The urban imprint on plant phenology

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The modification of the surface radiation and energy balance in urban areas causes the temperatures in these areas to exceed those of the surrounding countryside. 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. Here we investigated changes in the timing of plant phenology and temperature across study sites that differed in the degree of urbanization using publicly available pan-European datasets for the period 1981–2010. We found a significant advancement in the phenological phases of leaf development, flowering and fruiting with higher degrees of urbanization, whereas a significant delay was observed for phenological phases of leaf senescence. In addition to these phenological changes, an increase in 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. On the basis of 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 with the temperature sensitivity inferred from temporal changes in phenology and temperature. We conclude that gradients in urbanization represent a poor analogue for the temporal changes in plant phenology, apparently owing to confounding factors associated with urbanization.

Because the timing of periodic plant life cycle events, such as leaf unfolding, flowering or leaf colouring, is sensitive to variations in environmental factors—such as temperature—plant phenology has emerged as an important bioindicator for climate change1. Given the widespread enhancement of air temperature in urban areas compared to the surrounding countryside—an effect dubbed the urban heat island (UHI)—a great many studies, using both in situ observations and remotely sensed changes in greenness, have reported advancements in spring and summer and delays in autumnal phenological phases in urban compared to rural areas14, matching the widely studied temporal response of plant phenology to global warming4,5.

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 change4–9. 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 modified10, affecting plant–water relations11 and plant–nutrient relationships; however these effects may be counteracted by irrigation and fertilization. Concentrations of greenhouse gases (for example, CO2)9,12 and primary pollutants (such as NO, NO2, CO, SO2 and particulate matter that is 10 µm or less in diameter) are higher in urban areas owing to the proximity of emission sources13, whereas the concentrations of secondary pollutants, such as O3, are often higher in downwind, rural, areas14. Plant phenology has been shown to react both with delay (for example, flowering) and advancement (for example, earlier senescence) to pollutants that are typical of urban environments15–17. Artificial light, ubiquitous in urban areas, has been shown to delay plant flowering and leaf senescence18,19. Biotic plant–plant and plant–animal interactions are highly modified in urban areas because of, for example, artificial biocenosis compositions and habitat fragmentation20. Finally, rural and urban plant populations may exhibit genetically based phenotypic differences20. The extent to which these differences confound the phenological response to the UHI is poorly quantified. In addition, many urban phenology studies, particularly those based on in situ measurements, have been criticized for not properly reporting the metadata required for placing observed phenological differences in context with the degree of urbanization1, a shortcoming that is also widespread in the UHI literature1. 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 geographical areas22–24, 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 phenology25 and air temperature26, which we analyse with respect to the degree of urbanization to validate the space-for-time substitution approach.

Results and discussion

To quantify how changes in urban fraction (UF) affect plant phenology, we conducted a multiple linear regression (MLR) in which we controlled, in addition to the UF, for the three other main factors that affect plant phenology through changes in temperature, that is latitude, elevation and time22 (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: (1) the CORINE land cover (COR), which quantifies land cover in 44 classes; (2) the imperviousness degree (IMD), which quantifies the degree of soil sealing; and (3) the European settlement map (ESM), which quantifies the percentage of built-up area cover (see Supplementary Figs. 2 and 3 for a comparison of UF metrics).

The resulting UF regression coefficients (βUF; equation (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

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advanced with increasing UF (88–95% of all cases) for the leaf development, flowering and fruiting phenological phases, whereas 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), whereas 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 UF derived from COR) on spring phenological phases in three German cities5; although this study was limited to nine 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 that UF values of the IMD mostly cover the low to medium range (Supplementary Fig. 2).

Effects of changes in UF on pre-season temperature—that is, the air temperature averaged for the preceding 30 days—were also analysed 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 (\( \beta \); equation (2)) exhibited a pronounced seasonal course with minimum values from October to April and maximum values from May to September6 (Fig. 2b). The change in air temperature per unit change in UF 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 flowering 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 occurs together with an advancement (leaf development, flowering and fruiting phenological phases) and delay (leaf senescence) in plant phenology (Fig. 1). This led us to ask (1) how these urbanization-related phenological changes compare against the widely studied phenological changes over time and (2) 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, yielding two apparent temperature sensitivities (days per K), one based on the degree of urbanization (\( \lambda_u \); equation (4)) and one based on time (year; \( \lambda_t \); equation (3)) (see equations (5)–(22) and associated text for a theoretical derivation and justification of the statistical comparison of the \( \lambda \) coefficients).

