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

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Abstract

We analysed the leaf phenology of European beech (*Fagus sylvatica*) in Slovenia and its variation due to spatial and temporal climatic variability, using a modified data set of the phenological network. We used first leaf unfolding (LU) and general leaf colouring (LC) time series of 47 sites (altitudes from 55 to 1050 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 (ARSO). Across the network average, LU occurred from 13 April until 13 May, and LC from 2 October until 29 October. LU proved to be delayed by 1 day when the altitude increased by 38.3 m and LC by 1 day when the altitude decreased by 53 m. Year to year variation of LU was significantly correlated to variations in March and April temperatures. March temperatures had a greater effect at lower and April ones at higher elevations. LC was related to August and September temperatures, and occured later if the temperatures were higher. In the studied period, March and April temperatures showed an increasing trend. Consequently, LU occured 1.52 days earlier per decade at 1,000 m a.s.l. and 0.67 days earlier at 500 m a.s.l. August temperatures were also increasing and LC was becoming delayed but the trends were not significant and were not clearly related to altitudinal gradient. This all shows that changes in climate affect phenological behaviour at higher altitudes to a greater degree than at lower ones.

Key words: European beech = *Fagus sylvatica* / phenology / temperature / leaf unfolding / leaf colouring / climate change

Introduction

Phenology is the study of the seasonal timing of plant and animal life cycle events (phenophases), which are very sensitive to small variations in climate. It provides information on organisms and on environmental conditions and site climate regime.

Plant phenology has been proposed as a climatic difference and global change indicator by the European Environment Agency and the Intergovernmental Panel on Climate Change, IPCC (IPCC 2007; Menzel et al. 2006; Parmesan and Yohe 2003). Lately, a growing number of ecological studies have provided evidence of phenological alterations from a wide range of ecosystems (Estrella et al. 2007; Gordo and Sanz 2009; Hudson and Keatly 2010).

Leaf phenology describes the seasonal cycle of leaf functioning and is essential for understanding the interactions between the biosphere and the climate (e.g., Dittmar and Elling 2006). Long-term phenological records in trees, such as leaf unfolding, leaf fall, flowering or fruit ripening, provide historical information about plant response to different climatic conditions (Morin et al. 2009). If we want to predict the future response of tree species to a changed climate, we need to explore how they have responded to climate in the past.

The global average temperature increased by about 0.8 degrees Celsius from 1850 to 2005 but the current warming trend is 0.13 to 0.16 degrees per decade and is projected to continue to rise at a rapid rate (Richardson et al. 2009). In terrestrial ecosystems, this rise in global temperature leads to earlier timing of spring events and poleward and upward shifts in plant and animal ranges are linked with very high confidence to recent warming (IPCC 2007).

However, trends in different phenological events may differ due to the divergent effects of climate on each phase of the plant life cycle, as well as to the heterogeneous temporal trends of different climatic elements within the year (Gordo and Sanz 2010). In a similar way, phenological responses also vary geographically due to the heterogeneous geographical variability of warming (Chmielewski and Rötzer 2001; 2002; Doi and Takahashi 2008; Rötzer et al. 2000). For this reason, the last AR4 report (IPCC 2007) suggests that we should now focus on detailed sub-regional studies, particularly in those areas that represent transitional climate areas.

Slovenia is a transitional climate area due to its intermediate position between the Alps, the Mediterranean and continental Europe (PRUDENCE 2005). Consequently, the Slovenian climate is characterized by wide local climate variability, with fairly large gradients of climatic factors (Ogrin 1996). In such conditions, we need high spatial coverage with climate and phenological data to define transitions between different sectors, in order to explore spatial and temporal changes in climate and phenology accurately.

European beech (*Fagus sylvatica* L.) is the basic structural element of Slovenian forests. It grows in most forest associations from the lowlands up to the high mountains. It forms more than one third of the wood stock and its proportion is currently increasing, particularly where forests with a high percentage of conifers are being converted into more natural mixed forests (Bončina et al. 2003; Brus 2005). However, it has recently been reported that the future competitiveness of beech might be considerably reduced due to climate change (e.g., Geßler et al. 2007) or that the changing climate might even cause a retreat of beech populations (e.g., Jump and Peñuelas 2006; Vitasse et al. 2009).

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 analysed 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 exist in phenological series and whether they can be explained by changes (trends) in key climatic factors.

