Changes in plant phenology—the seasonal timing of developmental events—are probably the best documented observed responses to ongoing climate change. Studies based on large global data sets have shown unequivocally that spring has advanced in the northern hemisphere (Parmesan and Yohe 2003, Root et al. 2003, Menzel et al. 2006), with an overall estimate across species of almost 3 days per decade (Parmesan 2007). Other studies have related the advancement linearly to the change in mean annual temperature (Wolkovitch et al. 2012). However, although these results provide convincing evidence that climate change is indeed affecting phenology of natural ecosystems, they shed little light on how to make forward predictions of phenological changes. The observed rates largely depend on the data set at hand (Parmesan 2007, Wolkovitch et al. 2012), and in any case, future predictions of warmer temperatures would involve extrapolation (Morin et al. 2009). On the other hand, the underlying mechanisms and causal relationships between environmental cues and phenological events still remain poorly understood (Morin et al. 2009, Pau et al. 2011).

In this issue, Jochner et al. (2013) set out to investigate the possibility of utilizing urbanization gradients of temperature as an analogue of climate change, to provide insights into climate change impacts on phenology. The case of birch (Betula pendula Roth) flowering is used as an example. Urbanization gradients are characterized by a decrease in temperature from the city centre towards the rural surroundings, but importantly, combined with simultaneous trends in CO$_2$ concentrations and other factors that are expected to accompany climate change (e.g., Zhang et al. 2004, Carreiro and Tripler 2005). While the inner-city parts of the urban gradient could be used to mimic the future environment in the area, the complete data sets with spatial trends could substitute time series with corresponding temporal trends. It has therefore been suggested that the urban gradient could be used to inform models about the quantitative relationships between climate and phenological events in current and future environments (Chung et al. 2009). To what extent the urban gradients actually represent predictions of future environmental factors still remains unclear, but more accurate information is becoming available that would allow for such comparisons (Rummukainen 2010).

Urban gradients are an example of the method of space-for-time (SFT) substitution that has been widely used in ecology and forest science (Fukami and Wardle 2005). Important applications to forestry, growth and yield tables have been constructed under the assumption that the spatial distribution of age classes of stands represents the temporal development of an individual stand (Picket 1989). In climate change studies, climate envelope models represent an important application of the SFT substitution (Heikkinen et al. 2006). They have been used, in particular, for projecting changes in species distributions under climate change on the basis of how the current geographical distributions are related to climatic variables (Fukami and Wardle 2005, Heikkinen et al. 2006). For phenology studies, however, it is necessary to separate the warming effect from the effect of daylength, both of which are known to affect phenological events but are strongly mutually correlated in large-scale geographical data. Altitudinal and urban gradients relying on data from more confined geographical areas could therefore be better suited for studying climate change impacts on phenology (Dunne et al. 2004, Zhang et al. 2004), but the role of the additional environmental factors co-varying...
with temperature along the urban gradient still remains to be
investigated (Carreiro and Tripler 2005). The objective of
Jochner et al. (2013) is to assess to what extent the SFT
approach involving urban gradients could lead to a better
understanding of phenological responses, eventually allowing
for projections across large spatial scales.

The prediction of phenological events, like any plant
responses, requires that (1) an adequate model exists and that
(2) the model can be parameterized and validated against data
relevant for the intended application. Phenological models for
temperate and boreal species, whether statistical or process-
oriented, are usually based mainly on temperature (Hänninen
and Kramer 2007, Fu et al. 2012), although daylength plays a
role at least in the choice of the time span of the temperature
variables (Linkosalo et al. 2006, Fu et al. 2012). The global
studies providing evidence of observed climate change impacts
have used a simple linear relationship between the timing of
phenological events and mean annual (Wolkovitch et al. 2012)
or seasonal (Buyantuyev et al. 2012) temperature, while a more
process-oriented approach to the progress of the annual cycle
is based on the accumulation of thermal time (or its variants)
through a sequence of stages in the ontogenetic development
cycle (Chuine et al. 2006, Hänninen and Kramer 2007).

The study by Jochner et al. (2013) interestingly sheds light
on the relative significance of model versus data for predicting
phenological events. First, they utilize two data sets on birch
flowering in southern Germany: a spatial data set across an
urbanization gradient from two consecutive years, and a tem-
poral data set covering 20 years of phenological observations
from four adjacent sites. Second, they test two models: a sim-
ple linear relationship between March–April temperature and
flowering date, and a process-oriented model including the
ontogenetic phases of dormancy induction, chilling and forcing
(Caffarra et al. 2011). Both models are parameterized using
(part of) the spatial data set, then validated against the tempo-
ral data set. For comparison, the linear model is also fitted to
the temporal data.

The results of the exercise seem somewhat contradictory.
First, the linear models based on the spatial and temporal data
differ, and the difference is statistically significant, even though
the temporal data exhibit wide scatter. Second, the predictions
using the spatially fitted models are reasonably good on the
temporal data, and the results are similar for both the linear
model and the process-oriented model. However, neither model
succeeds in explaining the considerable scatter of the temporal
data set. The results further emphasize that care should be
taken when different types of data are combined, and the limita-
tions of both the models and the data should be thoroughly
analysed before further conclusions are drawn.

It is particularly interesting that the more complex, process-
oriented model was not able to improve considerably on the
predictions of the simple linear model. Is this because even the
more complex model structure is inadequate, or because the
data are not sufficiently informative? Studies applying Bayesian
model comparison show that increasing model complexity does
not necessarily increase a model’s predictive power, even if the
simple models are theoretically justified, unless the data are
sufficient for adequately quantifying the model (Fu et al. 2012,
von Oijen et al. 2013). In line with this, Jochner et al. (2013) sug-
gest that 2 years of spatial data within a confined geographical
area may not have been enough for adequately parameterizing
the model, especially as regards the responses of trees to chill-
ing and photoperiod, and their interaction. If this was the case,
longer time series of data from urbanization gradients, as well as
pooling several locations, should prove fruitful for improving the
predictive power of the process-oriented model.

It is also possible that daily mean temperature is not suffi-
cient for predicting the general pattern of phenological events
across different data sets, even if the temperature response as
such was based on a thorough mechanistic understanding of
ontogenetic development. Jochner et al. (2013) discuss the
possibility of factors outside the model such as soil properties,
air pollution effects, tree age and genetic traits. Some studies
have also found evidence of the impact of water availability
(Pinto et al. 2011) or within-day temperature variation (Chung
et al. 2009) on the timing of phenological events. In a limited
data set additional causal variables may be sufficiently con-
stant across the entire data, or they may be correlated with the
explanatory variable(s) included in the model, such that their
exclusion does not reduce the predictive power of the model in
similar data sets (Mac Nally 2000, Heikkinen et al. 2006). That
predictions based on one type of data set fail for another
hence indicates that some causal variables are missing from
the model, and that they could be identified by analysing the
differences in the correlation structures of candidate explana-
tory variables in the two data sets. A special characteristic of
spatial data is its tendency of autocorrelation, i.e., values of
particular variables in neighbouring sites are more similar or
less similar than in a random sample (Heikkinen et al. 2006).

The study by Jochner et al. (2013) has provided interesting
insights into timely questions on how to improve our under-
standing of processes related to phenological events, and how
to utilize this understanding in building better predictive mod-
els. On the surface, their key finding that caution should be
exercised when interpreting the results from urbanization gra-
dients in terms of climate change impacts may sound disap-
pointing. However, the study has also demonstrated the utility
of combining spatial and temporal data sets as a means for
extracting more information about causal relationships related
to phenology.

Conflict of interest

None declared.
References


