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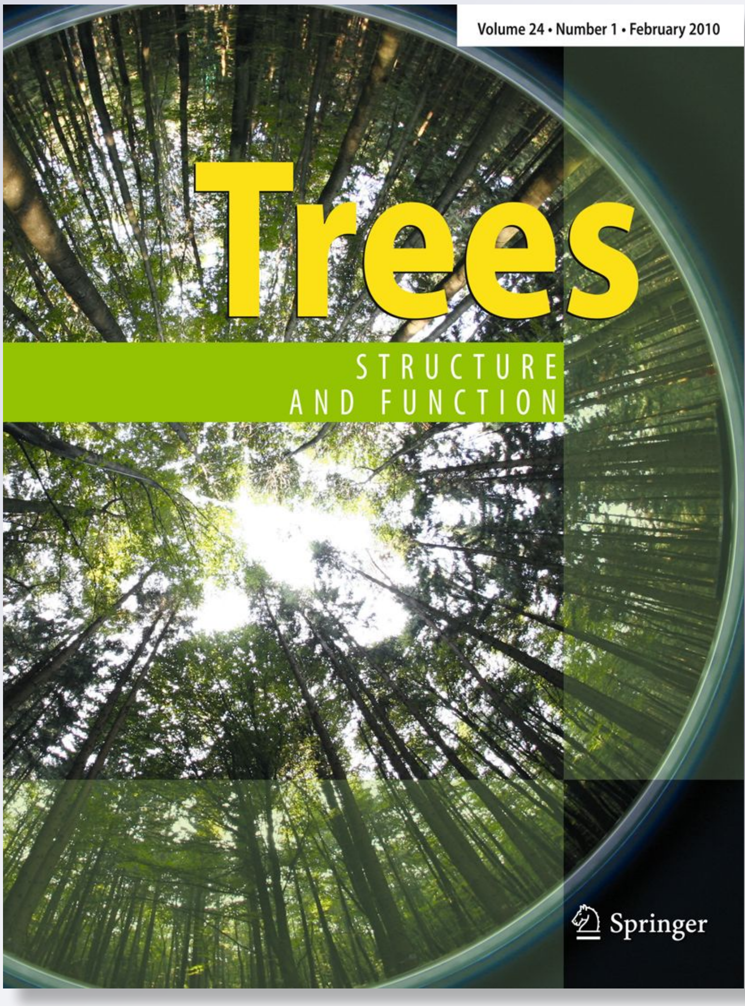


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ORIGINAL PAPER

# Temporal shifts in leaf phenology of beech (*Fagus sylvatica*) depend on elevation

**Katarina Čufar · Martin De Luis · Miguel Angel Saz · Zalika Črepinšek · Lučka Kajfež-Bogataj**

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**Abstract** We analyzed the leaf phenology of European beech (*Fagus sylvatica*) and its variation due to spatial and temporal climatic variability, using a modified data set of the phenological network in Slovenia. We used first leaf unfolding (LU) and general leaf colouring (LC) time series of 47 sites (altitudes from 55 to 1,050 m a.s.l.) and corresponding climate series (52 of precipitation and 38 of temperature) for the period 1955–2007, collected by the Environmental Agency of the Republic of Slovenia. Across the network in average, LU occurred from 14 April until 13 May, and LC from 3 October until 29 October. LU was delayed by 2.6 days and LC was promoted by 1.9 days when the altitude increased by 100 m. Year-to-year variation of LU was significantly correlated with March and April temperatures. March temperatures had a greater effect at lower elevations and April ones at higher elevations. LC was related to August and September temperatures, and occurred later if the temperatures were higher. Recently, March and April temperatures showed an increasing trend and LU occurred 1.52 days earlier per decade at 1,000 m a.s.l. but no significant shifts were observed at lower altitudes. August temperatures were also increasing but the trends of LC were not significant and were not clearly related to altitude. Our detailed sub-regional data from a relatively small area with high geographic variability showed that changes in climate affect phenological response, mainly leaf unfolding, to a greater degree at higher altitudes than at lower ones.

**Keywords** European beech (*Fagus sylvatica*) · Phenology · Temperature · Leaf unfolding · Leaf colouring · Climate change

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## Introduction

Plant phenology, studying the seasonal timing of plant life cycle events (phenophases), has been proposed as an indicator of climatic difference and global change by the European Environment Agency and the Intergovernmental Panel on Climate Change, IPCC (2007). Long-term phenological records in trees, including spring events such as leaf unfolding and autumnal events of leaf colouring, have shown that a rise in global temperature generally leads to earlier timing of spring events and poleward and upward shifts in plant ranges (IPCC 2007; Kramer et al. 2000; Menzel et al. 2006; Parmesan and Yohe 2003).

Trends in different phenological events may also vary due to the divergent effects of climate on each phase of the plant life cycle, as well as heterogeneous temporal trends of different climatic elements within the year (Gordo and Sanz 2010). In addition, phenological responses vary geographically, due to the heterogeneous geographical

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variability of warming (Chmielewski and Rötzer 2001, 2002; Doi and Takahashi 2008; Rötzer et al. 2000). The last AR4 report (IPCC 2007) therefore suggests that we should now focus on detailed sub-regional studies, particularly in areas that represent transitional climate areas.

