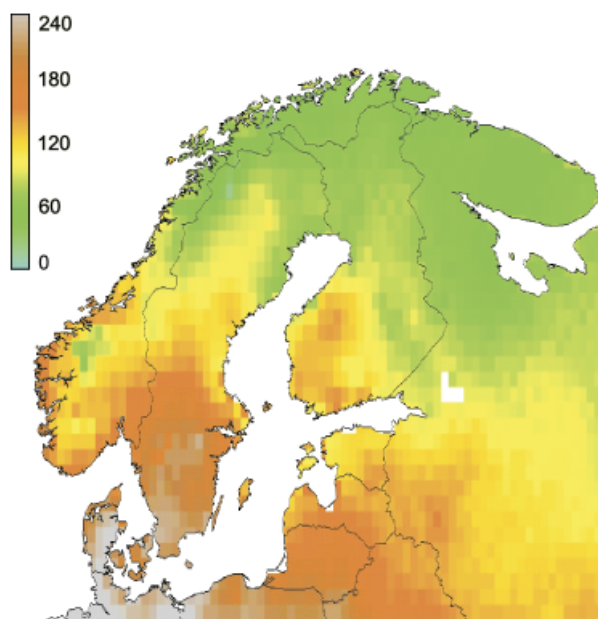
Fig. 5 Map of predicted degree day requirement for bud-burst (above 3 °C threshold) in *Betula pubescens* produced by applying the linear relationship in Fig. 3 to 1961–1990 climate.

potential range of *B. pubescens* beyond its current latitudinal and altitudinal limits in the region (Dalen & Hofgaard, 2005), and it is assumed here that the region as a whole remains climatically suitable for the species.

The map of degree day requirements (Fig. 5) predicts that the degree day threshold for bud-burst follows geographical gradients in latitude, altitude and continentality, with thresholds decreasing at higher altitudes, higher latitudes and in more continental climates; this general pattern is consistent with published observations (Myking & Heide, 1995; Thompson & Clark, 2006). Applying the degree day requirements to the HadGEM1 A2 climate scenario predictions, we expect bud-burst to occur progressively earlier during the 21st Century than during the 1961–2090 period, by 2–14 days by 2010–2039, 11–22 days by 2040–2079 and 36–56 days by the period 2070–2099. The greatest magnitude of change is predicted in northern, mountainous and oceanic regions (Fig. 6).

The model predicts that current exposure to spring frost after bud-burst is more frequent in more northern and higher altitude regions (Fig. 7a), following the Finnish phenological data used to parameterize the model. The earlier bud-burst shown in Fig. 6b–d is offset by increasing minimum temperatures at the time of bud-burst with the frequency of exposure to spring frost across most of the region decreasing by up to two frost days for all time periods (Fig. 7a–d). However, notable exceptions to this trend occur in the Scandina-vian mountain range, especially in the high mountains of Northern Sweden and Southern Norway. These are regions with an extremely short growing season, low average temperatures and relatively oceanic climates with low seasonal amplitude, and include mountain ranges where *B. pubescens* currently reaches its altitudinal limit. It is only in these regions that there is a predicted increase in frost exposure of up to two frost days. This is due to low predicted degree day requirements for bud-burst in these regions, which leads to predicted bud-burst occurring soon after daily temperatures exceeds the 3 °C threshold. Although the future climate projections predict a lengthening growing season, as a consequence of the oceanic climate, spring temperatures remain relatively low for a period following bud-burst, and hence the mean exposure to spring frost increases.

Figure 8 shows the difference between the bud-burst date predicted on the basis of the optimal GDD requirements from the 1961 to 1990 climate (Fig. 3) and that predicted from optimal GDD requirements calculated from the predicted climate for each time period. Generally, if there is no adaptation to climate change, we expect bud-burst to occur earlier than the 'optimal' date for a particular climate, with the largest differences in the south of the region and in the mountainous regions mentioned above. In the short-term (2010–2039) some regions are predicted to experience bud-burst slightly *later* than the climatically optimal date, whereas in the longer-term all regions are predicted to experience bud-burst earlier than the optimal date.

