Urban warming advances spring phenology but reduces the response of phenology to temperature in the conterminous United States

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Urbanization has caused environmental changes, such as urban heat islands (UHIs), that affect terrestrial ecosystems. However, how and to what extent urbanization affects plant phenology remains relatively unexplored. Here, we investigated the changes in the satellite-derived start of season (SOS) and the covariation between SOS and temperature (R_T) in 85 large cities across the conterminous United States for the period 2001–2014. We found that 1) the SOS came significantly earlier (6.1 ± 6.3 d) in 74 cities and R_T was significantly weaker (0.03 ± 0.07) in 43 cities when compared with their surrounding rural areas ($P < 0.05$); 2) the decreased magnitude in R_T mainly occurred in cities in relatively cold regions with an annual mean temperature <17.3 °C (e.g., Minnesota, Michigan, and Pennsylvania); and 3) the magnitude of urban–rural difference in both SOS and R_T was primarily correlated with the intensity of UHI. Simulations of two phenology models further suggested that more and faster heat accumulation contributed to the earlier SOS, while a decrease in required chilling led to a decline in R_T magnitude in urban areas. These findings provide observational evidence of a reduced covariation between temperature and SOS in major US cities, implying the response of spring phenology to warming conditions in nonurban environments may decline in the warming future.

phenology | urbanization | temperature response | urban heat island

Phenology, the timing of recurring events in a plant's life cycle, is sensitive to biotic and abiotic environmental variations (e.g., community structure and temperature) (1, 2). Extensive studies have demonstrated earlier spring green-up (i.e., the start of season [SOS]) driven by warming conditions, especially in northern extratropical ecosystems (3, 4). However, criticism of current testing methodologies, such as relatively short observational periods and the use of saplings or twigs instead of mature trees in experimental observations, has prompted further investigation of phenology changes (5). Moreover, although the phenological studies using in situ or satellite measurements have provided convincing evidence of earlier spring leaf-out over the last several decades, they have shed little light on future phenological changes when temperatures are projected to go beyond the range of historical or present-day variability (6, 7).

Urbanization has transformed the environmental conditions of urban terrestrial ecosystems. A well-known phenomenon associated with urbanization is the urban heat island (UHI) effect, characterized by elevated air temperatures in cities relative to their rural surroundings. Because the intensity of the UHI effect is similar to that of projected temperature changes in the near future (8), cities can serve as natural laboratories for examining the effects of future warming conditions on ecosystems (9). A comparison between urban and rural phenology thus likely offers a distinctive analog for possible phenological responses under projected higher temperatures, facilitating investigation of the underlying mechanisms (10).

Numerous studies have observed earlier flowering in urban areas relative to that in rural areas. Field observations and herbarium records have documented that leaves tend to emerge 4 to 17 d earlier on urban trees than on rural trees for the same species in the United States, Europe, and China (11–13). However, these studies were restricted to a limited numbers of sites or to simple urban–rural comparisons and thus did not capture much of the interurban variation in phenological change. Satellite retrievals have expanded observations from isolated sites to wide spatial areas, enhancing the capability to explore urban–rural phenology variations at broader scales. Satellite data revealed that the photosynthetic activity started 5.6 ± 0.7 d earlier in cities among 880 urban–rural gradients across the Northern Hemisphere (14, 15); SOS came earlier at sites closer to the urban core (16). The extent to which urban climate (e.g., background climate and UHI) modulates the spatial pattern of SOS remains less well known. Recent studies reported a link between radiative land surface temperature (LST) and phenology, showing that SOS shifted 9 to 12 d earlier per 1 °C increase of LST

Significance

Cities and their associated urban heat islands are ideal natural laboratories for evaluating the response of plant phenology to warming conditions. In this study, we demonstrate that the satellite-derived start of season for plants occurred earlier but showed less covariation with temperature in most of the large 85 cities across the conterminous United States for the period 2001–2014. The results show a reduction in the response of urban phenology to temperature and imply that, in nonurban environments, the onset of spring phenology will likely advance but will slow down as the general trend toward warming continues.