During the leaf development, flowering and fruiting phenological phases, the apparent temperature sensitivities based on the temporal trend (\( \lambda_t \)) were significantly (P < 0.05) more negative compared to those based on differences in UF (\( \lambda_u \)) (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 (IQRs) overlapped with zero, as a result of a weakly negative and highly variable temporal trend in leaf senescence phenology (Supplementary Fig. 8), which has also been reported in previous studies8. By contrast, positive apparent temperature sensitivities (that is, a delay per unit of increase in temperature) 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 (that is without UF; see Supplementary Fig. 8 for the full MLR results). As shown in Fig. 4, the temporal trend coefficients were not statistically significantly different for the low and high UF datasets 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 UF 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 combinations.
of species and phenological phases in both low and high UF classes (see Supplementary Fig. 10). Given that the warming trend is similar in rural compared to urban sites\(^2\), these findings suggest a linear response of plant phenology to temperature.\(^2\)

**Conclusions**

In summary, our analysis shows that even though plant phenology and air temperature followed expected patterns across sites that differed in the degree of urbanization (Figs. 1 and 2), the corresponding phenological temperature sensitivities were either much smaller (spring and summer phenological phases) or reversed (autumn phenological phases) compared to the 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 is a poor quantitative predictor of the UHI. The most likely explanation for this observation is the presence of confounding factors that affect plant phenology along with the degree of urbanization, in particular air\(^2\),\(^2\)\(^,\)\(^2\)\(^,\)\(^3\)\(^,\)\(^4\)(11-19) and light pollution\(^1\)\(^,\)\(^1\)\(^,\)\(^5\)\(^,\)\(^6\)(16-17), modifications of the soil\(^1\)\(^,\)\(^7\)\(^,\)\(^8\)(18-19) and biotic interactions\(^9\), and genetic variation\(^9\). Future studies should aim to quantify the magnitude and direction of these multi-factorial effects.\(^1\) Most importantly, 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\(^9\). Particularly at intermediate UFs, where the complex interplay between natural surfaces and urban fabric may result in significant spatial microclimatic heterogeneity\(^9\), 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\(^10\),\(^11\), 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 datasets, which are often based on the work of volunteers\(^7\),\(^9\), 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\(^7\). (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)\(^1\). The downloaded dataset included 256 plant species (including cultivars) at 19,985 sites and a total of 11,922,878 phenological entries. From the dataset, 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, Bundesstoffenentamt und Chemische Industrie) scale\(^2\). For each phenology station, the degree of urbanization was derived as described below. For the analysis, the dataset was restricted to the period 1981–2010, as this is the most recent climatological time period that is 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 dataset to 6,765,348 entries, which was then statistically analysed as described below. For the ease of interpretation, the output of the statistical analyses was, as described previously\(^1\),\(^,\)\(^1\)\(^,\)\(^5\)\(^,\)\(^6\)(16-17), 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 geographical 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 at which phenological observations are made. Large-scale phenological studies thus typically relate phenology to gridded air temperature products\(^7\),\(^9\) to derive apparent phenological temperature sensitivities. Gridded air temperature products capture broad climatological patterns, but would be unsuitable for 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 were downloaded from the European climate assessment and dataset (ECAD; www.ecad.eu)\(^5\) database in June 2018 and used in a MLR approach as described below. We extracted information on the latitude, longitude, elevation and unique identifier of the station along with daily average air temperature. For the analysis, to be consistent with the phenological observations, the dataset 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 UF were outside (with a 5% tolerance) the elevation and/or UF range of the phenological stations present in that grid cell.

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**Fig. 4 | Coefficients of the MLR analysis describe unique changes in plant phenology over time.** a–d. Significant MLR coefficients ($\beta$, equation (1)) for the leaf development (a), flowering (b), fruiting (c) and leaf senescence (d) phenological phases and three UF metrics with data stratified into low and high UF classes. Significant (P < 0.05, Wilcoxon rank-sum test) differences between UF metrics are indicated by the same letters, between low and high UF metrics by an asterisk. Box plots show the IQR (box), the median (horizontal line in box) and 1.5× the IQR (whiskers); outliers are omitted for clarity.
This reduced the number of air temperature stations to 1,174. For each temperature station, the degree of urbanization was derived as described below.