European beech (*Fagus sylvatica* L.) is an important and widespread forest tree species in Europe. Several recent studies have shown that it might retreat from vulnerable ecosystems, especially at the edge of its natural range (Geßler et al. 2007; Jump et al. 2006; Kramer et al. 2010). It belongs to a group of woody plants that have been the focus of phenological observations within the framework of the European International Phenological Gardens program and has been included in several phenological studies dealing with past and possible future effects of changing climate on this species in different areas (e.g., Caffarra and Donnelly 2011; Delpierre et al. 2009; Dittmar and Elling 2006; Donnelly et al. 2006; Vitasse et al. 2011).

In Slovenia, beech grows in a great variety of forest associations, from the lowlands up to the high mountains. It is one of the most important wood species in the region and forms more than one-third of the wood stock. Its proportion is currently increasing, particularly where forests with a high percentage of conifers are being converted into more natural mixed stands (Bončina et al. 2003; Poljanec et al. 2010).

The climate in Slovenia is characterized by wide local variability, with fairly large gradients of climatic factors, due to the position between the Alps, the Mediterranean and continental Europe (PRUDENCE 2005). Beech in Slovenia is also included in the European International Phenological Gardens program and, it was among others included in a European wide study of the phenological response of plants to climate change, in which it was shown that its mean national trends match the pattern of temperature increase in March (Menzel et al. 2006).

When studying beech phenology, we need to understand how this species interacts with the environment. Various experimental studies have shown that cessation of winter dormancy and subsequent leaf unfolding in beech are affected by chilling during dormancy, as well as forcing temperatures and photoperiod during reactivation, even though some results are controversial (Caffarra and Donnelly 2011; Heide 1993; Murray et al. 1989). Phenological models for predicting the behaviour of beech usually perform worse than for other species (e.g., Vitasse et al. 2011). Leaf colouring and leaf fall in beech as affected by climatic factors, as in other species, have been less studied than leaf unfolding, although various authors have reported that mainly lower temperatures, shorter day length and summer drought promote the senescence of leaves (e.g., Črepinšek et al. 2006; Delpierre et al. 2009).

Since temperatures affect spring and autumn phenological phases, it is also important to know how altitude affects leaf phenology (e.g., Dittmar and Elling 2006; Vitasse et al. 2010). This has not been shown precisely for beech in Slovenia, but it is known that tree ring widths in beech in Slovenia and surrounding countries respond to climate depending on elevation (Di Filippo et al. 2007; Čufar et al. 2008a), and that cambium reactivation with the formation of new xylem cells takes place immediately after bud breaking (Čufar et al. 2008b). It is still not known how the leaf phenology of beech varies on different sites and elevations affected by different climatic conditions. Slovenia with good spatial coverage for climatic and phenological data provides good possibilities for exploring the spatial and temporal effects of climate changes on phenology.

The aim of the present study was to analyse spatial variability in *Fagus sylvatica* leaf phenology in Slovenia in relation to climate and its temporal changes. For this purpose, we analyzed 47 series of leaf unfolding and general leaf colouring for the period 1955–2007 and identified key climatic factors affecting them. Furthermore, we explored whether trends (shifts) exist in phenological series and whether they can be explained by trends in key climatic factors.

## Materials and methods

### Phenological data

We used phenological data, first leaf unfolding (LU) and general leaf colouring (LC) of European beech (*Fagus sylvatica* L.) in Slovenia. The data originated from the phenological archive of the Slovenian National Phenological Network of the Environmental Agency of the Republic of Slovenia (ARSO) within the Ministry of the Environment. They included 47 localities distributed all over Slovenia, with altitudes ranging from 55 to 1,050 m a.s.l. and with different site and climatic characteristics (Fig. 1, Table 1 supplementary material).

The selection of trees and the observations were made in accordance with Guidelines for Plant Phenological Observations (Koch et al. 2007). Monitoring of different phases, as suggested for perennial plants, was carried out on individual trees in naturally established populations. The observations were always made on the same trees for as many years as possible. If one of the selected trees died or was removed, it was replaced with a new, nearby one in line with the criteria for phenological monitoring. The location of the trees to be observed was selected so that it was representative of the observation area, which excluded micro locations associated with the extreme development,