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in cities (17, 18). Although highly correlated with air temperature in most cases, the LST could cause large biases in quantifying the temperature response of phenology. This is because LST mainly reflects the temperature of impervious surfaces instead of vegetative surfaces in the city and thus is often much higher than the air temperature, especially during sunny and calm days (19).

How and why the response rate of SOS to temperature differs in urban and rural areas remain largely unexplored. One way to characterize it is through the interannual covariation of SOS with temperature, expressed as a partial correlation coefficient between SOS and preseason mean air temperature (R_T) (20), after statistically controlling for precipitation and shortwave radiation. Thus, R_T represents how much SOS is correlated to interannual changes in temperature. Recent studies have found that R_T declined in natural vegetation systems during the satellite era (21, 22). However, the extent to which these declining trends will continue in the future remains unclear. The study of urban phenology as an analog could offer a unique opportunity to investigate the changes in natural R_T in warmer conditions.

In this study, we focused on the following questions: 1) How have SOS and R_T changed in large US cities? 2) Were these phenological changes and their magnitudes influenced by the background climatic conditions and the modified local environments (e.g., UHI intensity)? 3) What physiological mechanisms drove these phenological changes?

We first assessed the changes in satellite-derived SOS and R_T among 85 large cities (*SI Appendix*, Fig. S1) in the conterminous United States for 2001–2014 using the Moderate Resolution Imaging Spectroradiometer (MODIS) phenology products (23) and gridded climate data from Topography Weather (TopoWx) (24) and Daymet (25) datasets. The confounding effects of other climate variables (i.e., precipitation and shortwave radiation) were excluded from R_T using partial correlation analysis. We also explored possible underlying mechanisms affecting such phenological changes using two process-based phenology models (*Materials and Methods* and *SI Appendix*).

Results

Across the selected 85 cities, the SOS was 6.1 ± 6.3 d (mean ± SD) earlier in urban areas (SOS: 71.3 ± 13.1 d of year) than in corresponding rural areas (SOS: 77.4 ± 15.2 d of year) with a slope of 1.06 ($P < 0.001$; Fig. 1*A*) during 2001–2014. In 87% of the study cities (74 cities), the 14-y mean SOS in urban areas was notably earlier than in rural SOS ($P < 0.05$; *SI Appendix*, Fig. S2). Significantly negative SOS correlations with preseason temperature (but not with precipitation or shortwave radiation) were identified in all study cities ($P < 0.05$; Fig. 1*B* and *SI Appendix*, Figs. S3 and S4*A*). Moreover, the R_T was 0.03 ± 0.07 weaker (i.e., less negative) in urban areas, compared with rural ones (slope = 0.85, $P < 0.001$; Fig. 1*B*). Of the study cities, 51% (43 cities) further demonstrated significantly weaker urban R_T than the rural ones ($P < 0.05$; *SI Appendix*, Fig. S4*B*). Similar results were obtained after removing the influence of extreme years on R_T (urban R_T was, on average, 0.04 ± 0.15 weaker than rural R_T; *SI Appendix*, Fig. S5) using a temporal bootstrapping approach. The R_T with different preseasons (i.e., January to March, February to March, March, and March to April) was also examined, and the results showed similar weaker urban R_T although with different amplitudes (i.e., 0.02 ± 0.1, 0.02 ± 0.1, 0.03 ± 0.1, and 0.05 ± 0.1, respectively; *SI Appendix*, Fig. S6).

