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The urban imprint on plant phenology

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Abstract

The modification of the surface radiation and energy balance in urban areas causes their temperatures to exceed those of the surrounding countryside[1]. It has thus been suggested that urban environments may serve as field laboratories for studying the effects of a warming climate on biota in a space-for-time substitution[2–5]. We investigated changes in the timing of plant phenology and temperature across study sites differing in the degree of urbanization using publicly available pan European data sets for the period 1981-2010[6,7]. We found a significant advancement in leaf development, flowering and fruiting phenological phases with higher degrees of urbanization, while a significant delay was observed for leaf senescence phenological phases. Along with these phenological changes an increase of air temperature with higher degrees of urbanization was observed. This increase was largest during the periods of leaf development, flowering and fruiting and smallest during the period of leaf senescence. Based on these results we show that the apparent temperature sensitivity of phenological phases to urban warming is either significantly dampened (leaf development, flowering and fruiting) or reversed (leaf senescence) compared to the temperature sensitivity inferred from temporal changes in phenology and temperature. We conclude that gradients in urbanization represent a poor analog for the temporal changes in plant phenology, apparently due to confounding factors associated with urbanization.

Because the timing of periodic plant life cycle events, such as leaf unfolding, flowering or leaf coloring, is sensitive to variations in environmental factors, notably to temperature, plant phenology has emerged as an important bioindicator for climate change[8]. Given the widespread enhancement of air temperature in urban areas compared to the surrounding

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Data availability

The phenological data used in this study are available from www.pep725.eu, the air temperature data from www.ecad.eu. The data underlying the CORINE land cover, the imperviousness degree and the European settlement map are available from the Copernicus Land Monitoring Service (https://land.copernicus.eu/pan-european).

Code availability

The Matlab (The MathWorks, Inc., Natick, Massachusetts, United States) scripts used to analyze data are under the following doi: 10.5281/zenodo.3422079.

Author contributions

G.W. conceived the study, analyzed the data and wrote the manuscript together with the E.T. and A.H.

Competing interests

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countryside[9], an effect dubbed the urban heat island (UHI)[1], a great many studies, using both *in situ* observations and remotely sensed changes in greenness, have reported advancements in spring/summer and delays in autumnal phenological phases in urban as compared to rural areas[3,10], matching the widely studied temporal response of plant phenology to global warming[11].

It has thus been suggested that rural to urban gradients may, in a space-for-time substitution, represent unique outdoor laboratories for studying the response of plants (and other biota) to climate change [2–5]. Urban environments, however, differ from their non-urban counterparts in many other aspects that may confound the temperature-related response in phenology: Soils in urban areas are highly modified[12] affecting plant-water[13] and plant-nutrient relationships, which may however be counteracted by irrigation and fertilization. Concentrations of greenhouse gases (e.g. CO_2)[5,14] and primary pollutants (NO, NO_2, CO, SO_2, PM_{10}, etc.) are higher in urban areas due to the proximity of emission sources[15], while concentrations of secondary pollutants, such as O_3, are often higher in downwind, rural, areas[16]. Plant phenology has been shown to react both with delay (e.g. flowering) and advancement (e.g. earlier senescence) to pollutants typical of urban environments[17–19]. Artificial light, ubiquitous in urban areas, has been shown to delay plant flowering and leaf senescence[20,21]. Biotic plant-plant and plant-animal interactions are highly modified in urban areas due to for example artificial biocenosis compositions and habitat fragmentation[2]. Finally, rural and urban plant populations may exhibit genetically-based phenotypic differences[22]. The extent to which these differences confound the phenological response to the UHI is, if at all, poorly quantified. In addition, many urban phenology studies, particularly those based on *in situ* measurements, have been criticized for not properly reporting meta data required for putting observed phenological differences into context with the degree of urbanization[3], a shortcoming widespread in the UHI literature as well[23]. Finally, many of the *in situ* studies have relied on a small number of plant species, focused on few phenological phases and/or were restricted to relatively small geographic areas[24–26], limiting the generalizability of the results.

In this study we advance previous efforts in quantifying the effect of urbanization on plant phenology by using pan European *in situ* observations of plant phenology[6] and air temperature[7], which we analyze with respect to the degree of urbanization in order to validate the space-for-time substitution approach.

Results and Discussion

In order to quantify how changes in urban fraction (UF) impact plant phenology we conducted a multiple linear regression (MLR) in which we controlled, in addition to the UF, for the three other main factors affecting plant phenology through changes in temperature, that is latitude, elevation and time[25] (see Supplementary Fig. 5 for an example and Supplementary Fig. 6 for the full results of the MLR). As it is not obvious how to best quantify the UF in the context of plant phenology, we chose three complementary metrics: (i) the CORINE land cover (COR), which quantifies land cover in 44 classes, (ii) the imperviousness degree (IMD), which quantifies the degree of soil sealing, and (iii) the

European Settlement Map (ESM), which quantifies the percentage of built-up area cover (see Supplementary Fig. 2 and 3 for a comparison of UF metrics).