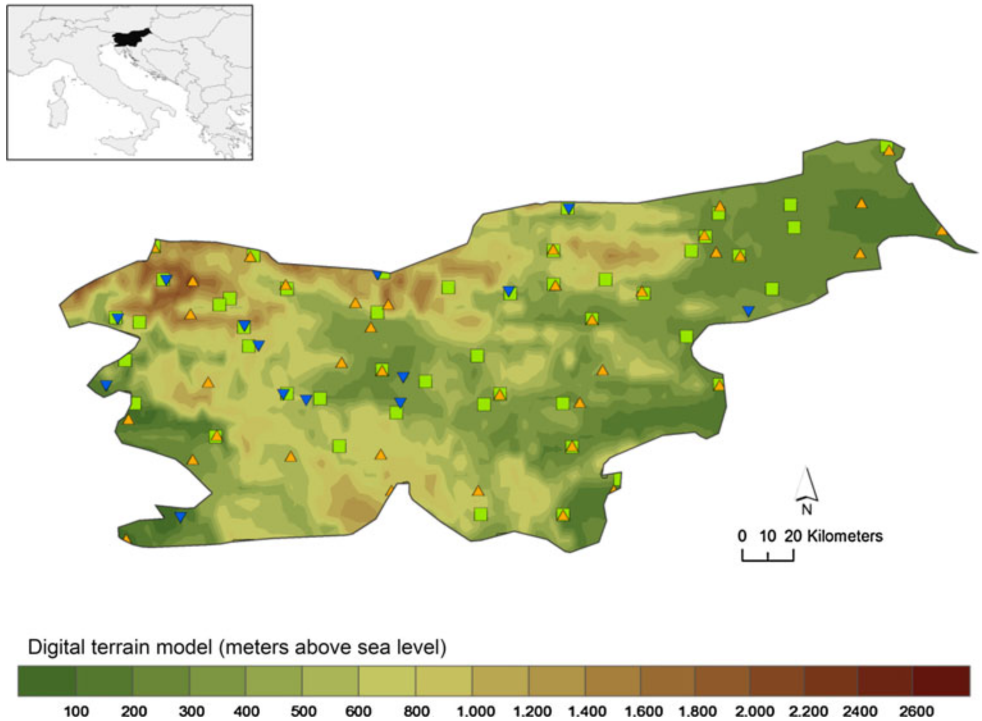


**Fig. 1** Map of Slovenia with locations of phenological observations (*squares*) and climate stations with temperature and precipitation data (*upright triangles*) and with precipitation data only (*inverted triangles*). *Inset* shows Slovenia in Europe. For details see also Table 1 supplementary material

which was very early or very late in comparison to other trees. The observed time-segment of bud bursting and leaf development in beech in spring was about 4 weeks, and during this time the observations were carried out daily.

According to the Guidelines for Plant Phenological Observations, the data are characteristic of the larger region around the observation area locations. The day of LU was recorded as the first regular surfaces of leaves were becoming visible in 3–4 places on the observed tree (BBCH scale 11) and LC when 50% of leaves had turned yellow on the observed tree (BBCH scale 94). The period of observation was 1955–2007.

## Climatic data

Climatic data, mean monthly air temperatures and monthly amount of precipitation, for the same period 1955–2007, were obtained from 52 precipitation and 38 temperature stations of ARSO (Fig. 1). These weather stations are located at or close to the phenological observation sites (median value 5 km from the phenological observation sites). The climatic parameters of the stations vary with regard to the annual amount of precipitation (800–3,500 mm), mean annual air temperatures (from −1.4 to 12.2°C); the distribution corresponds to Continental, Alpine or Sub-Mediterranean climatic regimes (PRUDENCE 2005).

In the network, mean temperatures and precipitation vary across the altitudinal gradient. In average, mean annual precipitation increases by 7% if the altitude increases by 100 m. On the other hand, mean annual temperatures decrease by 0.75°C if the altitude increases by 100 m. At the seasonal scale, the decrease in temperatures with increasing altitudes is higher in spring (−0.91°C per 100 m) and lower in winter (−0.54°C per 100 m). A detailed description of climate characteristics of the study sites can be found in Table 1 (supplementary material).

## Statistical analyses

Phenological and climatic original datasets obtained from the ARSO were set up following an exhaustive quality control process designed to detect suspicious data and inhomogeneous series.

We originally obtained 56 phenological data sets from ARSO, which contained gaps or missing data representing on average 26% of the database. We therefore first selected 47 series, which contained information for more than 20 years within the analyzed period 1955–2007. They showed high correlation with neighbouring series, so filling of gaps was possible by applying the general procedures used to construct the climatic database for the Iberian Peninsula (De Luis et al. 2010; González-Hidalgo et al. 2010). The general procedure is based on the construction of a set of reference series for each original station. To construct the reference series, neighbouring stations were selected according to the following criteria: distance less than 50 km, minimum overlap of more than 10 years and all positive monthly correlations and average monthly correlations higher than 0.5. To avoid introducing an uncontrolled bias during the creation of the reference series, average standardizations were applied to all neighbouring series using a common overlap period with the candidate one. Finally, the calculation of each reference series was carried out by means of a weighted average of $(1/d)^2$, where $d$ is the distance of the candidate in kilometres. After comparing the original with the reference series, suspicious data were discarded (see details in González-Hidalgo et al. 2010) and homogeneity was checked with the standard normal homogeneity test (SNHT) (Alexandersson 1986). Reconstruction of the final time series was performed with a new set of reference series from the final homogeneous data, using a maximum distance of 10 km; a second set of references at 25 km was used to fill in any gaps. The overall procedure was performed with specific software developed for climate analysis (AnClim and ProClim software, Stepanek 2008a, b).

Thereafter, mean values of LU and LC over the period 1955–2007 were calculated on each phenological station to explore their spatial variability. We used stepwise multiple regression models, using altitude, latitude, longitude and distance to the Adriatic Sea as independent variables to identify key geographical elements explaining such spatial variations.