Discussion

B. pubescens is the dominant tree species at the latitudinal and altitudinal tree line in the north and west of Fennoscandia, and a widespread tree throughout northwestern Europe. Bud-burst in *B. pubescens* has been used as a phenology indicator for the region (Karlsen *et al.*, 2006) and has been shown to be well correlated with satellite-derived greening indices (Shutova *et al.*, 2006; Karlsen *et al.*, 2008). The species exhibits a high degree of genetic variation in northern Europe, two subspecies being recognized: *B. pubescens* ssp. *pubescens* (Downy Birch *s.s.*) and *B. pubescens* ssp. *czerepanovii* (Mountain Birch), an introgressive hybrid between *B. pubescens* ssp. *pubescens* and *Betula nana* (Eriksson & Jonsson, 1986). Several traits, including relative growth rate, dehardening and bud-burst timing, have been shown to have a high degree of heritability in *Betula* (Billington & Pelham, 1991; Kramer, 1995; Myking & Heide, 1995; Weih & Karlsson, 2001; Karlsson *et al.*, 2003; Taulavuori *et al.*, 2004). Billington & Pelham (1991) considered that projected rates of climate change
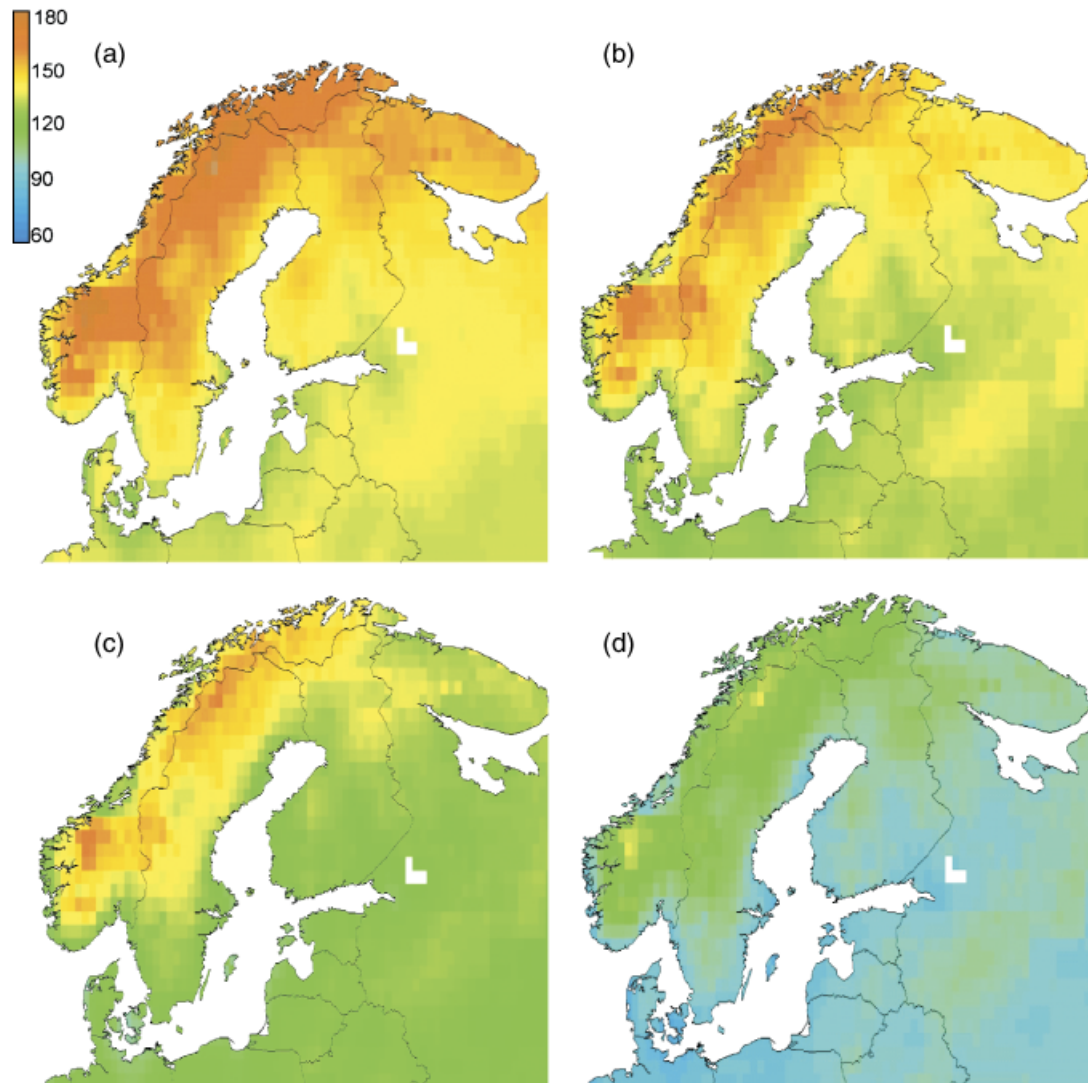
Fig. 6 Maps of predicted day of bud-burst for *Betula pubescens* derived by applying degree day requirement to future climate projections: (a) 1961–1990 climate; (b) 2010–2039; (c) 2040–2069; (d) 2070–2099.

will be too rapid for native populations of *B. pubescens* to adapt their bud-burst strategy in the absence of gene flow from external populations.