It should be noted that European beech belongs to a group of woody plants, subjected to phenological observations running within the framework of the European International Phenological Gardens program, of which the Slovenian network is part. In this context, the obtained results could help to complete the picture of tree phenology changes across Europe (Ahas and Aasa 2006; Chmielewski and Rötzer 2001; Dittmar and Elling 2006; Estrella and Menzel 2006; Gordo and Sanz 2010; Vitasse et al. 2009).

Materials and Methods

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 1050 m a.s.l. and with different site and climatic characteristics (Fig. 1). According to the Guidelines for Plant Phenological Observations, they are characteristic of the larger region around the observation area locations. The day of LU was recorded as the first regular surfaces of leaves 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, 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 in regard to the annual amount of precipitation (800 – 3500 mm), mean annual air temperatures (from -1.4°C to 12.2°C); the distribution corresponds to Continental, Alpine or Sub-Mediterranean climatic regimes (PRUDENCE 2005).

Phenological and climatic original datasets were set up following an exhaustive quality control process designed to detect suspicious data and inhomogeneous series. We applied for this 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 than10 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 by 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 to the candidate in kilometres. After comparing the original with the reference series, suspicious data were discarded (see details in Gonzalez-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 in order 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) in order 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).

Insert Figure 1

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 13 April (DOY 103) 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 2 October (DOY 275) to 29 October (DOY 302) across the network. Extreme values of LC were 5 September (DOY 248) and 13 November (DOY 317) (Fig. 2).

Spatial variation of LU was significantly related to altitude. According to the model on Figure 2, LU was delayed by 1 day if the altitude increased by 38.3 m. The spatial variation of LC was also significantly related to altitude and was delayed by 1 day if the altitude decreased by 53 m.

The influence of the altitude, however, was more intense in the case of LU (slope 0.0261) than of LC (slope -0.0189). According to these findings, LU occured earlier and LC later on lower elevated sites. The model also showed that the trees on different locations had leaves from DOY 115 to DOY 214. The period in which trees on the lower elevated sites had leaves (and could conduct photosynthesis) was therefore up to 3 months longer than on those at higher elevations.

According to the obtained models, the earliest LU occured in the central, south-western and north-eastern 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, south-western and north-eastern parts of Slovenia (Fig. 3b).

Insert Figures 2, 3

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 earlier LU. At higher altitudes, LU was better correlated with April temperatures; the correlation was also negative (Figure 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 the main climatic parameter controlling variations in LU in the lowlands of north-eastern, central and south-western Slovenia, while April temperature variations played the decisive role at higher elevations, especially in the north-eastern and south-western parts (Alps and the Dinaric mountains) (Fig. 4 c, 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 in the whole area and their importance did not vary with altitude (Figure 5 a, 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 are lower than normal (Fig. 5 c, d). The amount of monthly precipitation was not significantly correlated with LU and LC.

Insert Figures 4, 5

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

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. and 0.67 days per decade at 500 m a.s.l. Significant earlier LU was therefore mainly detected in northern Slovenia, on the Alpine sites (Fig. 6 b).

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. 6 c, 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.

Insert Figure 6

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 analysed stations. There was also no significant pattern across the altitudinal gradient (Fig. 7 a, 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).

Insert Figure 7

Discussion

Although various studies have suggested that the leaf phenology of beech is less sensitive to environmental variability than in some other tree species (Menzel 2000; Vitasse et al. 2009), we found that beech in the relatively small area of Slovenia (ca. 20,000 km^2) showed a considerable phenological variability at different elevations. The variation of LU along the altitudinal gradient was in line with the observations of Dittmar and Elling (2006), who investigated the leaf phenology of beech from a number of stations all over Germany, although they did not observe altitudinal differences in phenological shifts related to changing climate.

The altitudinal differences are to a large degree related to different temperature regimes along the altitudinal gradient. Many studies have shown that air temperature affects phenological events, especially spring phases such as flowering and leaf unfolding (Chmielewski and Rötzer 2002; Črepinšek et al. 2006; Menzel et al. 2006; Vitasse et al. 2009). Another study in beech on a site in central Slovakia showed that March and April temperatures were most important for the time of leaf unfolding (Schieber et al. 2009). Our study in Slovenia also showed that LU is correlated with March and April temperatures but, in addition, we showed that March temperatures have a greater effect on LU at lower elevations, whereas April temperatures play a more important role at higher elevations.