The SOS significantly advanced with an increase in annual mean air temperature (T_{avg}, slope = −1.98 d/°C, $P < 0.0001$) but not with annual precipitation (P_{rcp}) (Fig. 2*A* and *SI Appendix*, Figs. S7 *A* and *C* and S8*A* and Table S1). However, the magnitude of R_T significantly decreased (less negative) with the advancement of SOS (slope = −0.005/d, $P < 0.0001$), increase in T_{avg} (slope = 0.009/°C, $P < 0.001$), and decrease in P_{rcp} (slope = −0.0008/mm, $P < 0.01$; Fig. 2*A* and *SI Appendix*, Figs. S7 *A* and *C* and S8 *A* and *C* and Table S1). The urban–rural difference in R_T (ΔR_T) significantly negatively correlated with the urban–rural difference in SOS (ΔSOS, slope = −0.015/d, $P < 0.001$; Fig. 2*B* and *SI Appendix*, Table S1). In other words, with the increase in the magnitude of urban–rural difference in SOS, the magnitude of urban–rural difference in R_T increased for cities in quadrant II and decreased for cities in quadrant III. Positive ΔR_T (i.e., reduced magnitude in urban R_T) was found mainly in cities associated with relatively low T_{avg}, and conversely negative ΔR_T (i.e., enhanced magnitude in urban R_T) was predominantly found in cities with high T_{avg} (Fig. 2*B* and *SI Appendix*, Fig. S8*D*). The T_{avg} threshold distinguishing the cities with positive ΔR_T from those with negative ΔR_T was 17.3 °C, which captured the sign of ΔR_T in 88% of cities in quadrant II and 72% of cities in quadrant III, respectively (*SI Appendix*, Fig. S9). This T_{avg} threshold was further used below to differentiate phenological responses to UHI in cold versus warm regions. Geographically, the cities showing advanced SOS but reduced R_T magnitude (quadrant II) were mainly in the northeastern temperate and boreal regions (e.g., Minnesota, Michigan, and Pennsylvania; *SI Appendix*, Fig. S8 *B* and *D*), while the cities showing advanced SOS and enhanced magnitude in R_T (quadrant III) were largely in the southwestern or coastal regions (e.g., Texas, Louisiana, and Florida; *SI Appendix*, Fig. S8 *B* and *D*).

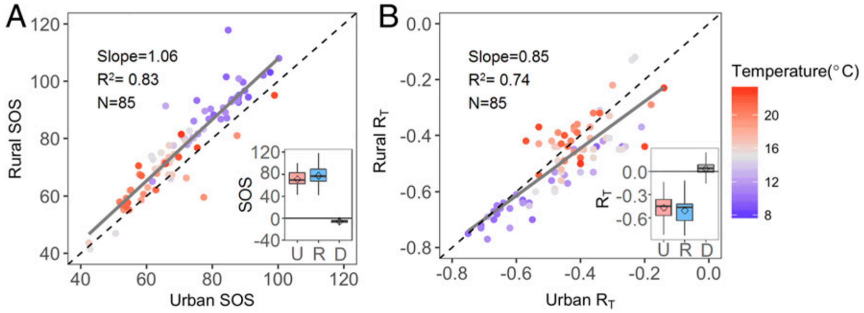

Fig. 1. Urban and rural (*A*) SOS and (*B*) R_T in 85 study cities. In *A*, SOS is the 14-y mean during 2001–2014 for each city. Point color represents background climate, i.e., 14-y averaged annual mean temperature; 1:1 line (black dashed) and fitted linear regression (gray solid, $P < 0.001$) are shown. The slopes of the linear regression, R^2 and *N* (sample size) of rural versus urban (*A*) SOS and (*B*) R_T are also shown. The points (*A*) above or (*B*) below the 1:1 line represent an earlier SOS or reduced magnitude in R_T in urban areas. (*Insets*) A boxplot for SOS or R_T. U and R stand for urban and rural (*A*) SOS and (*B*) R_T, and D is the urban–rural difference (D = U − R). The central line and the rhombus represent the median and mean, respectively. The lower and upper hinges correspond to the 25th and 75th percentiles, respectively.