Phenological models parameterized by a survival/capacity trade-off as described here have the theoretical advantage over spatially uniform STT models that they allow spatial variation in bud-burst strategy and reproduce known genetic clines in bud-burst along latitudinal, altitudinal and continentality gradients. Furthermore, the prediction of bud-burst timing is based on reasonable assumptions concerning the trade-off between capacity and survival adaptation. It allows predictions to be made assuming that the spatially variant plant strategies will not adapt at the rate of future climate change, leading to nonoptimal strategies in the future. While this form of

parameterization still requires field data, it has been shown in this study to improve the ability of a budburst model parameterized in one area (in this case Finland) to be extended over a larger area (Fennoscandia and northern Russia). A similar approach could be taken for other species where thermal time models are appropriate and a capacity/survival trade-off is applicable, as long as sufficient data from phenotypes along climatic gradients is available. In the absence of more detailed physiological knowledge, not only of the mechanisms behind bud-burst timing, but also of the trade-offs involved in bud-burst strategy and cold adaptation (Howe *et al.*, 2003), this approach is an improvement on current methods. It is, however, based on a number of assumptions, which are assessed critically below.
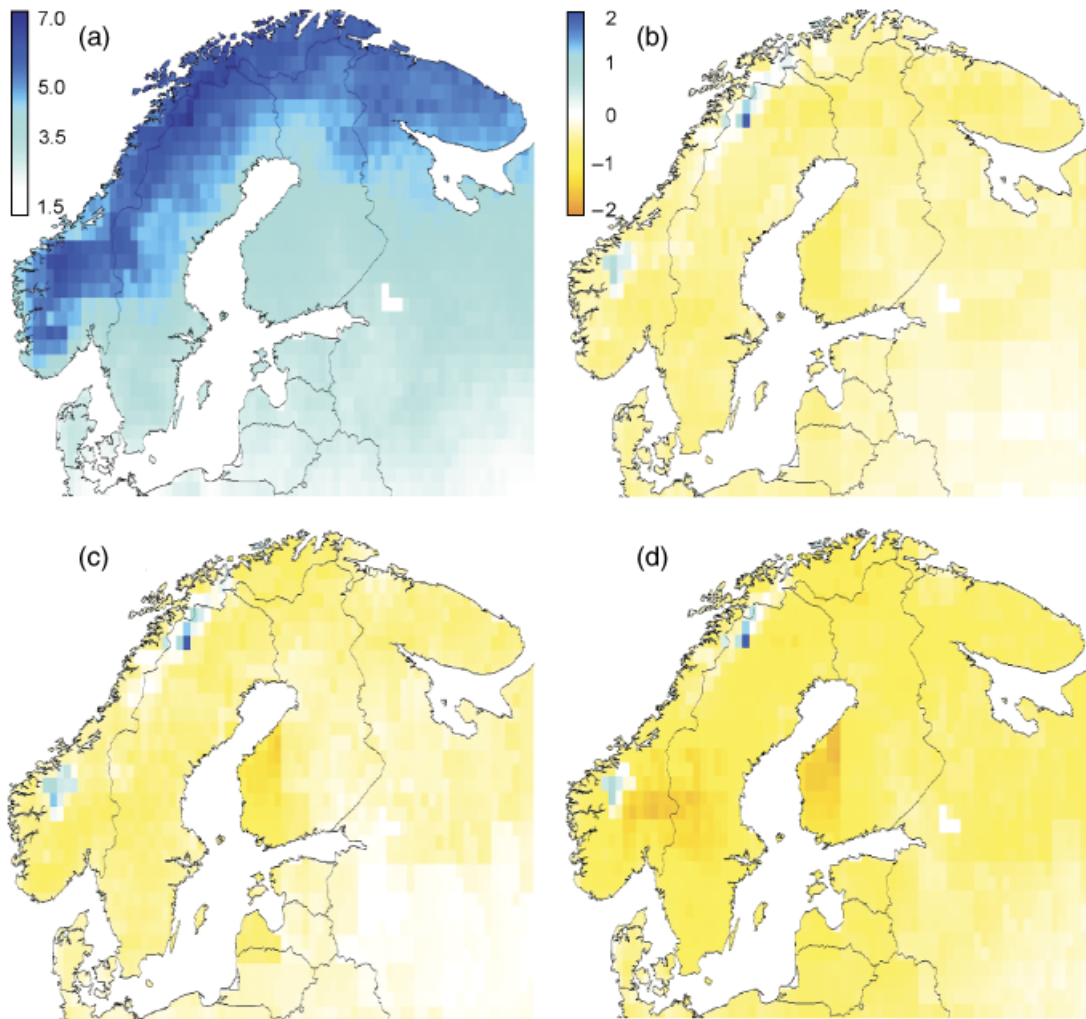
Fig. 7 (a) Map of average number of spring frost days following bud-burst for 1961–1990 climate. (b)–(d) predicted change in number of spring frost days for the periods 2010–2039, 2040–2069 and 2070–2099 respectively (scale as in b).
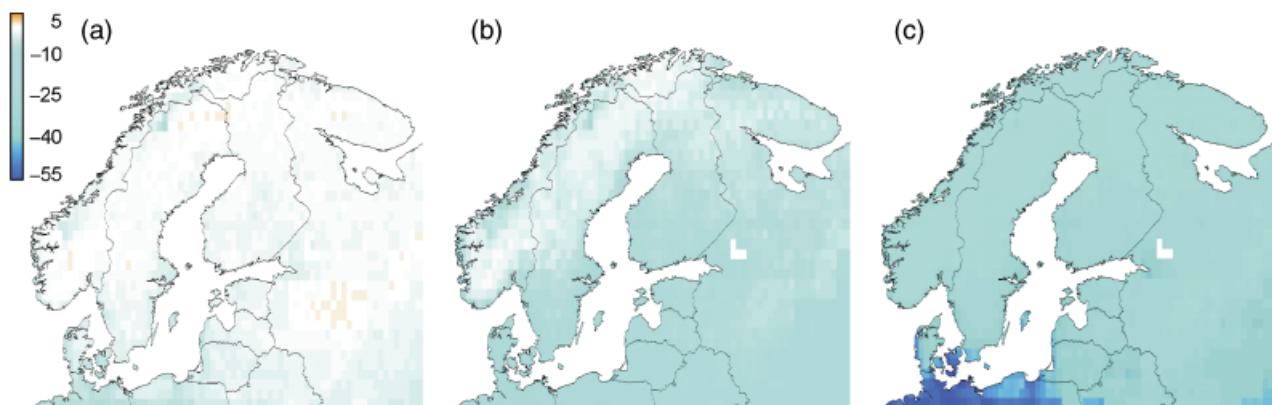
Fig. 8 Difference between predicted bud-burst date assuming no adaptation to changing climate (i.e. degree day requirements as in Fig. 4) and predicted date assuming 'optimal' adaptation to future climate, for the periods: (a) 2010–2039; (b) 2040–2069; and (c) 2070–2099.