**UF data.** As it is not obvious how to best quantify the degree of urbanization, three different, publicly available datasets, were used in this analysis (Supplementary Fig. 2). First, COR quantifies the land cover in 44 distinct classes and was downloaded as a 100-m GeoTIFF from https://land.copernicus.eu/pa/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 (MathWorks). Second, IMD quantifies the percentage of soil sealing and was downloaded as a 100-m GeoTIFF from https://land.copernicus.eu/pa/pan-european/high-resolution-layers/imperviousness for the COR product, UF was calculated as the percentage of built-up area coverage and was downloaded as a 100-m GeoTIFF from https://land.copernicus.eu/pa/pan-european/GSHL/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 datasets, a 500 m × 500 m (that is 5 pixels × 5 pixel) average was calculated centred on the pixels in which the phenological/temperature stations are situated. For the COR product, UF was calculated as the percentage of COR classes 1–6 (urban fabric and industrial, commercial and transport units) within each 500 m × 500 m area. The frequency distribution of the three UF metrics is compared in Supplementary Fig. 2. 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 1,100 m × 1,100 m (that is, 121 ha) spatial scale instead of the chosen 500 m × 500 m (that is, 25 ha) spatial scale. As shown in Supplementary Fig. 7, compared to Supplementary Fig. 6, results are robust, apart from additional significant differences between the three UF metrics during leaf senescence, despite a factor five difference in spatial scale.

For the two datasets that 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).

**Overview of the statistical analyses.** Typically, plant phenological studies analyse changes at a given place, for a given plant species and phenological phase over time. By contrast, this study aimed to quantify changes in phenology over space, specifically across varying degrees of urbanization. Because stations that differ in the degree of urbanization may also differ in other factors that affect phenology, such confounding factors need to be accounted for and this is done within the framework of a 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, data from air temperature stations are instead used and a general MLR regression approach is used to control for confounding factors. The results of these two independent MLR analyses are then combined to infer the unique phenological temperature sensitivity, that is, the change in phenological entry dates per unit change in air temperature.

**Statistical analyses of phenology.** To extract the unique influence of the degree of urbanization (U) on plant phenology (P), phenological data were, separately for each phenological phase–species combinations, subjected to a MLR using the fitlm function of MATLAB (MathWorks), controlling additionally for station latitude (L), elevation (E) and year (Y), to account for factors known to affect phenology through corresponding changes in temperature, that is

\[
P = \beta_0 + \beta_L L + \beta_E E + \beta_Y Y + \beta_U U
\]

Here \(\beta_0\) and \(\beta_L, \beta_E, \beta_Y, \beta_U\) 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 environmental conditions during the corresponding pre-season, daily air temperature data were, as described previously, averaged over the preceding 30 days. Apparent phenological temperature sensitivities (see next section) are robust to this particular choice for the pre-season averaging period, as demonstrated in Supplementary Figs. 11 and 12, which are identical to Fig. 5, 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 (MathWorks). These were then weighted with the frequency of phenological phases from Fig. 2 to produce MLR coefficients for each aggregated phenological phase. The coefficients representing the unique influence of UF on air temperature \(\beta_U\) are shown in Fig. 2, the full results of the MLR are shown in Supplementary Fig. 9.

**Statistical analyses of the apparent phenological temperature sensitivity.** Apparent phenological temperature sensitivities were derived by dividing the phenological coefficients for changes over time \(\beta_L, \beta_E, \beta_Y\) (days per year) and UF \(\beta_U\) (days per UF) (Supplementary Fig. 6) by the temperature coefficients for changes over time \(\beta_T\) (K per year) and UF \(\beta_T\) (K per UF) (Supplementary Fig. 9) in a bootstrapping framework \((n = 1,000)\), yielding two apparent temperature sensitivities, one based on changes over time \((L, E, \beta_L, \beta_E, \beta_Y, K)\) and one based on the degree of urbanization \((L, E, \beta_U, K)\) (Fig. 3).

**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 UF, and phenology a linear function of temperature only, that is**

\[
T = \beta_L L + \beta_E E + \beta_Y Y + \beta_U U
\]

Replacing temperature in equation (7) with the right side of equation (5) yields the following expression for phenology, which is conceptually identical to equation (1):

\[
P = \beta_0 + \beta_L L + \beta_E E + \beta_Y Y + \beta_U U
\]

with the following definition for the \(\beta_U\) coefficients:

\[
\beta_U^L = \beta_U^E = \beta_U^Y
\]

\[
\beta_U^L = \beta_U^E = \beta_U^Y
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\beta_U^L = \beta_U^E = \beta_U^Y
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\beta_U^L = \beta_U^E = \beta_U^Y
\]