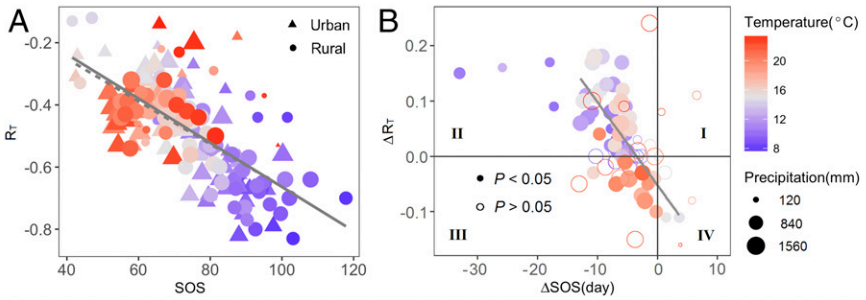

Fig. 2. The relationship between (*A*) SOS and R_T and (*B*) ΔSOS and ΔR_T. (*A*) The points are the 14-y mean SOS and R_T for urban (triangle) and rural (circles) areas in each city during 2001–2014. Fitted linear regression lines for urban (solid) and rural (dashed) areas are shown. (*B*) $\Delta SOS = SOS_{Urban} - SOS_{Rural}$ and $\Delta R_T = R_{T\mathrm{Urban}} - R_{T\mathrm{Rural}}$. Negative ΔSOS represents an earlier urban SOS, and positive ΔR_T represents a decreased magnitude in urban R_T. Solid points indicate a significant ($P < 0.05$) difference in R_T between urban and rural areas. Fitted linear regression line for cities for which ΔSOS is larger than−12.4 d and ΔR_T is significant ($P < 0.05$) are shown (slope= −0.015/d, $P < 0.001$). Point color and size represent background climate, that is, 14-y mean annual average temperature, and annual precipitation in each city.

In addition to background climates, the modified local climatic conditions characterized by UHI were closely associated with the magnitudes of change in SOS and R_T. All of the cities except two (98%) showed significant UHI effects (ΔT, i.e., $T_{\mathrm{Urban}} - T_{\mathrm{Rural}}$, 0.6 ± 0.7 °C, $P < 0.05$; *SI Appendix*, Fig. *S7E*). However, the responses of ΔSOS and ΔR_T to ΔT differed from cold regions to warm regions separated by 17.3 °C as the threshold (see above). For cities in cold regions, ΔSOS and ΔR_T significantly decreased at −7.0 d/°C ($P < 0.01$; Fig. 3*A*) and increased at 0.04/°C ($P = 0.05$; Fig. 3*C*), respectively, with the intensification of UHI. In warm regions, the intensification of UHI significantly strengthened the urban R_T reduction at 0.07/°C ($P < 0.05$; Fig. 3*D*) but not SOS ($P = 0.06$; Fig. 3*B*). It's worth noting that ΔR_T was negative when ΔT was less than 0.5 °C (Fig. 3*D*). Such enhanced urban SOS response to temperature gradually changed to a reduced one (positive ΔR_T) with the intensification of UHI in warm regions. These contrasting patterns show that the ΔSOS and ΔR_T widened in cold regions, but more complex changes occurred in warm regions with UHI intensification.

Two process-oriented phenology models, namely, the alternating (ALT) (26) and parallel (PAR) (27) models, were used to examine the possible causes underlying the SOS and R_T changes in cities. These two models, which have been shown to agree well with both in situ and remote sensing observations, require daily air temperature as the only input to predict spring budburst (28). They assume that plants accumulate chilling and forcing during