The degree day requirement for bud-burst of a phenotype is assumed to be under genetic control, and to have been subject to adaptation in response to the recent climatic conditions under which the phenotype has evolved. The choice of late 20th Century climatic data to determine the current 'optimal' relationship between frost days and degree days may be restrictive because phenotypes, especially of relatively long-lived organisms, may not be in equilibrium with the current climate. However, it should be noted that temperatures during the 1961–1990 period were close to the average for the 20th Century in the region (Jylhä *et al.*, 2004), and fluctuations over recent centuries were of relatively small magnitude compared with forecast changes during the 21st Century.

Following the STT model, it is assumed that bud-burst is triggered by warm temperature in the spring, and the effects of other meteorological or environmental factors are secondary. In particular, we have not included a requirement for a period of temperatures below some threshold value in order to break winter dormancy, although such a chilling requirement has been found to be a prerequisite for bud-burst. This adaptation is presumed to be a defence against bud-burst occurring during unseasonably warm periods in winter or early spring. Chilling requirements determined from controlled experiments are usually exceeded under normal field conditions before the bud-burst dates, and establishing chilling requirements from field data are therefore problematic. However, under future climates, warm periods during winter and early spring are likely to increase in frequency; chilling requirements thus may have an important effect on the future response of bud-burst. It is not clear how changes in the frequency of extreme or unusual events (as opposed to climatic averages) will affect the balance of strategies.

