

Complex climate-mediated effects of urbanization on plant reproductive phenology and frost risk

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Summary

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- Urbanization can affect the timing of plant reproduction (i.e. flowering and fruiting) and associated ecosystem processes. However, our knowledge of how plant phenology responds to urbanization and its associated environmental changes is limited.
- Herbaria represent an important, but underutilized source of data for investigating this question. We harnessed phenological data from herbarium specimens representing 200 plant species collected across 120 yr from the eastern US to investigate the spatiotemporal effects of urbanization on flowering and fruiting phenology and frost risk (i.e. time between the last frost date and flowering).
- Effects of urbanization on plant reproductive phenology varied significantly in direction and magnitude across species ranges. Increased urbanization led to earlier flowering in colder and wetter regions and delayed fruiting in regions with wetter spring conditions. Frost risk was elevated with increased urbanization in regions with colder and wetter spring conditions.
- Our study demonstrates that predictions of phenological change and its associated impacts must account for both climatic and human effects, which are context dependent and do not necessarily coincide. We must move beyond phenological models that only incorporate temperature variables and consider multiple environmental factors and their interactions when estimating plant phenology, especially at larger spatial and taxonomic scales.

Introduction

Human populations have grown immensely over the last century, precipitating massive global environmental change (Harte, 2007; United Nations, Department of Economic and Social Affairs, Population Division, 2019). In particular, continued population growth has resulted in an expansion of urban environments with high human population density. This is greatly exacerbated by people increasingly migrating to urban centers around the world, further fueling their growth (Satterthwaite, 2009; United Nations, Department of Economic and Social Affairs, Population Division, 2017, 2019). Urbanization can alter local environmental conditions. For instance, urbanization has been demonstrated to increase temperature (i.e. the urban heat island effect) and drought stress (Oke, 1973, 1982; Van Loon *et al.*, 2016; Lüttge & Buckeridge, 2020), thus changing the structure and function of ecosystems (Boivin *et al.*, 2016). Indeed, studies have suggested that the climatic impact of urbanization is equivalent to decades of global warming (Imhoff *et al.*, 2010), and thus it has been posited that urban environments may represent (un)natural

experiments that can be used to study the response of plants to climate change (Harrison & Winfree, 2015; Jochner & Menzel, 2015).

Plant phenology, or the timing of recurring life-history events, has been shown to be especially sensitive to changes in climate. Changes in the timing of phenological events can have significant consequences for an organism's fitness, survival, and reproduction (Donohue, 2005; Willis *et al.*, 2008). As plants form the basis of all terrestrial ecosystems, phenological shifts have potentially cascading impacts on critical ecological and biogeochemical processes (Cleland *et al.*, 2007; Richardson *et al.*, 2009; Piao *et al.*, 2019). Recent studies have demonstrated that urbanization generally advances both the vegetative (Meng *et al.*, 2020; Qiu *et al.*, 2020) and reproductive phenology of plants (reviewed in Neil & Wu, 2006; Jochner & Menzel, 2015). However, plant phenological responses to climate may vary substantially across species' ranges (Park *et al.*, 2019), and broad investigations of *in situ* and remotely sensed phenology observations have demonstrated that the effects of urbanization on plant phenology can differ across temperature regimes as well (Li *et al.*, 2019; Wohlfahrt *et al.*, 2019). Specifically, advanced plant flowering and leaf

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out, and delayed leaf senescence were associated with higher human population density in colder areas, but these effects were reversed in warmer areas (Li *et al.*, 2019, 2021). Interestingly, studies examining the effect of temperature on plant phenology have often found the opposite pattern – increases in temperature generally advanced phenology to greater degrees in warmer areas (Menzel *et al.*, 2006; Sherry *et al.*, 2007; Wolkovich *et al.*, 2012; Love & Mazer, 2021; Xie *et al.*, 2022). This suggests that urbanization-driven plant phenological shifts are not simply because of local increases in temperature (i.e. the urban heat-island effect) and may be the result of more complex interactions with the environment.