The resulting UF regression coefficients (β_U^P; Eq. 1) represent the unique changes in phenological entry dates for a unit change in UF (note that because UF is bound between zero and unity, UF regression coefficients correspond to the maximum possible change in phenology) and were significantly ($p < 0.05$) different from zero in 68-89 % (leaf development, flowering and fruiting phenological phases) and 60-75 % (leaf senescence) of all phenological phases species combinations. Phenological entry dates significantly advanced with increasing UF (88-95 % of all cases) for the leaf development, flowering and fruiting phenological phases, while a significant delay was observed for the leaf senescence phenological phases (75-80 % of all cases). A unit change in UF caused leaf development, flowering and fruiting phenological phases to advance by 1.0 2.8 days (median values), while leaf senescence phenological phases were delayed by 1.3-2.7 days (median values) (Fig. 1) across all UF metrics. These values are at the lower end of those reported in the only other study that used a comparable approach (MLR using elevation and urban fraction derived from COR) on spring phenological phases in three German cities[25], which was however limited to 9 plant species. Phenological phases were significantly (except for leaf senescence) more sensitive to UF when quantified on the basis of the IMD compared to the COR and the ESM (Fig. 1), which is expected given UF values of the IMD mostly cover the low to medium range (Supplementary Fig. 2).

Effects of changes in UF on pre-season temperature, i.e. the air temperature averaged for the preceding 30 days[11], were also analyzed on the basis of a MLR, again accounting for confounding effects by latitude, elevation and time (see Supplementary Fig. 9 for full MLR results). The unique change in air temperature for a unit change in UF derived from the MLR (β_U^T; Eq. 2) exhibited a pronounced seasonal course with minimum values from October through to April and maximum values from May to September (Fig. 2b)[9]. The change in air temperature per unit UF change was largest when UF was based on the ESM (maximum of 1.3 K per unit change in UF) and smallest for the COR (maximum of 0.4 K per unit change in UF) (Fig. 2b). When weighted with the probability of occurrence of the various phenological phases (Fig. 2a), the temperature change per unit change in UF was highest for the fruiting phenological phases, followed by flowering and leaf development and smallest for the leaf senescence phenological phases (Fig. 2c-f). During all four aggregated phenological phases differences between the three UF metrics were significant ($p < 0.05$).

Taken together, the analysis so far clearly demonstrates a positive relationship between air temperature and the degree of urbanization (Fig. 2), which goes along with an advancement (leaf development, flowering and fruiting phenological phases) and delay (leaf senescence) in plant phenology (Fig. 1). The ensuing questions are (i) how these urbanization-related phenological changes compare against the widely studied phenological changes over time and (ii) whether the temporal trend differs in dependence on the UF. To address the first question we combined the results of the two previous MLR analyses by convolving the phenological coefficients with the temperature coefficients in a bootstrapping framework,

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yielding two apparent temperature sensitivities (days/K), one based on the degree of urbanization (λ_U; Eq. 4) and one based on time (year) (λ_Y; Eq. 3) (see Eq. 5 – 22 and associated text for a theoretical derivation and justification of the statistical comparison of the λ coefficients).

During the leaf development, flowering and fruiting phenological phases, the apparent temperature sensitivities based on the temporal trend (λ_Y) were significantly ($p < 0.05$) more negative compared to those based on differences in UF (λ_U) (Fig. 3). Plant phenology thus advanced much more (by a factor of 2 9 based on medians) per degree temperature change over time than per unit UF. The median apparent temperature sensitivities of the leaf senescence phenological phases based on the temporal trend were negative, but the interquartile ranges overlapped with zero, as a result of a weakly negative and highly variable temporal trend in leaf senescence phenology (Supplementary Fig. 8) reported also in earlier studies[11]. In contrast, positive apparent temperature sensitivities (i.e. delay per unit temperature increase) were observed when these were derived from the degree of urbanization (Fig. 3).

The question whether temporal trends in phenology differ depending on UF was addressed by stratifying the phenology data into low and high UF sites and repeating the MLR with latitude, elevation and time as independent variables (i.e. without UF; see Supplementary Fig. 8 for the full MLR results). As shown in Figure 4, the temporal trend coefficients were statistically not significantly different for the low and high UF data sets for the leaf development, flowering and fruiting phenological phases. For the leaf senescence phenological phases a tendency towards more positive temporal trend coefficients was observed in the high UF class, with significant differences observed for the IMD (Fig. 4). These results are not due to differences in species composition between low and high urban fraction sites, as results remained unchanged (except for the flowering phenological phase in combination with the IMD UF data) if the analysis was restricted to the same species-phenological phases combinations in both low and high urban fraction classes (see Supplementary Fig. 10). Given that the warming trend is similar at rural compared to urban sites[27], these findings suggests a linear response of plant phenology to temperature[28].

Conclusions

In summary, our analysis shows that even though plant phenology and air temperature followed expected patterns across sites differing in the degree of urbanization (Fig. 1-2), the corresponding phenological temperature sensitivities were either much smaller (spring/summer phenological phases) or reversed (autumnal phenological phases) compared to temperature sensitivities derived from the temporal trend (Fig. 3). We thus conclude that spatial variability in temperature caused by the UHI is not suitable for investigating how plant phenology will react to a likely warmer future climate and conversely that plant phenology makes for a poor quantitative predictor of the UHI. The most likely explanation for this observation is the presence of confounding factors affecting plant phenology along with the degree of urbanization, in particular air[5,14,15] and light pollution[20,21], modifications of the soil[12] and biotic interactions[2], and genetic variation[22]. Future studies should aim at quantifying the magnitude and direction of these multi-factorial effects[3]. Most importantly,

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however, future studies need to overcome the major weakness of the underlying data, that is the widespread lack of co-located phenology and temperature observations[28]. In particular at intermediate urban fractions, where the complex interplay between natural surfaces and urban fabric may result in significant spatial microclimatic heterogeneity[29], co-located temperature observations can be expected to considerably improve the interpretation of phenological records. Another area that requires further research is the definition of the UF metric[30,31], as our study demonstrates that the use of different UF metrics yields qualitatively similar, but quantitatively (often significantly) different results.