Although it is known that, in addition to air temperature, precipitation and other climatic parameters such as air humidity, soil temperature, snow cover or radiation can also influence phenological development (Chmielewski and Rötzer 2002; Schieber et al. 2009), temperature proved to be the most significant factor affecting leaf phenology at Slovenian sites and we found no significant effect of precipitation. This is possibly because the effect of precipitation is more pronounced in dry areas, for instance in the Mediterranean, where the phenology of coniferous forests is mainly driven by water availability, which affects the development of leaf/needle area (Kramer et al. 2000). The low importance of precipitation on leaf phenology in Slovenian beech indicates that water availability is not a limiting factor there. Črepinšek et al. (2006) came to similar conclusions when evaluating phenological models for predicting spring flowering and leafing models in various plant species in Slovenia.

A large number of phenological studies have reported on shifting phenology, mostly on earlier spring and later autumn phenophases, due to changing climate (Ahas and Aasa 2006; Beaubien and Freeland 2000; Menzel 2000; Studer et al. 2007)**.** Such trends have been mainly attributed to the increase in temperatures (Menzel et al. 2006; Peñuelas and Filella 2001; Root et al. 2003).

In a wide European study, phenological network data sets of more than 125,000 observed series of 542 plant and 19 animal species in 21 European countries (1971–2000) have shown that 78% of all leafing, flowering and fruiting records advanced (30% of them significantly) and only 3% were significantly delayed (Menzel et al. 2006). The same authors found that spring now arrives six to eight days earlier across Europe than in the early 1970s and that warmer temperatures have delayed autumn, by an average of three days in the past 30 years.

On the global scale, remote sensing data have validated these ground observations (Studer et al. 2007), suggesting that the growing season has become two weeks longer during past decades in Eurasia and North America (Peñuelas and Filella 2001).

We can generally confirm that, in the studied period of 1955-2007, LU in Slovenian beech advanced and we explained this by increasing March and April temperatures. On the other hand, LC did not prove to be significantly delayed, in spite of observed increases in August and September temperatures. The observed trends in leaf phenology of beech from Slovenia are therefore only partially in line with the aforementioned large studies in Europe and North America dealing with shifting phenology.

Moreover, our study showed that, on a relatively small area with high geographic variability, such trends are not uniform and that phenological events greatly differ along altitudinal gradients. Thus, at higher altitudes, even small changes in climate trigger a more significant change in phenological behaviour than those caused by more intense changes in climate at lower altitudes.

Our study thus demonstrates that phenological behaviour at higher altitudes is more sensitive to temperature variations, probably because LU occurs there later than in the lowland, i.e., when other environmental factors such as photoperiod are less limiting.

The implication of the observed changes may be of great importance because an alteration in tree phenology also affects other processes in the tree and plant communities. It can be related to biogeographical shifts and affects the future distribution and survival of beech (Di Filippo et al. 2007; Kramer et al. 2010). In addition, it can also affect temporal matching with herbivores and/or pollinators, which may have serious consequences for trophic interactions and the viability of populations (Harrington et al. 1999; Memmott et al. 2007; Visser and Both 2005).

Nevertheless, it is still not fully understood how these changes in leaf phenology may modify tree growth. Visible leaf unfolding in beech coincides with the onset of wood production by the cambium at breast height, while, on the other hand, wood formation stops at least two months before general leaf colouring occurs (Čufar et al. 2008a). However, climate variables affecting wood formation differ from those that affect leaf phenology. It was shown for a lowland beech site in central Slovenia that LU depends on late winter temperatures and LC on late summer temperatures, while radial growth (wood formation) depends mainly on June-July conditions (Čufar et al., 2008a). We can thus assume that, at higher altitudes, the length of the growing season may increase because of increased temperatures in March and April but the growth rate may even decrease due to divergent trends in the months crucial for wood formation (June and July). Changes in growth rates cannot therefore be directly inferred from phenological trends.

In conclusion, our results in *Fagus sylvatica* in Slovenia, which grows on a great variety of sites affected by altitudinal gradient and by different distance from the Adriatic Sea (Di Filippo et al. 2007; Čufar et al. 2008b), show great variability of leaf phenology, which can be explained to a considerable degree by altitude and changing climate. Recent trends show advanced LU, which is more significant at higher elevations; it is nearly 3 times greater at an altitude of 1,000 m a.s l. than at 500 m a.s.l. The results indicate that, at higher altitudes, even small changes in April mean temperatures produce a significant change in the temporal pattern of LU. LC is generally delayed but the trends are not significant. This all may provoke 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.