Previous studies examining the effect of urbanization on plant phenology have largely focused only on temperature. However, it has been suggested that phenological sensitivity to urban warming across space does not provide a good analog of phenological sensitivity to warming over time (i.e. global warming; Wohlfahrt *et al.*, 2019). These results suggest the existence of other factors associated with urbanization that may influence phenology, including light pollution (Neil & Wu, 2006), soil modification (Herrmann *et al.*, 2018), biotic interactions (Harrison & Winfree, 2015), and precipitation (Qiu *et al.*, 2020). Precipitation, in particular, has been shown to affect phenological timing, yet has not been broadly explored in the context of urbanization despite the existence of large impervious surfaces in urban environments that may greatly alter hydrology (Rathcke & Lacey, 1985; Pavón & Briones, 2001; Peñuelas *et al.*, 2004; Zipper *et al.*, 2017; Li *et al.*, 2021). Water stress may delay plant phenology, especially under warmer or more arid conditions (Adams *et al.*, 2015). Furthermore, few studies address the potential consequences of urbanization-driven phenological change for species fitness or for ecological processes (Diamond *et al.*, 2014; Gim *et al.*, 2018). In particular, it has been posited that though global warming has generally advanced both final frost dates in spring (i.e. last day of frost) and flowering times, the net result may be an overall decrease in frost risk (Park *et al.*, 2021). This implies that frost and flowering respond differently to changes in climate, and thus they may respond differently to urbanization as well. Indeed, it has been suggested from a case study of two shrub species that urbanization may reduce the risk of frost damage to spring flowers (Gim *et al.*, 2018). However, this hypothesis has not been tested on a wide scale, across diverse taxa and climatic conditions.

Here, we explicitly examine how urbanization influences the reproductive timing of a phylogenetically diverse group of angiosperm species across gradients of temperature and precipitation across the eastern US. We collected a large historical (1895–2018) phenological dataset by crowdsourcing over 70 000 digitized herbarium specimens collected across 120 yr and 20 degrees of latitude, spanning a period of rapid urbanization across the most populous regions of the United States (U.S. Census Bureau, 2020). Herbarium specimens comprise information on phenological events across great spatial, temporal, and taxonomic breadth (Davis *et al.*, 2015). Previous studies mainly assessed the effects of urbanization on plant phenology across spatial gradients (i.e. rural to urban gradients) because of the general lack of long-term phenology observations (Zhang *et al.*, 2004; Li *et al.*, 2019;

Meng *et al.*, 2020). Phenological sensitivity to climate has also been demonstrated to vary within species across their ranges, potentially complicating such inferences (Renner & Zohner, 2018; Park *et al.*, 2019). The use of herbarium records has the advantage of allowing us to pair multiple phenological observations from the same general area with corresponding changes in urbanization as determined by human population density. In other words, specimens can allow us to examine the effects of urbanization across both space and time simultaneously. Indeed, herbarium specimens have been successfully used to uncover variation in plant phenological responses to climate across wide spatial scales (Park *et al.*, 2019, 2022) and to study the effects of urbanization, albeit at much smaller spatial and taxonomic scales (Primack *et al.*, 2004; Lavoie & Lachance, 2006; Neil *et al.*, 2010). Such efforts have been greatly facilitated by increasing digitization and mobilization of natural history collections (Hedrick *et al.*, 2020) and are examples of how the herbarium of the future and the ‘global metaherbarium’ are facilitating expansive and novel science (Davis, 2022).

Using these data, we test the hypothesis that the direction and magnitude of urbanization effects on flowering and fruiting phenology vary across species ranges because of the interaction between urbanization and local temperature and precipitation levels. In colder, wetter conditions, the heat generated by urbanization may advance reproductive phenology, whereas in warmer, drier conditions, urbanization may delay phenology by increasing water stress and the time it takes to meet vernalization requirements. We also assess how climate-mediated effects of urbanization may alter frost risk to flowers.