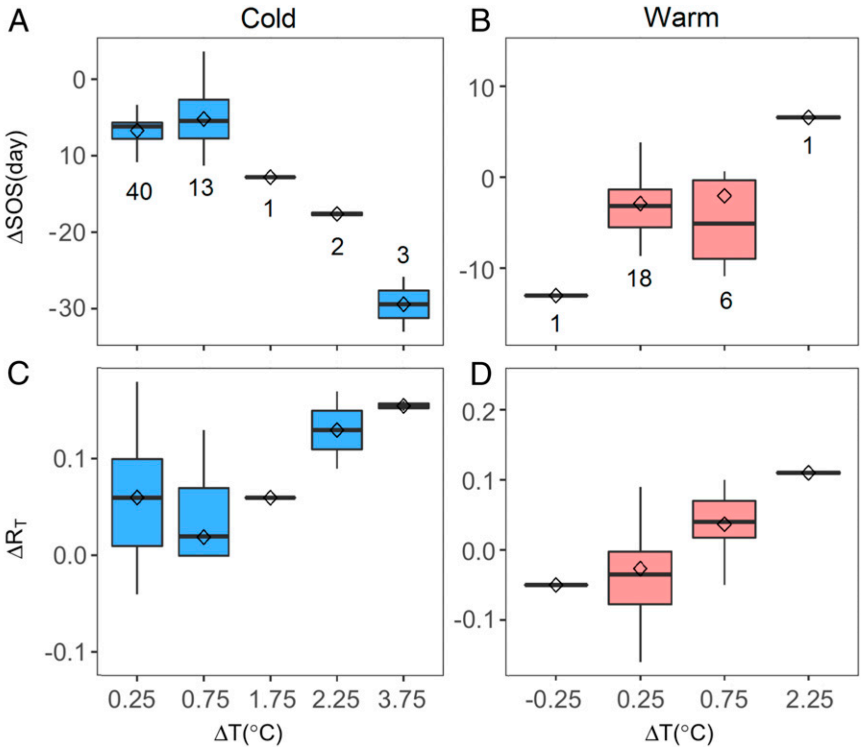

Fig. 3. Changes in (*A* and *B*) ΔSOS and (*C* and *D*) ΔR_T with ΔT in cold and warm regions. $\Delta SOS = SOS_{Urban} - SOS_{Rural}$, $\Delta R_T = R_{T\mathrm{Urban}} - R_{T\mathrm{Rural}}$, and $\Delta T = T_{\mathrm{Urban}} - T_{\mathrm{Rural}}$. Negative ΔSOS represents an earlier urban SOS, and positive ΔR_T represents a decreased magnitude in SOS response to temperature in urban areas. Positive ΔT represents UHI effect. Results are shown at 0.5 °C bin of ΔT. The *x* axis is the mean ΔT in each bin. The central line and the rhombus represent the median and mean values, respectively. The lower and upper hinges correspond to the 25th and 75th percentiles, respectively. *A* and *C* are the results for cold regions (blue), and *B* and *D* are the results for warm regions (red). Sample sizes are indicated using numbers for each bin (shown in *A* and *B*).

winter and spring, and spring budburst occurs when forcing and chilling accumulations meet certain requirements (*SI Appendix*). Both models captured the interannual variation and spatial variability of SOS with a correlation of 0.85 between observation and prediction during the independent validation for 2012–2014 ($P < 0.001$; *SI Appendix*, Table S2 and Fig. S10). The models also reproduced the ΔSOS as observed, albeit with underestimated magnitudes (*SI Appendix*, Fig. S11). Compared with those in rural areas, urban plants were simulated to accumulate more forcing and less chilling for 78% (ALT) and 67% (PAR) of cities and years (quadrant II; *SI Appendix*, Fig. S12). Similar results were obtained when comparing 14-y mean forcing and chilling accumulations in urban versus rural areas in 85 cities; that is, 85% (ALT) and 67% (PAR) of cities showed more forcing and less chilling accumulations in urban areas (quadrant II; *SI Appendix*, Fig. S13). How the changes in forcing and chilling account for the changes in SOS and R_T is discussed below.

Discussion

This study provides direct evidence that urban warming not only advanced SOS but reduced the magnitude of SOS response to temperature in 85 large US cities. Such urbanization-induced phenological changes are broadly consistent with recently reported research on natural ecosystems (21, 22, 29). As a preview of possible impacts of future warming on phenology, this finding suggests that, while spring phenology will likely continue to advance in natural ecosystems, the rate of SOS advancement will slow down under anticipated climate warming conditions (6, 7, 21, 22). To explain the reduced R_T magnitudes, we consider four hypotheses: 1) thermal budget percentage (6), 2) insufficient chilling (7, 30), 3) reduced preseason length (31), and 4) photoperiod restriction (32).

The hypothesis of thermal budget percentage suggests that spring phenology is more sensitive to temperature in colder, higher-latitude sites than that in warmer regions because small absolute changes in temperature constitute greater relative changes in thermal balance under colder conditions. This theory thus justifies the reduced magnitudes of urban R_T. If we treat urban and rural areas as warm and cold conditions, respectively, rural SOS is more responsive to warming because a smaller increase in temperature constitutes a larger thermal balance in rural areas, leading to a relatively larger magnitude for rural R_T than that for urban R_T (i.e., positive ΔR_T).