Additionally, we used correlation function analysis (Biondi and Waikul 2004), to identify main climatic parameters explaining year-to-year variations in phenological series. At each site, time series of LU and LC were used as dependent variables and the monthly mean temperatures and the monthly sums of precipitation for each biological year from the previous September to the current November were the regressors. The program applies a bootstrap process (Guiot 1991) to assess the statistical significance of the correlation coefficients. Finally, we explored spatial variations for obtained statistically significant coefficients.

Finally, we studied temporal variations of phenological series and of key climate factors (identified previously) to establish whether the observed trends in phenological series can be explained by the observed trends in climate. The intensities of observed changes were estimated with linear regression techniques. The significance of these changes was assessed using the Pearson correlation coefficient ($p < 0.05$ level).

## Results

### Average time of leaf unfolding and general leaf colouring

In the period 1955–2007, the average day of the year (DOY) of the LU varied from 14 April (DOY 104) to 13 May (DOY 133) across the network. Extreme values of LU were 26 March (DOY 85) and 31 May (DOY 151). Average LC was observed from 3 October (DOY 276) to 29 October (DOY 302) across the network. Extreme values of LC were 5 September (DOY 248) and 13 November (DOY 317) (Fig. 2a, b).

The spatial variation of LU was significantly related to altitude. According to the model on Fig. 2a, LU was delayed by 2.6 (±0.24) days if the altitude increased by 100 m. The spatial variation of LC was also significantly related to altitude and was delayed by 1.9 (±0.20) days if the altitude decreased by 100 m (Fig. 2b).

According to the obtained models, the earliest LU occurred in the central, southwestern and northeastern parts of Slovenia (Fig. 3a). The areas with the latest LU were at higher altitudes in the mountains. The earliest LC was observed in the mountains and the latest in the central, southwestern and northeastern parts of Slovenia (Fig. 3b).

### Climatic factors and temporal shifts in phenological series

Year-to-year variation of LU was significantly correlated with inter-annual variations in March and April temperatures across the network. At lower altitudes, variations in LU were significantly negatively correlated with variations in March temperatures and higher March temperatures promoted

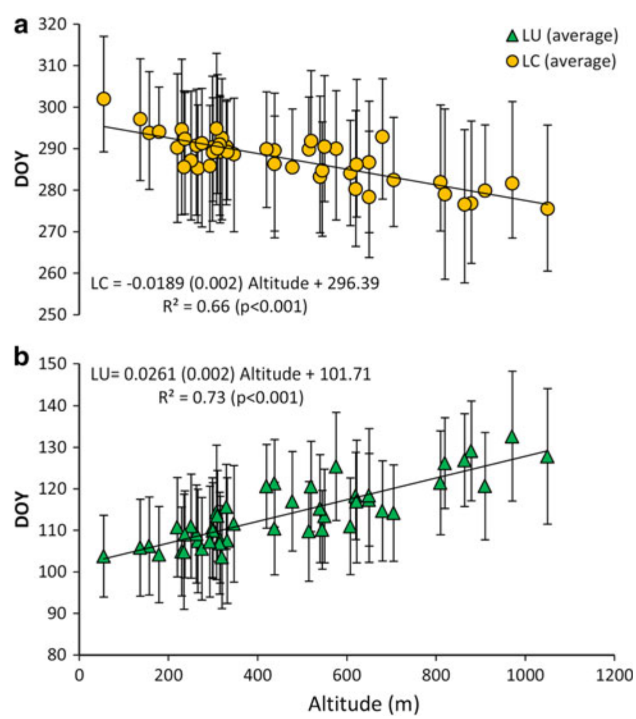


**Fig. 2** Leaf phenology of beech in Slovenia. Average day of the year (DOY) for **a** first leaf unfolding (LU) and **b** general leaf colouring (LC) related to altitude with equations showing the relations of LU and LC to altitude for the period 1955–2007, $R^2$ and significance level $p$. For details see also Table 1 supplementary material

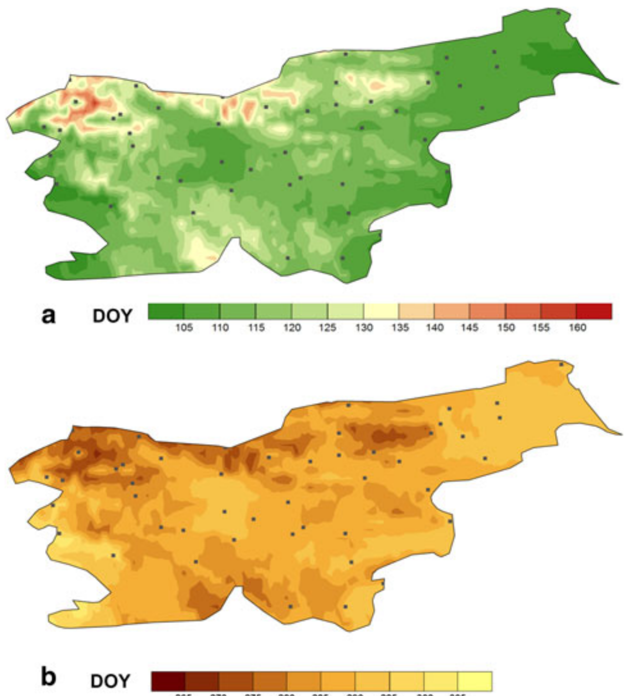


**Fig. 3** Modelled spatial distribution of timing (day of the year—DOY) of **a** first leaf unfolding (LU) and **b** general leaf colouring (LC) for beech in Slovenia

earlier LU. At higher altitudes, LU was better correlated with April temperatures; the correlation was also negative (Fig. 4a, b). The coefficients of correlation ($r$) reached maximum values of −0.72 for March and −0.71 for April.