Materials and Methods

Phenology data

We gathered data on the phenology of species using digitized herbarium specimen images from two comprehensively digitized regional floras: the Consortium of Northeastern Herbaria (CNH; <http://portal.neherbaria.org/portal/>) and Southeast Regional Network of Expertise and Collections (SERNEC; <http://sernecportal.org/portal/index.php>). Species that: included at least county-level location data; comprised at least 50 unique collections across space and time; and had relatively easily identifiable and quantifiable reproductive structures were selected for crowdsourcing (Supporting Information Table S1). Further details on sampling filters are in Park *et al.* (2019). Community-scientists hired through Amazon’s Mechanical Turk service (MTURK; <https://www.mturk.com/>) counted the number of buds, flowers, and fruits to assess phenological status. Each specimen was examined by three different people on average. These anonymous crowdworkers were compensated at an average rate of \$0.12 per image. See Park *et al.* (2019) and Willis *et al.* (2017) for detailed crowdsourcing methods.

To estimate measurement error, each 10-image set scored by a single crowdworker included nine unique images and a single duplicate image randomly selected from the other nine (Williams *et al.*, 2017). We calculated a reliability score for each participant

based on the data for each 10-image set by dividing the absolute difference in organ counts by the total count of that specimen across the two duplicate specimens and subtracting this value from 1 ($1 - (|count1 - count2| / (count1 + count2))$) (Park *et al.*, 2019). Reliability scores range from 0 (unreliable/inconsistent) to 1 (reliable/consistent). Participants who reported no organs on one sheet and a non-zero number of the same organ on the duplicate sheet were assigned a reliability score of 0 for that organ. We calculated a weighted average of the number of buds, flowers, and fruits on each specimen across the three crowdworker observations, using these reliability scores as weights with the 'weighted.mean' function in R 3.6 (R Core Team, 2020), and rounded them to integers. Specimens were then designated to be in flower or fruit if the rounded weighted average counts for flowers/fruits was at least 1 for the corresponding organs. Specimens were designated as being in peak flower if open flowers represented $\geq 50\%$ of the total reproductive structure count, and in peak fruiting if fruits represented $> 50\%$ of the total reproductive structure count. Our final dataset comprised 200 plant species across 71 278 herbarium specimens in 780 counties in the eastern US (Fig. 1a; Table S1).

Climate, frost risk, and population density data

We used historical climate data from 1895 to 2018 from PRISM (PRISM Climate Group, 2019), including monthly mean

temperatures and total precipitation. Total precipitation can comprise both snowfall and rainfall. We calculated spring mean temperature and total precipitation, and winter mean temperature over 124 yr (1895–2018) for each county in this study. Spring was defined as the time period during March, April, and May, and winter was defined as the time period during December in the preceding year, January, and February following common practices for phenological studies in the region (Primack *et al.*, 2015; Park *et al.*, 2019, 2022). To account for both spatial and temporal variation in climate, we calculated: the 124 yr long-term mean temperature and precipitation conditions in each county; and the 'anomalies' in temperature and precipitation – the deviation between long-term climatic conditions and those of the year of collection for each county. Previous studies have suggested that climate anomalies allow the quantification of inter-annual variation in precipitation and temperature independent of the spatial variation in climate across species ranges (Kharouba & Vellend, 2015; Munson & Long, 2017). The biological effects of precipitation anomalies of equal magnitude may vary among sites, as local precipitation conditions can vary greatly across species' ranges. Thus, precipitation anomalies were calculated as the proportional value to the long-term mean to standardize the precipitation effects across sites following Pearson *et al.* (2021). As precise locality data were not available for the majority of historic specimen records (Park & Davis, 2017), we used county as our geographic unit of analysis. For each county and year, we