Our results also show that unavoidable differences in UF between study sites in large-scale phenological data sets, which are often based on the work of volunteers[6], are not likely to compromise the interpretation of temporal trends in plant phenology, as these are largely, with the exception of leaf senescence, unaffected by the degree of UF[25] (Fig. 4).

Methods

Plant phenological data

In *situ* plant phenological data were downloaded in June 2018 from the database of the Pan European Phenology project (PEP725; www.pep725.eu)[6]. The downloaded data set included 256 plant species (inclusive of cultivars) at 19 985 sites and a total of 11 922 878 phenological entries. From the data set we extracted station data (elevation, latitude, longitude and unique station identifier) as well as for each plant species (cultivar) entry dates (day of year and year) for up to 47 phenological phases according to the BBCH (Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie) scale[32]. For each phenology station the degree of urbanization was derived as detailed below.

For the analysis, the data set was restricted to the period 1981-2010, as this is the most recent climatological time period reasonably covered by UF maps (see below), and was filtered for so-called false leaf-out events in autumn by removing database entries for BBCH classes 10-19 when the corresponding entry date was beyond day of year 200. In combination, both restrictions reduced the size of the data set to 6 765 348 entries, which was then statistically analyzed as described below. For the ease of interpretation, the output of the statistical analyses was, similar to Menzel, et al. [11], merged into broader phenological classes by aggregating functionally similar BBCH values (leaf development: BBCH values 10-19; flowering: BBCH values 51-59; fruiting: BBCH values 75-89; leaf senescence: BBCH values 92-97). The geographic distribution of the phenological stations in the study domain is shown in Supplementary Fig. 1.

Air temperature data

Air temperature is not routinely measured at the sites where phenological observations are made. Large-scale phenological studies thus typically relate phenology to gridded air temperature products[11,33] in order to derive apparent phenological temperature sensitivities. Gridded air temperature products capture broad climatological patterns, but would be unsuitable in this study, which seeks to quantify how temperature and phenology change with the degree of urbanization. Thus daily average 2 m air temperature data of 4 431 stations was downloaded from the European Climate Assessment and Dataset (ECA&D; www.ecad.eu)[7] database in June 2018 and used in a multiple linear regression approach as described below. We extracted station latitude, longitude, elevation and unique identifier along with daily average air temperature. For the analysis, to be consistent with the phenological observations, the data set was restricted to the period 1981-2010. In addition, we excluded air temperature stations if no phenological station was present in any 1 x 1° latitude/longitude grid cell or air temperature station elevation and/or urban fraction were outside (with a 5 % tolerance) the elevation/urban fraction range of the phenological stations present in that grid cell. This reduced the number of air temperature stations to 1 174. For each temperature station the degree of urbanization was derived as detailed below.

Urban fraction data

As it is not obvious how to best quantify the degree of urbanization, three different, publicly available, data sets were used in this analysis (Supplementary Fig. 2):

(i) CORINE land cover (COR): quantifies the land cover in 44 distinct classes and was downloaded as a 100 m GeoTIFF from https://land.copernicus.eu/pan-european/corine-land-cover for four time slices (1990, 2000, 2006 and 2012; v. 18.5) in June 2018 and linearly inter/extrapolated for the study period 1981-2010 using the *interp1* function of Matlab (The MathWorks, Inc., Natick, Massachusetts, United States).

(ii) Imperviousness degree (IMD): quantifies the percentage of soil sealing and was downloaded as a 100 m GeoTIFF from https://land.copernicus.eu/pan-european/high-resolution-layers/imperviousness for three time slices (2006, 2009 and 2012) in June 2018 and linearly inter/extrapolated for the study period 1981-2010 using the *interp1* function of Matlab The MathWorks, Inc., Natick, Massachusetts, United States).

(iii) European settlement map (EMS): quantifies the percentage of built-up area coverage and was downloaded as a 100 m GeoTIFF from https://land.copernicus.eu/pan-european/GHSL/european-settlement-map for the year 2012 (release 2016) in June 2018 and kept constant at this value for the study period 1981-2010.

For the IMD and ESM data sets, a 500 x 500 m (i.e. 5 x 5 pixel) average was calculated centered on the pixels in which the phenological/temperature stations are situated. For the CORINE land cover product, UF was calculated as the percentage of CORINE land cover classes 1-6 (urban fabric and industrial, commercial and transport units)[27] within each 500 x 500 m area. The frequency distribution of the three UF metrics is compared in Supplementary Fig. 2. In order to test for the sensitivity of the results to the particular choice of spatial scale, the MLR analysis of the phenological data was repeated with a 1100 x 1100 m (i.e. 121 ha) instead of the chosen 500 x 500 m (i.e. 25 h) spatial scale. As shown in Supplementary Figure 7, compared to Supplementary Figure 6, results are robust, apart from additional significant differences between the three UF metrics during leaf senescence, despite a factor 5 difference in spatial scale.

For the two data sets which account for temporal variability in urban area fraction (COR and IMD), it can be shown that over 90 % of all phenological sites exhibited no or at maximum slight changes in urban area fraction during the 1981-2010 study period (Supplementary Fig. 3).