It is assumed here that the fitness cost of frost damage may be estimated as a function of the mean number of nights during which the minimum temperature falls below 0 °C. Although dormant buds are able to survive exposure to extreme low temperatures during winter, (Ruohomäki *et al.*, 1997; Gansert *et al.*, 1999), actively growing tissue may be damaged by temperatures only a few degrees below zero. We assume that the frequency of temperatures below zero is well correlated with the potential for frost injury. It should be noted that a small shift in the average number of frosts following bud-burst may signify a considerable increase in the probability of prolonged periods of frost at the extreme tail of the distribution. The maximum average increase of two frost days predicted for high-altitude sites in Fig. 6 is likely to translate to a much higher frequency of cold springs in which postbudburst frosts are severe or prolonged. The use of values of β in Eqn (4), fitted from

current data, to predict frost frequencies under future scenarios assumes that, while minimum temperatures change, the variation in minimum temperature remains constant under changing climate. An analysis of GCM output would determine whether this is predicted to be the case.

This study assumes that the growing season ends when daily mean temperatures fall below 3 °C and so does not take into account leaf senescence occurring before this point. The timing of leaf senescence in autumn also influences the growing season length, and thus would be expected to influence the balance between capacity and survival adaptation. Leaf senescence dates are more conservative than bud-burst dates, however, and may be triggered predominantly by darkness duration. It is also assumed that the evolutionarily stable strategy is that which balances the fitness cost due to frost damage associated with early bud-burst with the fitness cost due to a shortened growing season associated with late bud-burst. This approach does not include the effects of other factors, including herbivory. The effects of both insect and mammalian herbivory may have significant effects on the carbon balance and ecological fitness of *B. pubescens* and may also influence phenology (Mjaaseth *et al.*, 2005).

Efforts are currently being made to generate and integrate phenological datasets with a wide (continental) geographical range and long (decadal) temporal coverage (Siljamo *et al.*, 2008). While valuable longer-term datasets exist (Aono & Kazui, 2008), they are usually limited in geographical coverage. There are at present few available medium- to long-term data sets that have a wide geographical spread along climatic gradients and incorporate comparable *in situ* observations of natural phenotypes in natural or seminatural environments. Phenological experiments frequently involve either two or more different genotypes in common garden, or a single standardized genotype grown across climatic gradients (Nordli *et al.*, 2008). While satellite data can be used to estimate 'greening up' of natural vegetation *in situ* (Myneni *et al.*, 1997; Botta *et al.*, 2000; Stöckli & Vidale, 2004; Ahl *et al.*, 2006; Fisher *et al.*, 2006; Karlsen *et al.*, 2006, 2008; Piao *et al.*, 2006; Shutova *et al.*, 2006), physiological interpretation of the spectral signal requires ground-truthing data and may require information on species composition or models specific to a given region or biome (Botta *et al.*, 2000; White & Nemani, 2006; Fisher *et al.*, 2007). In mixed-species stands of vegetation the remotely sensed signal may derive from a number of different bud-burst events from different species throughout the spring (Lechowicz, 1984; Wesolowski & Rowinski, 2006). In this context long term *in situ* phenological records from natural vegetation have a high value as data resources.

In addition to the need for data sets there is also clearly progress to be made in characterizing present and future climates, particularly rare and extreme events (Rigby & Porporato, 2008), elucidating the climatic and physiological factors driving phenological events (Linkosalo *et al.*, 2006), as well as the evolutionary forces that drive them. Improving predictive models of changes in regional and global phenology will require integration of a more probabilistic representation of climate with an improved understanding of both the physiological processes and the evolutionary trade-offs involved.

Summary

This study shows that current strategies for bud-burst may be suboptimal for future climates, and are expected to lead to bud-burst occurring in future considerably earlier than is predicted by an optimal strategy, particularly in maritime, mountainous and higher-latitude areas. However, across most of the study area the potential growing season is projected to increase considerably, while the exposure to frost risk is projected to decrease slightly under current strategies. Apart from the possible effects of extreme events, an increased incidence of frost damage to young shoots is unlikely in this context. Exceptions to this pattern occur in the high altitude, relatively maritime, areas of the Scandinavian mountains. In these areas, although growing season length is predicted to increase, the cool oceanic climate and low degree-day thresholds for bud-burst means that the exposure to frost risk is also predicted to increase considerably. This suggests that phenotypes with low degree day thresholds, adapted to current conditions at or near the altitudinal tree line in these mountains, will be vulnerable to increasing exposure to frost under projected changed climatic conditions late in the 21st Century. This is not predicted to be the case, however, in the more continental high-latitude tree line regions of Finland, Norway and Russia, where exposure to frost damage is predicted to decrease.

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