According to these results, March temperatures were shown to be the main climatic parameter controlling variations in LU in the lowlands of northeastern, central and southwestern Slovenia, while April temperature variations played the decisive role at higher elevations, especially in the northeastern and southwestern parts (Alps and the Dinaric mountains) (Fig. 4c, d).

Year-to-year variations of LC were positively and significantly correlated with variations in August and September temperatures across the network, but the correlation to temperature was weaker (maximum $r = 0.50$) than for LU. The influence of both was important over the entire area and their importance did not vary with altitude (Fig. 5a, b).

These results indicate that LC is generally delayed in all parts of Slovenia if August and September temperatures are higher than normal. On the other hand, LC is advanced when August and September temperatures are lower than normal (Fig. 5c, d). The amount of monthly precipitation was not significantly correlated with LU and LC.

## Trends in phenological and in climatic series

### Trends in first leaf unfolding and in significant climatic parameters

In addition to their spatial variation, the phenological series also exhibited changes during the analyzed period 1955–2007, which varied with altitude. In the most recent

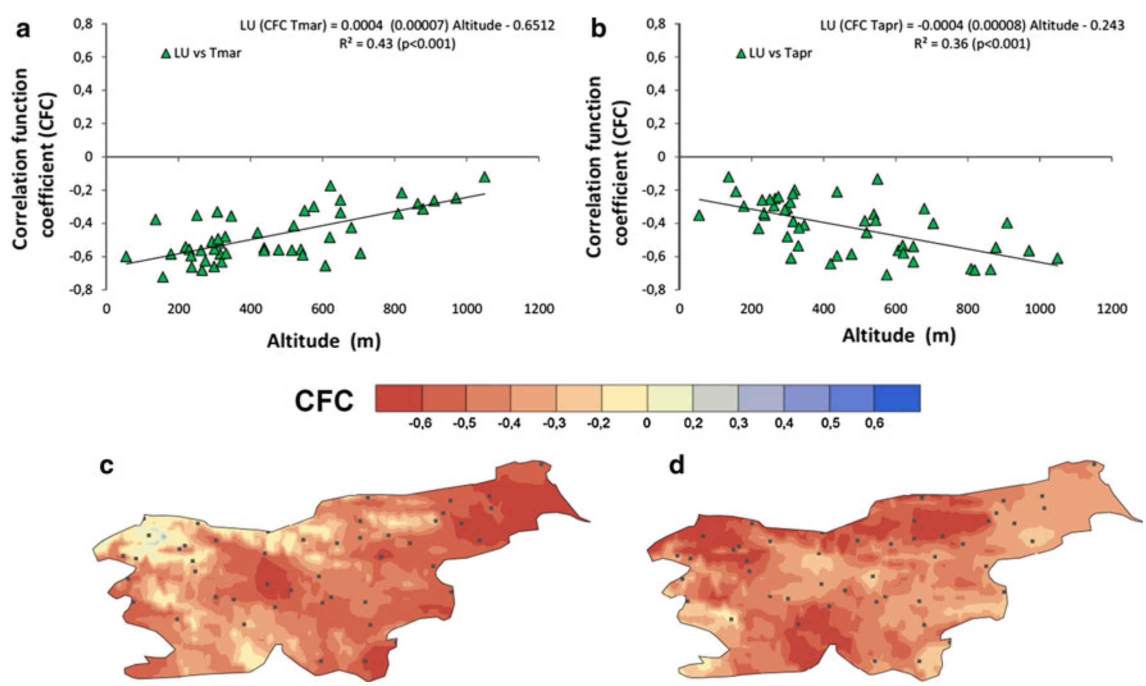


**Fig. 4** First leaf unfolding (LU) and its correlation to **a** March and **b** April temperatures. Spatial distribution of correlation function coefficients (CFC) for **c** March and **d** April temperatures in Slovenia