Statistical analyses - overview

Typically, plant phenological studies are concerned with changes at a given place, for a given plant species and phenological phase over time[11,33]. This study, in contrast, aims to quantify changes in phenology over space, specifically the degree of urbanization. Because stations differing in the degree of urbanization may also differ in other factors affecting phenology, such confounding factors need to be accounted for and this is done within the frame of a multiple linear regression (MLR) analysis. As gridded temperature products, which are typically related to temporal changes in phenology, are unable to resolve differences in temperature related to the degree of urbanization, air temperature station data are used instead and again a MLR regression approach is employed to control for confounding factors. The results of these two independent MLR analyses are then combined to infer the apparent phenological temperature sensitivity, i.e. the change in phenological entry dates per unit change in air temperature.

Statistical analyses - phenology

In order to extract the unique influence of the degree of urbanization (U) on plant phenology (P), phenological data were, separately for each phenological phase-species combination, subject to a MLR using the *fitlm* function of Matlab (The MathWorks, Inc., Natick, Massachusetts, United States) controlling in addition for station latitude (L), elevation (E) and year (Y), in order to account for factors known to affect phenology through corresponding changes in temperature, i.e.

$$\hat{P} = \beta_0^P + \beta_L^P L + \beta_E^P E + \beta_Y^P Y + \beta_U^P U \,. \tag{1}$$

Here β_0^P and $\beta_L^P, \beta_E^P, \beta_Y^P$ and β_U^P refer to the y-intercept and the coefficients representing the unique response of phenology to latitude, elevation, year and degree of urbanization, respectively. In order to avoid erratic MLR results, a minimum number of 30 records was imposed for the MLR. In addition data were, separately for each species-phenological phase combination, required to cover the following minimum interquartile ranges: 1 deg in latitude, 200 m in elevation, 5 years and 0.3 UF units. As shown in Supplementary Fig. 4, 95 % of all species-phenological phase combinations covered at least the following ranges within which 90 % of data are contained: latitude: 2 deg, elevation: 484 m, time: 9 years and urban fraction: 0.87 units (COR) or 0.44 units (IMD). MLR results were graphically controlled for independence, homoscedasticity and normal distribution of residuals. In this way, the size of the data set was further reduced to 4 835 669 entries and MLR results were obtained for 151 species-phenological phase combinations (leaf development: 28, flowering: 81, fruiting: 22, leaf senescence: 20), with the number of records used in each MLR ranging from 45 to 74 196 (the number of records exceeding 498 in 95 % of all species-phenological phase combinations). An example for the data underlying the MLR for a selected species-phenological phase combination is shown in Supplementary Figure 5. The coefficients representing the unique influence of UF on phenology (β_U^P) are shown in Fig. 1, the full results of the MLR in Supplementary Figure 6.

In a second step, the phenology data set was stratified into stations with low (UF < 0.2) and high (UF > 0.8) UF and the MLR as described above repeated for the two data sets with station latitude, elevation and year as independent variables. The coefficients representing the unique influence of year on phenology (β_Y^P) from this analysis are shown in Supplementary Figure 4, the full results of the MLR in Supplementary Figure 8.

Statistical analyses – air temperature

In order to extract the unique influence of the degree of urbanization (U) on temperature (T), air temperature station data were subject to a multiple linear regression (MLR) using the *fitlm* function of Matlab (The MathWorks, Inc., Natick, Massachusetts, United States) controlling in addition for station latitude (L), elevation (E) and year (Y), in order to account for factors known to affect temperature, i.e.

$$\hat{T} = \beta_0^T + \beta_L^T L + \beta_E^T E + \beta_Y^T Y + \beta_U^T U \,. \tag{2}$$

Here β_0^T and $\beta_L^T, \beta_E^T, \beta_Y^T$ and β_U^T refer to the y-intercept and the coefficients representing the unique response of air temperature to latitude, elevation, year and degree of urbanization, respectively. As it is well established that phenology responds to the environmental conditions during the corresponding pre-season, daily air temperature data were, following Menzel, et al. [11], averaged over the preceding 30 days. Apparent phenological temperature sensitivities (see next section) are robust against this particular choice for the pre-season averaging period, as demonstrated in Supplementary Figures 11 and 12, which are identical to Figure 3, except that the pre-season averaging period is 10 days and 60 days, respectively. As the coefficients of the MLR exhibited pronounced seasonal variation, the MLR was conducted in monthly blocks of data and later interpolated to daily values using the *interp1* function of Matlab (The MathWorks, Inc., Natick, Massachusetts, United States). These were then weighted with the frequency of phenological phases from Figure 2a to produce MLR coefficients for each aggregated phenological phase. The coefficients representing the unique influence of UF on air temperature $\left(\beta_U^T\right)$ are shown in Figure 2, the full results of the MLR in Supplementary Figure 9.

Statistical analyses – apparent phenological temperature sensitivity

Apparent phenological temperature sensitivities were derived by dividing the phenological coefficients for changes over time (β_Y^P; days/y) and UF (β_U^P; days/UF) (Supplementary Fig. 6) by the temperature coefficients for changes over time (β_Y^T; K/y) and UF (β_U^T; K/UF) (Supplementary Fig. 9) in a bootstrapping framework (n = 1000), yielding two apparent temperature sensitivities, one based on changes over time (λ_Y; days/K) and one based on the degree of urbanization (λ_U; days/K) (Fig. 3):

$$\lambda_Y = \frac{\beta_Y^P}{\beta_Y^T}, \text{ and} \tag{3}$$

$$\lambda_U = \frac{\beta_U^P}{\beta_U^T}. \tag{4}$$

If λ_Y and λ_U are statistically significantly different, it is concluded that the space-for-time substitution is ill-posed, as different apparent temperature sensitivities are obtained over time and the degree of urbanization.