The hypothesis of insufficient chilling assumes that, if the necessary chilling for dormancy break is not fully met (e.g., under warm winters), plants become less responsive to spring warming. Specifically, after growth cessation in early fall, plants need to be exposed to low chilling temperatures for a certain period to break dormancy. After that, phenological development (e.g., budburst) occurs as a result of high forcing temperatures above a threshold (33). If the necessary chilling is not fully met, the forcing process might be delayed or the forcing requirement might be increased, leading to a decreased magnitude in the temperature response of SOS. According to this hypothesis, the chilling requirement may not be fully achieved in urban areas, due to mild winters, causing an increased requirement for forcing and, taken together, reduced magnitude in temperature response of SOS in urban areas (i.e., less negative R_T or positive ΔR_T). Simulations from the two phenology models also support this hypothesis (*SI Appendix*, Figs. S12 and S13).

The hypothesis of preseason length suggests climate warming reduces the magnitude of R_T simply by reducing the length of the preseason, due to a faster progression toward budburst in spring (31). However, we did not find significant changes ($P = 0.18$) in preseason length from urban (2.0 ± 0.8 mo) to rural areas (1.9 ± 0.7 mo; *SI Appendix*, Fig. S14). Thus, the impacts of preseason length on R_T can be excluded in this study.

Photoperiod (i.e., the period that a plant is exposed to light in a day) has been proposed to restrict the advancement of phenology under warming by imposing a hard limit (5, 22, 34). However, we did not find evidence that a hard limit had been reached in this study. Photoperiod is a cue for the progression of phenology at a given location because it gradually increases from winter to summer and then decreases until the following winter (35). Unlike large fluctuations in temperature, photoperiod does not vary from year to year, and thus has a stabilizing effect on phenology (36). Experimental and modeling studies revealed that, although a warmer spring leads to an earlier budburst, the resulting shorter day length when budburst occurs might have an adverse effect on phenology by slowing down cell growth in the spring to protect leaves against frost damage (32). In this study, urban and rural areas were in close proximity and experienced nearly identical photoperiods on any given day under natural conditions; however, the urban SOS actually occurred earlier at times with progressively shorter day lengths. Photoperiod could therefore partially contribute to the reduced R_T magnitudes along with the insufficient chilling restriction. However, it is likely that the hard limit of photoperiod was not reached in this study, since SOS still showed a continuous advancement in warmer conditions.

Most cities in the cold region showed reduced R_T magnitudes, but many in the warm region showed enhanced R_T magnitudes (negative ΔR_T; quadrant III in Fig. 2*B*). Cities associated with enhanced R_T magnitudes were mainly located in southern or western coastal regions (e.g., Texas, Louisiana, and Florida; *SI Appendix*, Fig. S8*D*), where winters are usually mild and short, followed by hot and long summers. These cities also exhibited complex phenological responses to UHI effects compared with those in the cold regions (Fig. 3 *B* and *D*). Such complex phenological responses are possibly caused by the dependence of local vegetation on other environmental cues for spring green-up in addition to temperature. For example, *Prunus dulcis* (sweet almond), a species native to Iran but widely cultivated elsewhere (e.g., California and Utah), is particularly sensitive to the available soil water (37).

Both phenology models are representative of the forcing and chilling processes and are consistent with the second hypothesis discussed above. They captured most of the observed SOS variations over time and among cities (*SI Appendix*, Fig. S10) and, more importantly, the observed earlier urban SOS (*SI Appendix*, Fig. S11). As these models are dependent on temperature only, and although other factors may influence the urban phenology to a certain extent (discussed below), urban warming dominated the phenological changes in this study. Because forcing processes determine how fast buds develop in the spring (5), a more and faster accumulated forcing, as estimated in the urban areas (*SI Appendix*, Fig. S12), explains the earlier urban SOS (Fig. 1*A*). In contrast, the increased accumulated chilling reduces the forcing requirement for budburst (5), as described in both models (*SI Appendix*). Thus, with less chilling accumulated (*SI Appendix*, Fig. S12), urban plants require more forcing for budburst, which offsets the forcing-induced early SOS, to a certain extent, and accounts for the decreased R_T magnitudes (38) (Fig. 1*B*).