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Figure 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.

Figure 2. Leaf phenology of beech in Slovenia. Average day of the year (DOY) for first leaf unfolding (LU) and general leaf colouring (LC) related to altitude. Equations show

the relations of LU and LC to altitude for the period 1955-2007. Significance level *p<0.05

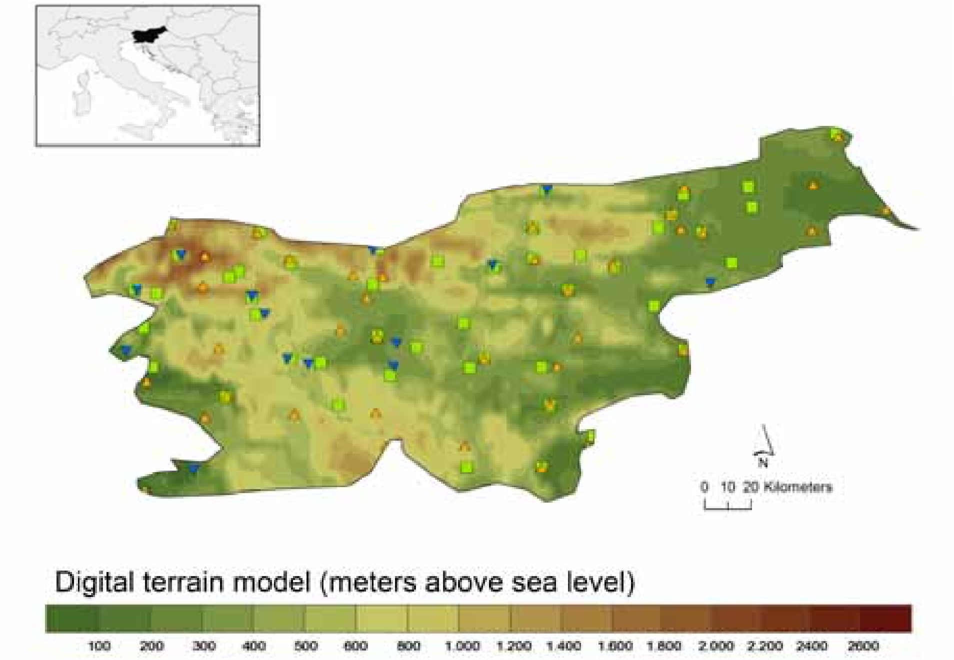
Figure 3. Modelled spatial distribution of timing (day of the year - DOY) of (a) first leaf unfolding (LU) and (b) general leaf colouring (LC) for beech in Slovenia.

Figure 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. Significance level *p<0.05

Figure 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.

Figure 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.

Figure 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.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100
200
300
400
500
600
800
1.000
1.200
1.400
1.600
1.800
2.000
2.200
2400
2600

Fig. 1

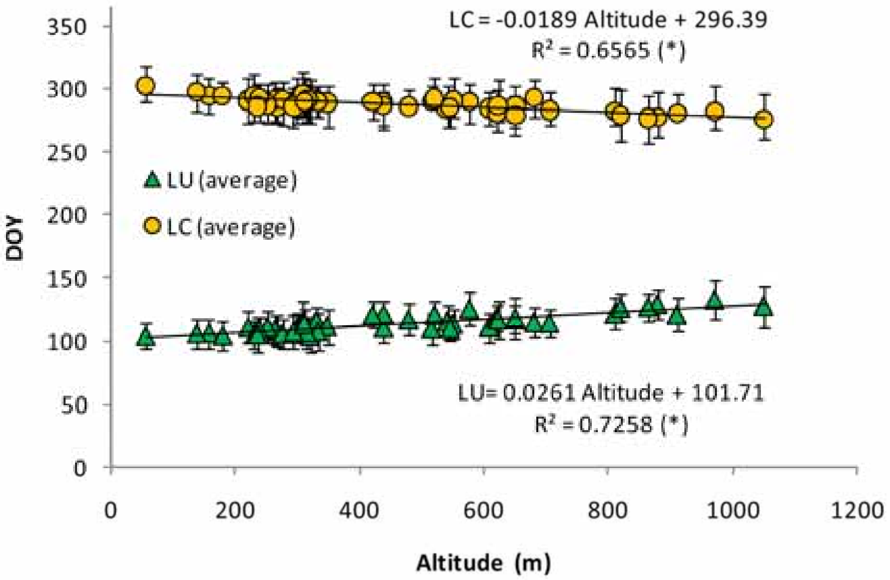

LC = -0.0189 Altitude + 296.39
R² = 0.6565 (*)
▲ LU (average)
● LC (average)
LU= 0.0261 Altitude + 101.71
R² = 0.7258 (*)
DOY
350
300
250
200
150
100
50
0
0
200
400
600
800
1000
1200
Altitude (m)

Figure 2.