Theoretical justification for this reasoning can be derived by considering a null model in which temperature is a multiple linear function of latitude, elevation, time and urban fraction, and phenology a linear function of temperature only, i.e.

$$T = \beta_0^T + \beta_L^T L + \beta_E^T E + \beta_Y^T Y + \beta_U^T U, \text{ and} \tag{5}$$

$$P = \beta_0^P + \beta_T^P T. \tag{6}$$

Replacing temperature in Eq. 6 with the right-hand side of Eq. 5 yields the following expression for phenology, which is conceptually identical to Eq. 1:

$$P = \widehat{\beta_0^P} + \widehat{\beta_L^P} L + \widehat{\beta_E^P} E + \widehat{\beta_Y^P} Y + \widehat{\beta_U^P} U, \tag{7}$$

with the following definition for the $\widehat{\beta^P}$ coefficients:

$$\widehat{\beta_0^P} = \beta_0^P + \beta_T^P \beta_0^T. \tag{8}$$

$$\widehat{\beta_L^P} = \beta_T^P \beta_L^T. \tag{9}$$

$$\widehat{\beta_E^P} = \beta_T^P \beta_E^T. \tag{10}$$

$$\widehat{\beta_Y^P} = \beta_T^P \beta_Y^T. \tag{11}$$

$$\widehat{\beta_U^P} = \beta_T^P \beta_U^T. \tag{12}$$

With Eqs. 11-12 it is then straightforward to show that the lambda coefficients have to be identical and reduce to the true (unknown) phenological temperature sensitivity:

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$$\lambda_Y = \frac{\widehat{\beta_Y^P}}{\beta_Y^T} = \frac{\beta_T^P \beta_Y^T}{\beta_Y^T} = \beta_T^P, \text{ and} \tag{13}$$

$$\lambda_U = \frac{\widehat{\beta_U^P}}{\beta_U^T} = \frac{\beta_T^P \beta_U^T}{\beta_U^T} = \beta_T^P. \tag{14}$$

If λ_Y and λ_U derived from Eqs. 3 and 4 are statistically significantly different, thus an alternative model including additional temperature-independent effects of time and urban fraction needs to be invoked:

$$P = \beta_0^P + \beta_T^P T + \beta_Y^P Y + \beta_U^P U. \tag{15}$$

Replacing temperature in Eq. 15 with the right-hand side of Eq. 5, we again arrive at Eq. 7 with the following new definition of the $\widehat{\beta^P}$ coefficients:

$$\widehat{\beta_0^P} = \beta_0^P + \beta_T^P \beta_0^T. \tag{16}$$

$$\widehat{\beta_L^P} = \beta_T^P \beta_L^T. \tag{17}$$

$$\widehat{\beta_E^P} = \beta_T^P \beta_E^T. \tag{18}$$

$$\widehat{\beta_Y^P} = \beta_T^P \beta_Y^T + \beta_Y^P. \tag{19}$$

$$\widehat{\beta_U^P} = \beta_T^P \beta_U^T + \beta_U^P. \tag{20}$$

The resulting λ_Y and λ_U are then given as:

$$\lambda_Y = \beta_T^P + \frac{\beta_Y^P}{\beta_Y^T}, \text{ and} \tag{21}$$

$$\lambda_U = \beta_T^P + \frac{\beta_U^P}{\beta_U^T}. \tag{22}$$

With this alternative model, statistically significantly different λ_Y and λ_U values derived from Eqs. 3 and 4 can be interpreted to result from additional, temperature-independent changes of phenology with time and/or urban fraction relative to the corresponding temperature changes. This interpretation also holds if the alternative model (Eq. 15) is

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formulated as a direct influence of temperature and either a direct influence of the variable year (i.e. $\beta_U^P = 0$) or urban fraction (i.e. $\beta_Y^P = 0$) only. Eqs. 21-22 yield identical results if $\frac{\beta_U^P}{\beta_U^T} = \frac{\beta_Y^P}{\beta_Y^T}$. In this special case the space-for-time substitution holds because the additional, temperature-independent changes of phenology with time and urban fraction relative to the corresponding temperature changes compensate each other.