In a second step, the phenology dataset was stratified into stations with low \((UF < 0.2)\) and high \((UF > 0.8)\) UF and the MLR as described above was repeated for the two datasets with station latitude, elevation and year as independent variables. The coefficients that represent the unique influence of year on phenology \(\beta_U\) from this analysis are shown in Fig. 4, the full results of the MLR are shown in Supplementary Fig. 8.
With equations (11) and (12), it is then straightforward to show that the λ coefficients have to be identical and reduce to the true (unknown) phenological temperature sensitivities:

$$\lambda_Y = \frac{\beta_Y}{\beta_T} = \frac{\beta_Y}{\beta_Y + \beta_T} \frac{\beta_Y}{\beta_T} = \beta_T$$

(13)

and

$$\lambda_U = \frac{\beta_U}{\beta_T} = \frac{\beta_U}{\beta_U + \beta_T} \frac{\beta_U}{\beta_T} = \beta_T$$

(14)

If $\lambda_Y$ and $\lambda_U$ derived from equations (3) and (4) are statistically significantly different, an alternative model including additional temperature-independent effects of time and UF needs to be invoked:

$$P = \beta_0 + \beta_T T + \beta_Y Y + \beta_U U$$

(15)

Replacing temperature in equation (15) with the right side of equation (5), we again arrive at equation (7) with the following new definition of the $\beta^c$ coefficients:

$$\beta^c_0 = \beta_0 + \beta_T \beta_T$$

(16)

$$\beta^c_Y = \beta_Y \beta_T$$

(17)

$$\beta^c_E = \beta_E \beta_T$$

(18)

$$\beta^c_Y = \beta_Y \beta_T$$

(19)

$$\beta^c_U = \beta_U \beta_T + \beta_T$$

(20)

The resulting $\lambda_Y$ and $\lambda_U$ are then given as:

$$\lambda_Y = \beta_Y + \beta_T \beta_T$$

(21)

and

$$\lambda_U = \beta_U + \beta_T \beta_T$$

(22)

With this alternative model, statistically significantly different $\lambda_Y$ and $\lambda_U$ values derived from equations (3) and (4) can be interpreted to result from additional, temperature-independent changes in phenology with time and/or UF relative to the corresponding temperature changes. This interpretation also holds if the alternative model (equation (15)) is formulated as a direct influence of temperature to the corresponding temperature changes. This interpretation also holds if the derived from equations (3) and (4) can be interpreted to result from additional, effects of time and UF needs to be invoked:

$$P = \beta_0 + \beta_Y T + \beta_Y Y + \beta_U U$$

(15)

Reporting Summary: Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability
The phenological data used in this study are available from www.pep725.eu and 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 (MathWorks) scripts used to analyse data are available at https://doi.org/10.5281/zenodo.3422079.

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**Author contributions**
G.W. conceived the study, analysed the data and wrote the manuscript together with E.T. and A.H.

**Competing interests**
The authors declare no competing interests.

**Additional information**
Supplementary information is available for this paper at https://doi.org/10.1038/s41559-019-1017-9.
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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

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Data collection No software was used for data collection.

Data analysis Matlab 2016b, The MathWorks, Inc., Natick, Massachusetts, United States

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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).
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Ecological, evolutionary & environmental sciences study design

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Study description
Publicly available plant phenological data were analyzed with regard/to publicly available air temperature and urban fraction data.

Research sample
All data originate from publicly available data bases: Plant phenological data originate from the Pep725 data base, air temperature station data originate from the ECAD data base, and urban fraction metrics originate from the Copernicus Land Monitoring service. See statement of data availability.

Sampling strategy
Not really applicable - sample size is given by the sample size of the data as deposited in the data bases used in this study.

Data collection
Not applicable - data are publicly available and were downloaded from established data bases.

Timing and spatial scale
Spatial scale is the local scale of the phenological and air temperature measurements. Spatial scale of the urban fraction data is 100m. Temporal scale is daily for air temperature and phenological data. Temporal scale varies for urban fraction data as detailed in the methods section.

Data exclusions
Data were excluded as detailed in the methods section. Briefly, only data from 1981-2010 were used. Plant phenological data were in addition filtered for a minimum n and other criteria as detailed in the methods section. Air temperature station data were filtered for a similar climate space as the phenological data, as detailed in the methods section.

Reproducibility
Results of this study are fully reproducible as these only involve computational analyses.

Randomization
Only applicable to Fig. 4 - here data were stratified by urban fraction < 0.2 and >0.8.

Blinding
Not applicable.

Did the study involve field work?
- Yes
- No

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