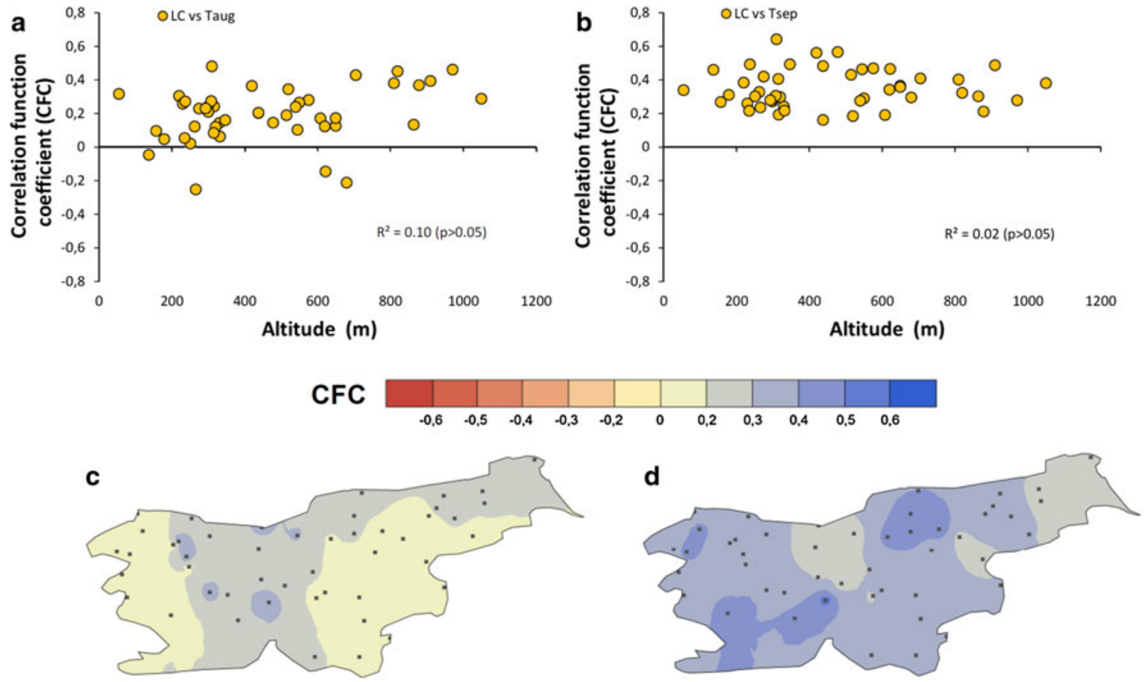


**Fig. 5** General leaf colouring (LC) and its correlation to **a** August and **b** September temperatures. Spatial distribution of correlation function coefficients (CFC) for **c** August and **d** September temperatures in Slovenia; *ns* not significant $p > 0.05$. For details see also Table 1 supplementary material

period, the leaves generally tended to unfold earlier but this trend was only significant at higher altitudes (Fig. 6a).

According to these results, LU advanced at a rate of 1.52 days per decade at an altitude of 1,000 m a.s.l. At 500 m a.s.l., the calculated value is 0.67 days per decade but the difference is not statistically significant. Significant earlier LU was therefore mainly detected in northern Slovenia, on the Alpine sites (Fig. 6b).

General trends in LU are partially in agreement with observed trends of main climate variables, which indicate that April and especially March temperatures significantly increased in the period 1955–2007 (Fig. 6c, d). However, climatic trends did not exhibit any significant pattern along altitudinal levels. This suggests that, at higher altitudes, even small changes in April mean temperatures (which are crucial there) produce a significant change in the temporal pattern of LU. On the other hand, at lower altitudes, more intense changes in March mean temperatures (which are crucial for LU at lower elevations) produce less intense changes in the temporal pattern of LU.

### Trends of general leaf colouring and of significant climatic parameters

During the period 1955–2007, significant trends were not detected in LC at most of the analyzed stations. There was also no significant pattern across the altitudinal gradient (Fig. 7a, b).

These results do not conform to observed trends in main climatic parameters that control LC. August temperatures significantly increased in most parts of Slovenia during the period 1955–2007 (Fig. 7c) but there were no significant trends in September temperatures (Fig. 7d).

## Discussion

Although the leaf phenology of beech is generally considered to be less sensitive to environmental variability than in some other tree species (e.g., Vitasse et al. 2009), the present study shows a considerable variability at different elevations.

Our study on a relatively small area of ca. 20,000 km$^2$ only partly confirmed the observations of large regional studies, which have shown that, due to recent global climate warming, spring arrives earlier but that changes in autumn events are more ambiguous (e.g., Menzel et al. 2006; Thompson and Clark 2008). We showed that changes in leaf phenology are not uniform and that they greatly differ along altitudinal gradients. In recent decades, leaves in beech in Slovenia have generally tended to unfold earlier but this trend has only been significant at higher altitudes. This indicates that, at higher altitudes, even small changes in climate may trigger a more significant change in phenological behaviour than at lower altitudes. To the best of our knowledge, no other study to