Significant differences between the three UF metrics, apparent temperature sensitivities based on the degree of urbanization and on time and low/high UF metrics were tested for with a two-sided Wilcoxon rank sum test at $p < 0.05$ using the *ranksum* function of Matlab (The MathWorks, Inc., Natick, Massachusetts, United States).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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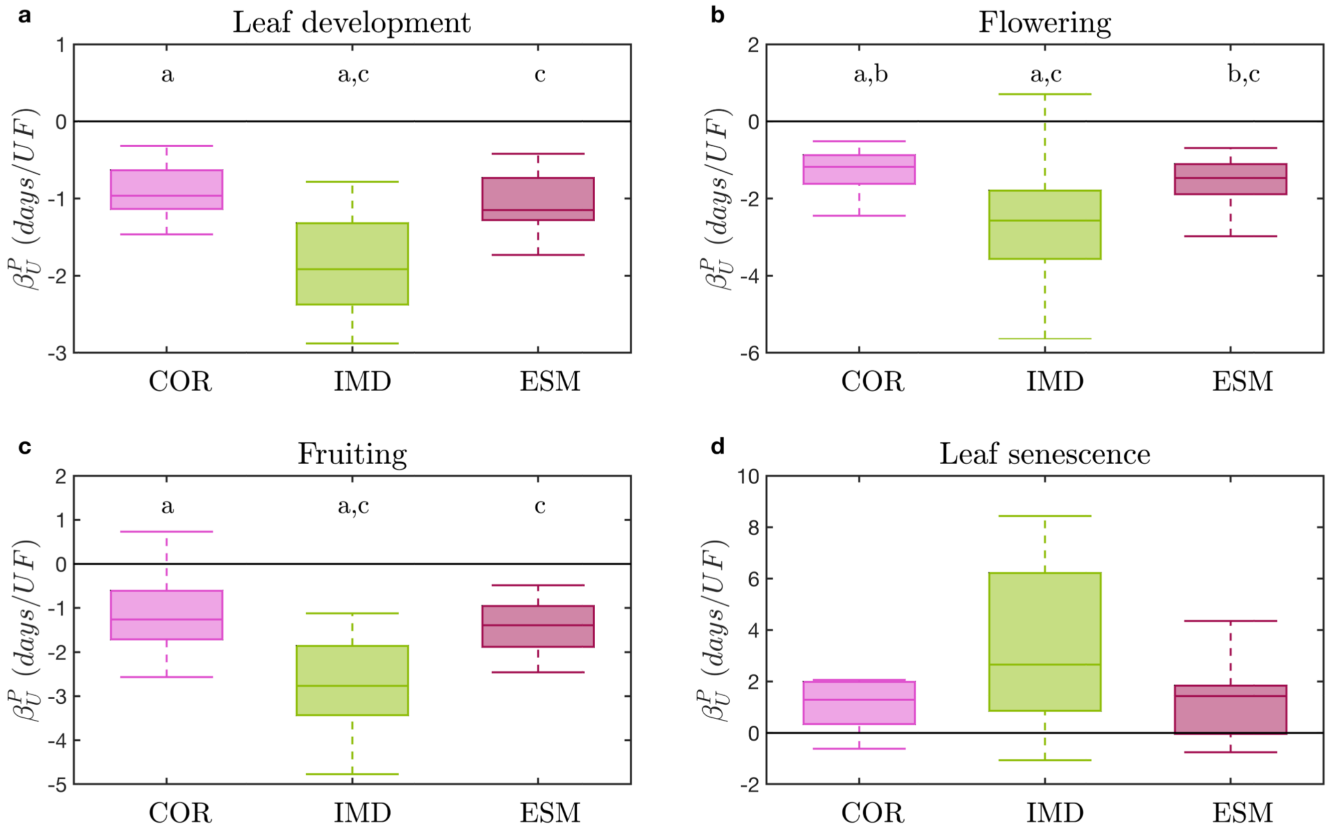

Figure 1. Coefficients of the MLR analysis describing unique changes in plant phenology with changes in urban fraction.

a-d, Significant MLR coefficients (β_U^P; Eq. 1) for four aggregated phenological phases and three urban fraction (UF) metrics (COR … CORINE land cover, IMD … imperviousness degree, ESM … European settlement map). Significant ($p < 0.05$, Wilcoxon rank sum test) differences between urban fraction metrics are indicated by the same letters. Boxplots show the interquartile range (IQR, box), the median (horizontal line in box) and 1.5 x the IQR (whiskers), while outliers are omitted for clarity.

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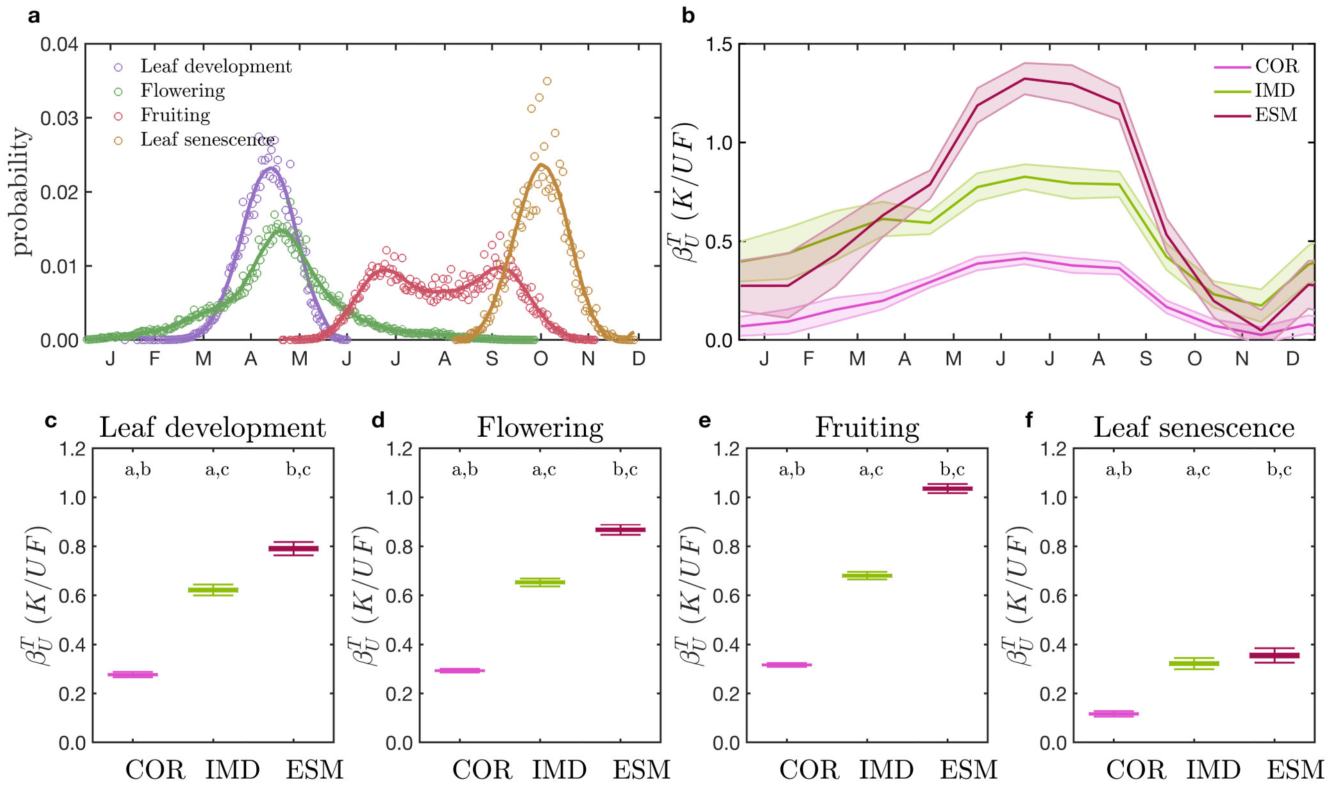