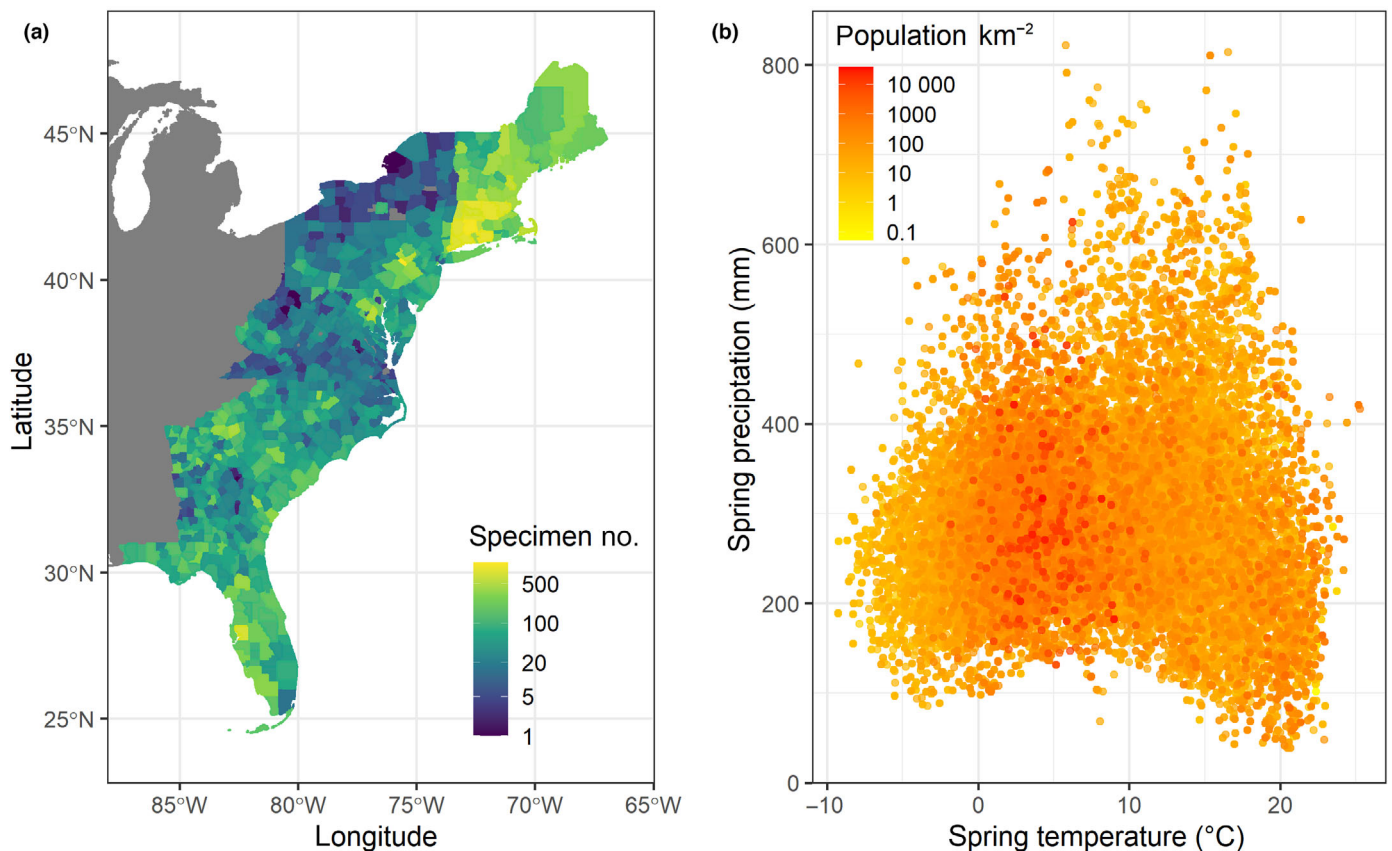


Fig. 1 Distributions of herbarium specimens of the 200 species used in this study. Specimens were collected from across 780 counties in the eastern United States (a). Associated distributions of spring temperature and precipitation with human population density from 1895 to 2018 (b).

estimated the mean of each climatic variable, and assigned these values to each specimen. Though counties can vary in size and climate: counties in states along the east coast of the United States are generally small in size and geographically homogeneous; mean county climate has been demonstrated to be closer to the climate of the true location than the climate of geographic centroids (Park & Davis, 2017); and within-county variation in climate did not significantly affect estimations of phenological response in this area in previous studies (Park *et al.*, 2019).