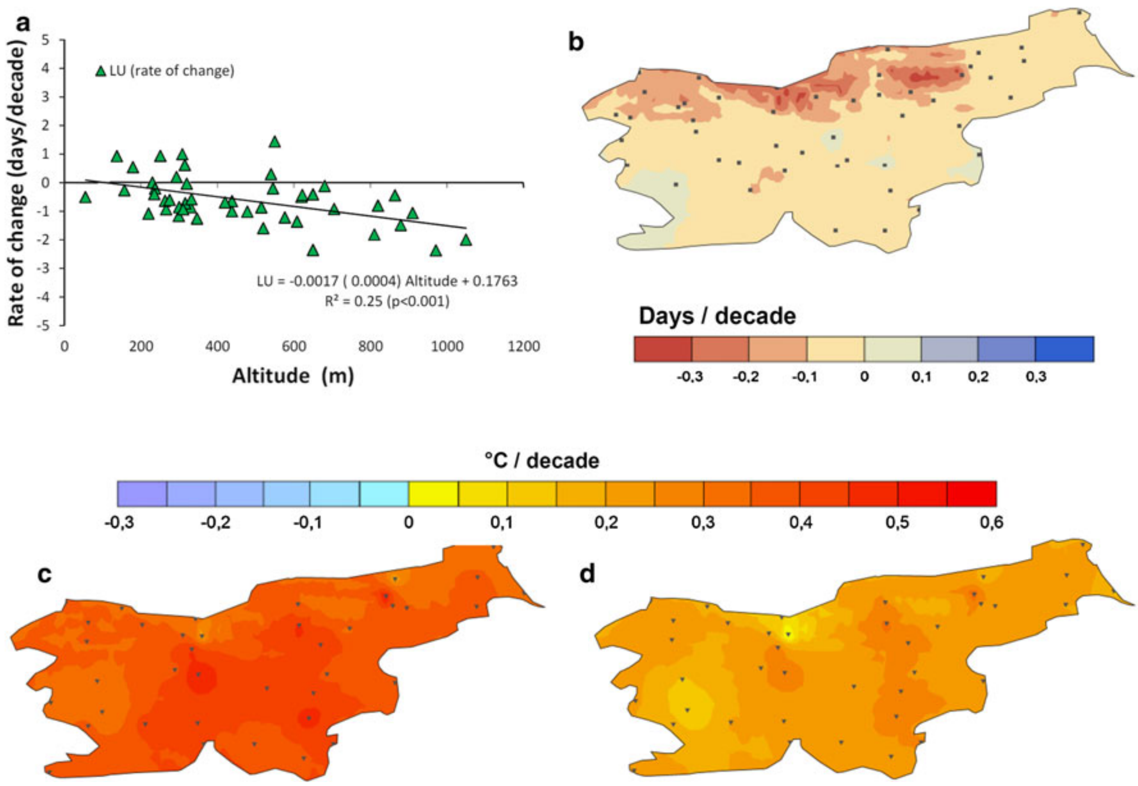


**Fig. 6** Trends of beech phenology and key climatic variables in Slovenia in the period 1955–2007: **a** first leaf unfolding (LU), **b** spatial distribution of LU changes across Slovenia, **c** trends in March temperatures and **d** trends in April temperatures

date has shown such clear differences in trends related to elevation.

LU in beech in Slovenia occurs from 26 March to 31 May. Beech needs an adequate period of chilling (generally at temperatures below about 10°C) for release of winter dormancy and, after this, exposure to warm temperatures (forcing temperatures) are needed to trigger budburst. In addition, beech requires a relatively long photoperiod (more than about 12 h of daylight) to resume growth in spring (Caffarra and Donnelly 2011; Körner and Basler 2010; Heide 1993).

Slovenian sites are characterized by harsh winter conditions, with mean temperatures in three winter months between −3.3 and 3.8°C. At the time of LU on Slovenian sites, daylength ranges from 13 h and half (on 14 April) up to nearly 15 h (on 13 May). On this basis, we assume that chilling and daylength requirements are fulfilled until mid March on all sites and forcing temperatures therefore seem to be most important for promoting LU. Furthermore, our results indicate that the best predictors for LU are the temperatures occurring during the month prior to budburst, i.e., in March at low elevations and in April at high elevations. March temperatures are therefore probably high enough at low elevations and too low at high elevations to act as forcing temperatures. In Slovenia, April and especially March temperatures have significantly increased in recent decades. Since the requirements of chilling and daylength are already fulfilled in March, at higher altitudes even small changes in April temperatures seem to trigger a significant change in LU. At the same time, at lower altitudes, changes in March temperatures do not cause significant shifts in phenology because chilling and/or photoperiod are possibly the limiting factors in March at low elevations. Towards the end of the growing season, the leaves undergo senescence and leaf fall which are important for the adaptation of trees to survive the cold winter period and to provide litter input to the ecosystem. Low temperatures and short days are considered to be among the most important environmental factors promoting leaf senescence (e.g., Delpierre et al. 2009; Estrella and Menzel 2006). Consistent with the low temperature trigger hypothesis, Menzel (2003), among others, reported on positive correlations between August and September mean temperatures and LC dates in *Fagus sylvatica,* which is consistent also with our observations. In addition, severe drought was also mentioned as a possible factor promoting leaf fall in deciduous species (e.g., Breda et al. 2006). However, in our case, we did not observe any significant effect of precipitation on leaf phenology. Estrella and Menzel (2006) also checked hypotheses proposed to predict the onset of LC. Most of the models used in comparison were temperature related and they often failed