Figure 2. Coefficients of the MLR regression analysis describing unique changes in air temperature with changes in urban fraction.

a, Probability of seasonal occurrence of four aggregated phenological phases. **b**, Seasonal variation of MLR coefficients (β_U^T; Eq. 2) for three urban fraction (UF) metrics (COR … CORINE land cover, IMD … imperviousness degree, ESM … European settlement map; mean and ± one standard deviation). **c-f**, Boxplots of MLR coefficients (panel **b**) weighted by probability of the four aggregated phenological phases (panel **a**). Significant ($p < 0.05$, Wilcoxon rank sum test) differences between urban fraction metrics are indicated by the same letters. Boxplots show the interquartile range (IQR, box), the median (horizontal line in box) and 1.5 x the IQR (whiskers), while outliers are omitted for clarity.

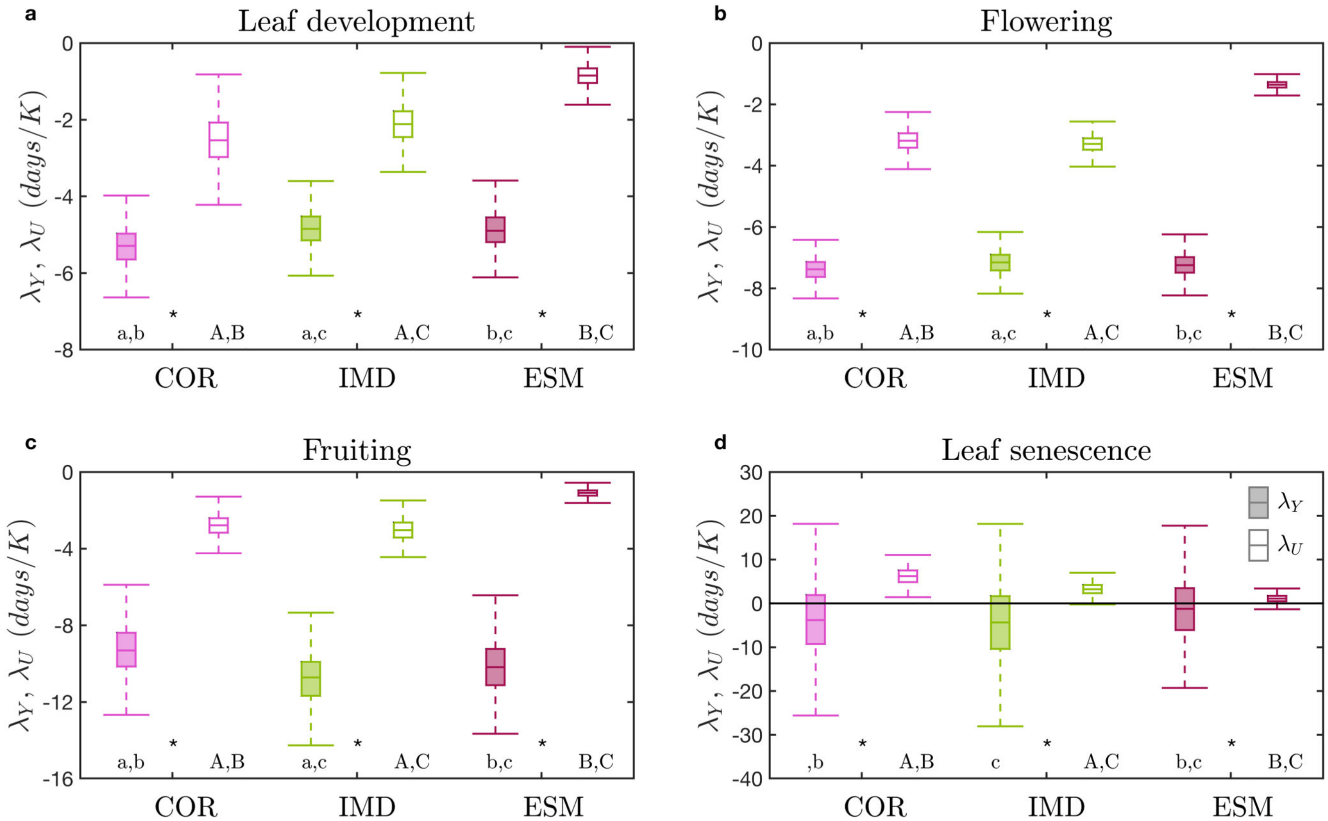

Figure 3. Apparent temperature sensitivities of aggregated phenological phases.