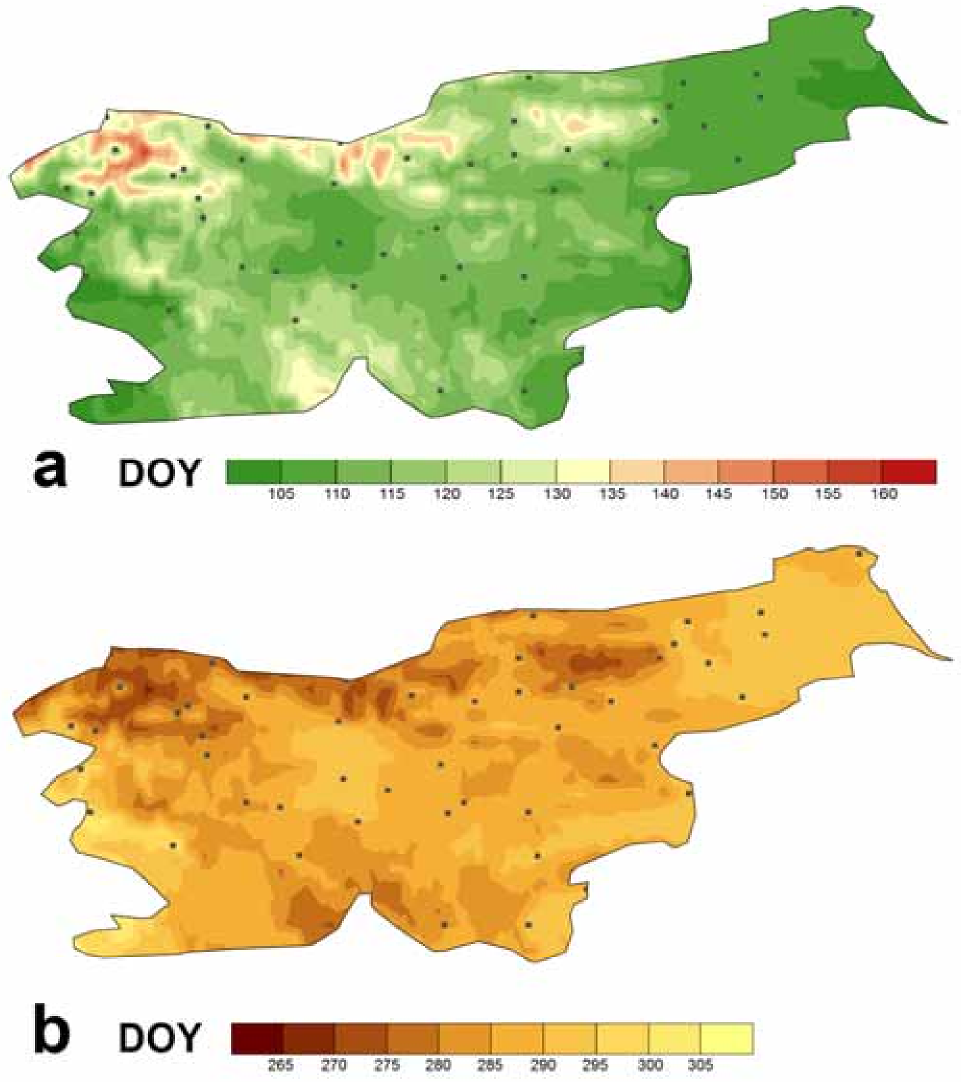

a
DOY
105
110
115
120
125
130
135
140
145
150
155
160
b
DOY
265
270
275
280
285
290
295
300
305

Figure 3.