The modeled Δ forcing and Δ chilling (*SI Appendix*, Figs. S12 and S13) also explained the widening gaps of urban−rural difference in SOS and R_T with intensified UHI for cold regions (Fig. 3 *A* and *C*). This is because the intensified UHI can cause continuous forcing gain and chilling loss for urban plants and thus further advance SOS and reduce R_T magnitudes. For warm regions, however, the ΔSOS and ΔR_T pattern (Fig. 3 *B* and *D*) could not be explained by such temperature-dependent phenology models (*SI Appendix*, Fig. S12). This is likely due to the complex response of spring phenology to various environmental cues as discussed above. In addition, the slopes of Δ forcing against Δ chilling in warm conditions were steeper than those in cold conditions (*SI Appendix*, Figs. S12 and S13). This suggests that, with the same amount of chilling loss in urban areas, the gained forcing is greater in a warm region than that in a cold region. Such differences in warm versus cold regions were mainly due to the differences in the relative proportion of forcing and chilling accumulations. For example, in cold regions, the chilling period is longer, and, consequently, the chilling accumulation is greater than that in warm regions. Therefore, with the same amount of chilling loss in urban areas, the relative portion of chilling lost is smaller in cold regions, causing a smaller forcing gain.

The influence of urban size (an indicator of urbanization level) on vegetation phenology was investigated, but no significant relationship was found between the urban size and ΔSOS or ΔR_T (*SI Appendix*, Table S1). A possible explanation is that various background climate conditions and associated plant functional types could cause different phenological responses to urban warming, even for cities of similar size (39). Other abiotic and biotic factors that were not considered in this analysis (e.g., urbanization-induced changes in nitrogen deposition, precipitation regimes, and plant species) could also affect urban phenology differently from temperature (9). For example, spring green-up dates vary greatly among different plant species. Because urbanization has partly altered the species and composition of vegetation in urban ecosystems (e.g., invasive species *Acer platanoides* in northeastern cities and the tropical species *Jacaranda* in California), diverse plant species may cause highly spatially heterogeneous phenology in cities (40). We nonetheless believe that our broader argument is valid. First, despite exotic species in cities, previous studies found that the rich variety of tree species, native or exotic, does not change significantly with urbanization gradient (41). With a considerable amount of native species in cities, such mixed phenological signals still reflect the phenology of tree communities in their geographic regions (e.g., rural areas) (42). Second, exotic species in cities have diverse phenology niches, some of which are earlier and others are later than those of native species (43). Because the employed satellite observations were derived from a mixed signal of all species within a grid at 500 m by 500 m spatial resolution, the exotic species could not account for the consistent SOS changes across most cities as documented in this study.

In summary, we reported an urban warming-induced advanced SOS and weakened SOS response to temperature change in 85 cities across the United States and demonstrated that increased forcing and reduced chilling were largely responsible for these phenological changes. These findings provide observational evidence of a weakened temperature response of SOS (i.e., decreased R_T magnitude) under urban warming conditions that deserves attention, along with the widely acknowledged earlier urban SOS. Moreover, such reductions in R_T magnitude were found to be mainly associated with cities in cold regions, and their changes correlated well with the intensity of UHI, whereas disparate R_T patterns existed in warm regions. These results suggest that the previously identified advancement in spring phenology in natural ecosystems may continue but that the rate of advancement will likely slow down under future warming, especially in cold areas.

Materials and Methods

The spring phenology indicator SOS during 2001–2014 was obtained from a MODIS Land Cover Dynamics (MCD12Q2) product (23). The climate data during 2000–2014 were obtained from the TopoWx dataset (24) and the Daymet dataset (25). The National Land Cover Database was used to classify pixels of urban areas, deciduous forest, evergreen forest, and mixed forest in this study (44). The urban extent was derived from the Defense Meteorological Satellite Program/Operational Linescan System nighttime light data (45). Cities with urban areas larger than 500 km^2 were selected in this study (46).

To understand the main driving climate factor(s) of SOS, covariations (i.e., partial correlation coefficients) between SOS and climate variables (i.e., T_{avg}, precipitation, and shortwave radiation) during 2001–2014 were calculated using partial correlation analysis. To estimate the uncertainty of the R_T obtained from the partial correlation analysis, we employed a nonparametric bootstrapping method (*SI Appendix, Materials*).

Data Availability. All data needed to evaluate the conclusions in the paper are present in the paper and/or *SI Appendix, Materials*. The datasets analyzed in this study are publicly available as referenced within the article.

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