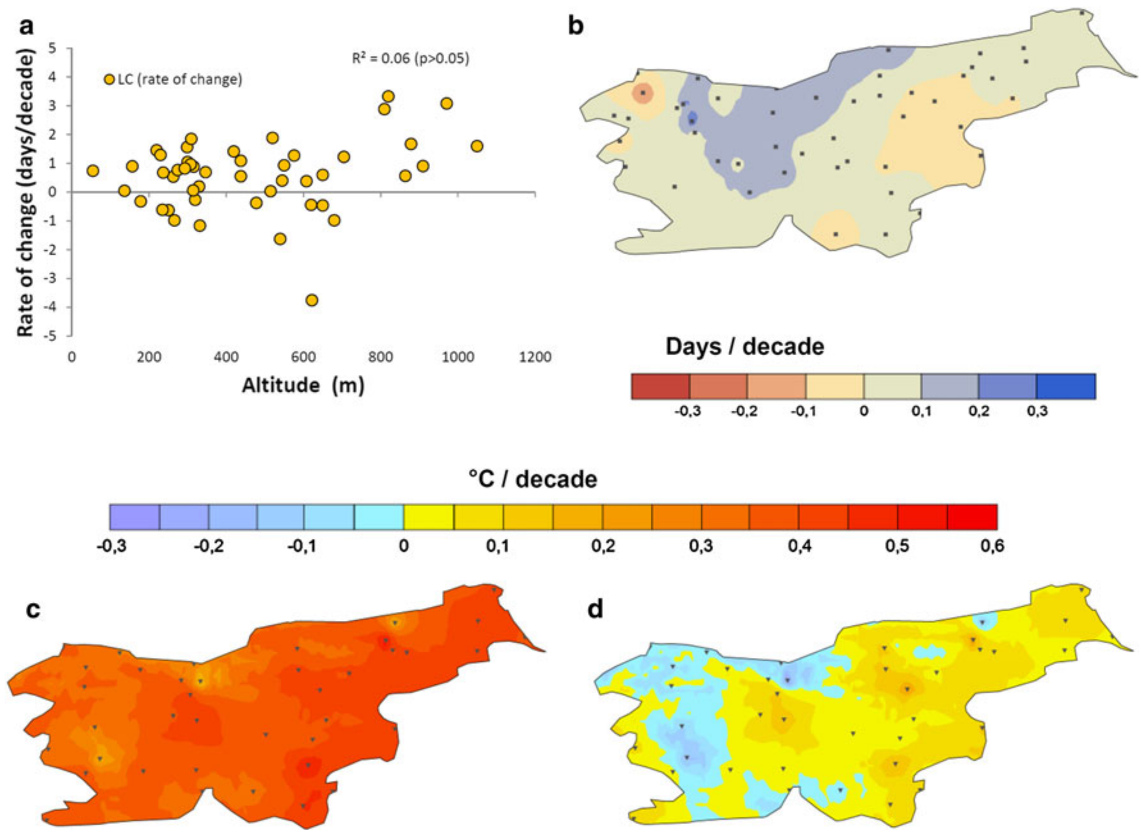


**Fig. 7** Trends of beech phenology and trends in key climatic variables in Slovenia in the period 1955–2007: **a** general leaf colouring (LC), **b** spatial distribution of LC trend changes across Slovenia, **c** trends in August temperatures and **d** trends in September temperatures

accurately to predict LC occurrence of deciduous tree species in a temperate climate.

On Slovenian sites, LC occurred from 3 October until 29 October and year-to-year variations of the average day of LC were positively and significantly correlated with variations in August and September temperatures. The influence of both was important over the whole area and their importance did not vary with altitude. Although August and September temperatures have increased in the last decades, LC was not significantly delayed.

LC probably did not vary with altitude because the temperature is not as important for leaf senescence as for LU. The particular climatic situation (temperature) on different sites does not seem to promote leaf senescence as much as daylength or other factors. LC is probably not significantly delayed because the increasing trends of August and September temperatures are not so clear.

Leaf phenology is important for the survival of trees and the dual dormancy control system (through temperature and daylength) has great adaptive significance. If the leaves unfold too early, they are more likely to be damaged by spring frost (Gomory and Paule 2011). With climatic warming, there is a tendency towards earlier budburst, which in beech increases the risk of spring frost injury due to cold spells following a warmer period, which promoted early leaf unfolding. Several studies suggest increased risk of frost damage as a possible effect of climatic warming (Hänninen 1991; Kramer 1994; Linkosalo et al. 2000). At middle altitudes, cold spells might become more frequent because of increased temperature variability and enhanced meridional exchanges between arctic and tropical air masses (Hänninen 1991).

A comparison of different tree species with different strategies of survival and capacity adaptation showed that beech has a strategy to avoid frost damage on account of vigorous growth at the beginning of the season (Caffarra and Donnelly 2011). We observed that at higher elevations earlier leaf unfolding is anticipated. The consequences of such shifted phenology might increase spring frost injuries and endanger the survival of beech at higher altitudes. The implication of the observed changes in phenology may also affect other processes in tree and plant communities. This all may cause changed productivity, biogeographical shifts and affect the future distribution and survival of beech, which is among the most common and important tree species in Slovenia and surrounding regions.

The present study has shown differences in phenological trends related to altitude and therefore confirms that focusing on detailed sub-regional studies in areas with a transitional climate can be helpful for predicting future phenological shifts and their consequences.

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