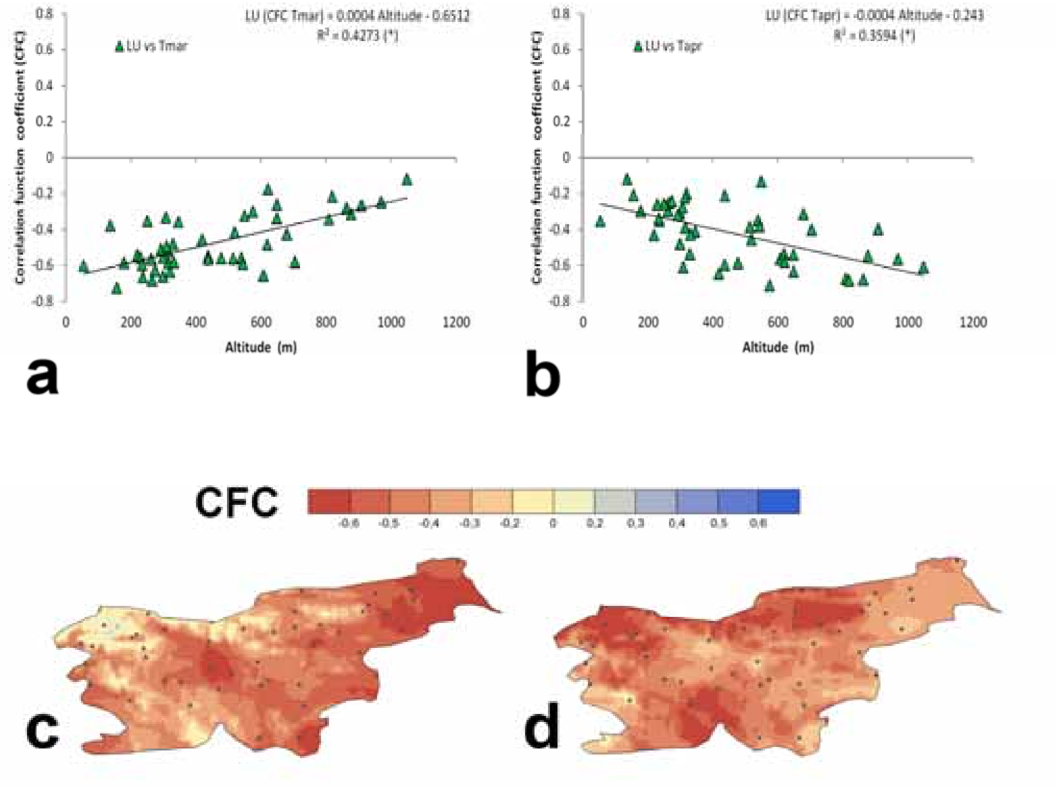
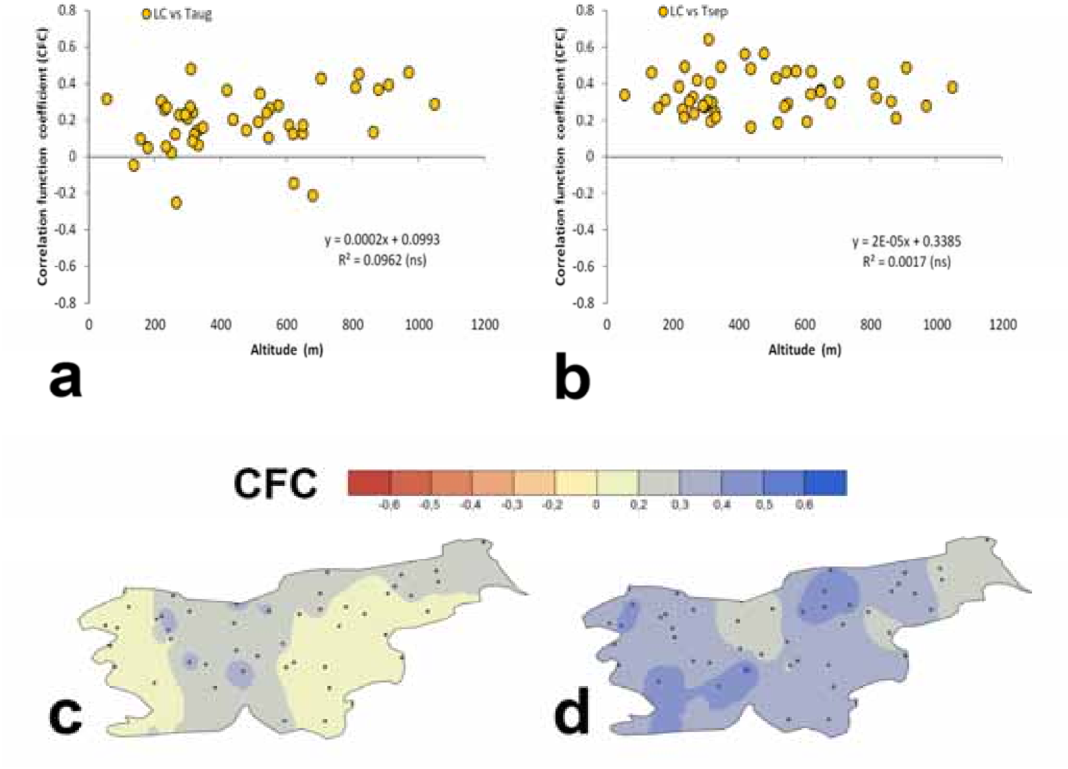