a-d, Change in entry dates of four aggregated phenological phases per degree air temperature change for three urban fraction metrics (COR … CORINE land cover, IMD … imperviousness degree, ESM … European settlement map). Apparent temperature sensitivities were calculated based on the temporal trend (λ_Y; Eq. 3; filled boxplots) and the spatial change in urban fraction (λ_U; Eq. 4; open boxplots). Significant ($p < 0.05$, Wilcoxon rank sum test) differences between urban fraction metrics are indicated by the same letters, between pairs of temperature sensitivities by an asterisk. Boxplots show the interquartile range (IQR, box), the median (horizontal line in box) and 1.5 x the IQR (whiskers), while outliers are omitted for clarity.

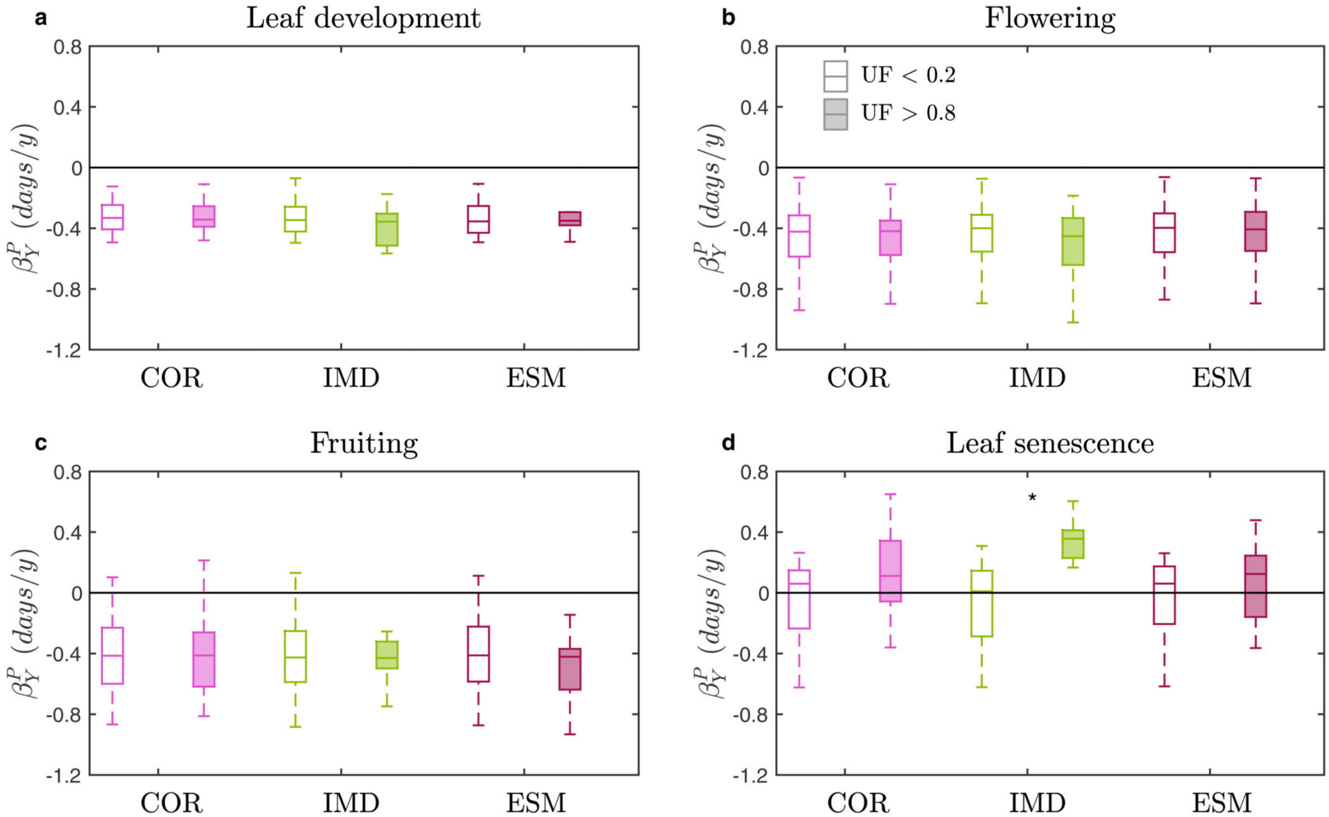

Figure 4. Coefficients of the MLR analysis describing unique changes in plant phenology over time.

a-d, Significant MLR coefficients (β_Y^P; Eq. 1) for four aggregated phenological phases and three urban fraction (UF) metrics (COR … CORINE land cover, IMD … imperviousness degree, ESM … European settlement map) with data stratified into low and high UF classes. Significant ($p < 0.05$, Wilcoxon rank sum test) differences between urban fraction metrics are indicated by the same letters, between low and high UF metrics by an asterisk. Boxplots show the interquartile range (IQR, box), the median (horizontal line in box) and 1.5 x the IQR (whiskers), while outliers are omitted for clarity.

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