LU (CFC Tmar) = 0.0004 Altitude - 0.6512
R² = 0.4273 (*)
LU vs Tmar
Correlation function coefficient (CFC)
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
0
200
400
600
800
1000
1200
Altitude (m)
a
LU (CFC Tapr) = -0.0004 Altitude - 0.243
R² = 0.3594 (*)
LU vs Tapr
Correlation function coefficient (CFC)
Altitude (m)
b
CFC
-0.6
-0.5
-0.4
-0.3
-0.2
0
0.2
0.3
0.4
0.5
0.6
c
d

Figure 4.



LC vs Taug
Correlation function coefficient (CFC)
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
0
200
400
600
800
1000
1200
Altitude (m)
y = 0.0002x + 0.0993
R² = 0.0962 (ns)
a
LC vs Tsep
Correlation function coefficient (CFC)
y = 2E-05x + 0.3385
R² = 0.0017 (ns)
Altitude (m)
b
CFC
-0,6
-0,5
-0,4
-0,3
-0,2
0
0,2
0,3
0,4
0,5
0,6
c
d

Figure 5.

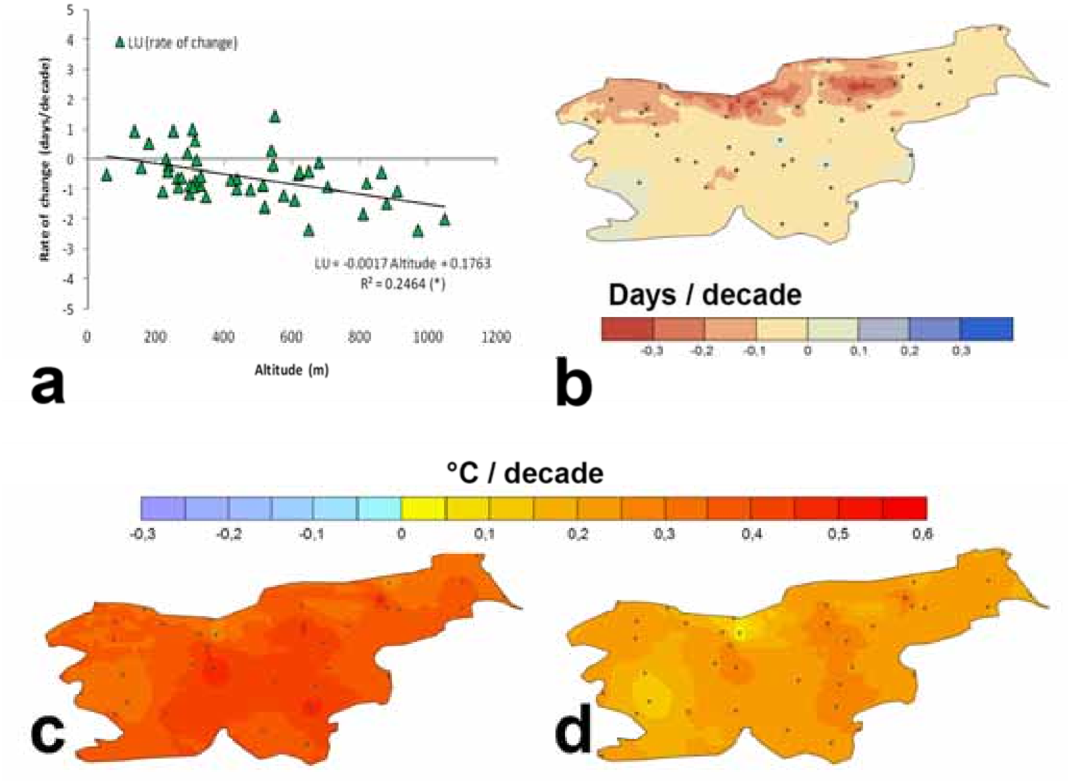

LU (rate of change)
Rate of change (days/decade)
5
4
3
2
1
0
-1
-2
-3
-4
-5
0
200
400
600
800
1000
1200
Altitude (m)
LU = -0.0017 Altitude + 0.1763
R² = 0.2464 (*)
a
Days / decade
-0,3
-0,2
-0,1
0
0,1
0,2
0,3
b
°C / decade
-0,3
-0,2
-0,1
0
0,1
0,2
0,3
0,4
0,5
0,6
c
d

Figure 6.

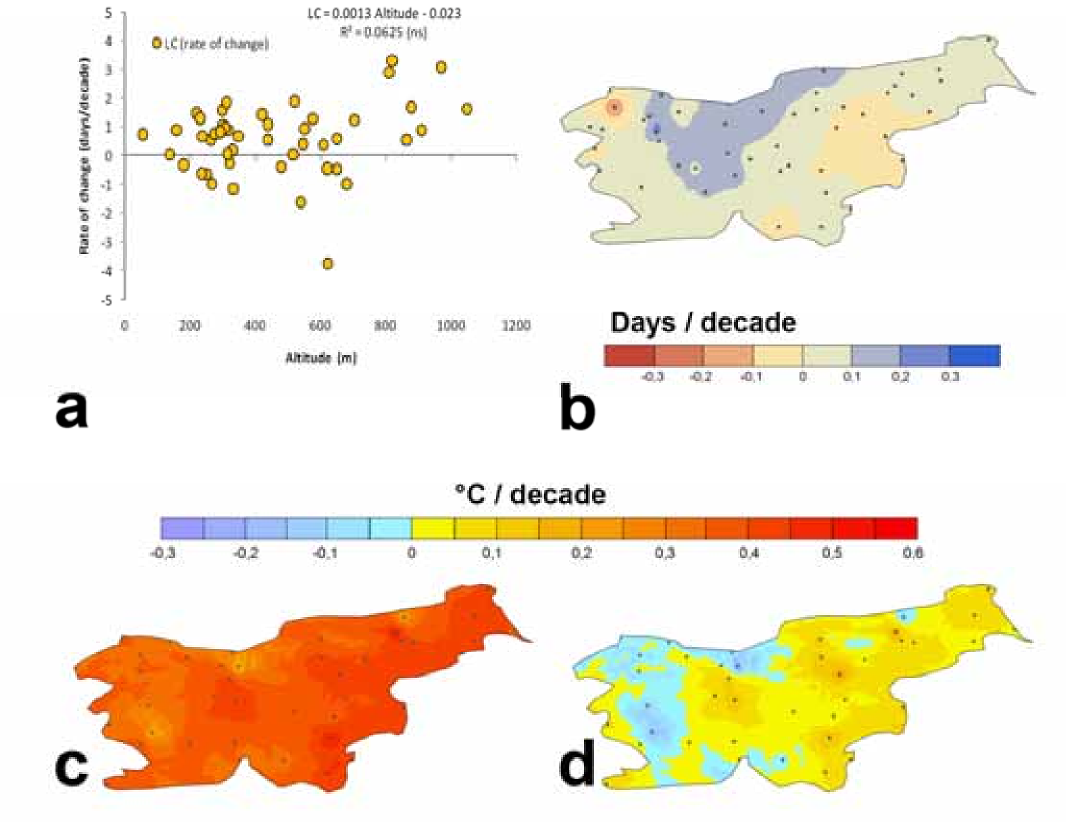

LC = 0.0013 Altitude - 0.023
R² = 0.0625 (ns)
LČ (rate of change)
Rate of change (days/decade)
5
4
3
2
1
0
-1
-2
-3
-4
-5
0
200
400
600
800
1000
1200
Altitude (m)
a
Days / decade
-0,3
-0,2
-0,1
0
0,1
0,2
0,3
b
°C / decade
-0,3
-0,2
-0,1
0
0,1
0,2
0,3
0,4
0,5
0,6
c
d

Figure 7.