We estimated frost risk to flowers using the number of days between the last frost date and the flowering date (Ge *et al.*, 2013). Specifically, frost risk was quantified by subtracting observed flowering dates from the last frost date for each species at a given county and year. The last frost date was defined as the day before the beginning of the frost-free period (i.e. bFFP) from CLIMATEANA, an application that downscales PRISM (Daly *et al.*, 2008) 1901–2020 gridded climate data (800 × 800 m) to scale-free point locations across North America (Wang *et al.*, 2016). The beginning date of the FFP for each specimen collection site in each year from 1901 to 2018 was also obtained from the CLIMATEANA (Wang *et al.*, 2016). Although frost tolerance can vary among plant species, the last frost dates defined by different temperature thresholds (i.e. 0°C to −4°C) are highly correlated with each other ($0.66 \leq r \leq 0.94$), and thus the rates at which frost risk varies should be similar regardless of species' different temperature thresholds (Park *et al.*, 2021).

The human population density of each county through time was used as a proxy for urbanization in this study, as it is: highly correlated with the degree of urbanization (Bagan & Yamagata, 2015); often used to represent the degree of urbanization or rural–urban gradients (McDonnell & Hahs, 2008; Balk *et al.*, 2018); and frequently used in this manner in studies of urbanization effects on phenology (Li *et al.*, 2019, 2021, 2022; Bonnet-Lebrun *et al.*, 2020). We calculated population density based on population size and county area collected in the decadal census data from the U.S. Census Bureau (2020). These data were associated with specimens from each decade based on their year of collection.

Statistical analyses

We used linear mixed-effect models to examine the effect of urbanization on plant reproductive phenology as estimated from herbarium specimens across species and locations. The general format of the models was:

$$Y_{ij} = X_{ij}\beta_k + Z_{ij}\gamma_m + \varepsilon_{ij}$$

where Y_{ij} represents the response variable of the i^{th} subject for the j^{th} group; $X_{ij}\beta_k$ is the fixed component in the model, for which X_{ij} is the design matrix of the fixed variables for the i^{th} subject for the j^{th} group and β_k corresponds to the vector of parameters associated with the fixed variables; $Z_{ij}\gamma_m$ is the random component in the model, for which Z_{ij} is a design matrix that represents the known values of the i^{th} subject for the j^{th} group and that has effects on the continuous response variable that vary randomly

across different groups, and γ_m represents the random coefficients associated with Z_{ij} ; and ε_{ij} represents the random errors to take account of the unexplained variation of the i^{th} subject for the j^{th} group in the response variable Y_{ij} . Both γ_m and ε_{ij} are assumed to be independent and normally distributed (Zuur *et al.*, 2009; Grevén & Kneib, 2010; West *et al.*, 2015).

Four phenophases (i.e. flowering, fruiting, peak flowering, and peak fruiting dates) across 200 species were fitted separately as response variables in the models. We fitted two models (i.e. urbanization and non-urbanization models) for each phenophase. Both models included long-term average climate and the anomaly variables as fixed effects in each model. Climatic variables included long-term averages and inter-annual anomalies of mean spring temperature, mean winter temperature, and total spring precipitation, and an interaction between temperature and precipitation anomalies selected by preliminary modeling. Urbanization models included population density as an additional fixed effect. This allowed us to compare model estimations and identify differences associated with the effect of population density. Interactions between climatic variables and population density were included in the urbanization models. In both models, we included two random intercept terms to incorporate the random effects of variation in phenology among species and counties in this study. Random slopes of temperature anomalies for each species were estimated in each model to account for species-specific phenological sensitivities to inter-annual climatic changes. Population density was natural-log transformed, and all explanatory variables including natural-log transformed population density were centered and scaled to a mean value of 0 and a standard deviation of 1. Correlation coefficients among all selected explanatory variables were lower than 0.5, which minimized the effect of multicollinearity and overfitting (Dormann *et al.*, 2013).

To examine how urbanization could affect frost risk to flowers, we fitted a separate model to predict the frost risk of flowering. We applied a linear mixed-effect model with the same random structure as mentioned earlier, but for the 133 species that had at least one flowering specimen with frost risk > 0. The frost risk to flowers for the 133 species across counties in 1901–2018 was the response variable in the model. The fixed component included long-term average climate, climate anomalies, human population density, and interactions between climatic variables and population density, the same as used for the flowering model described earlier. We randomly subset the data for model training and validation – 90% of data of each species were randomly selected for model training and the remaining 10% of data were used for model validation.

We used a top-down strategy (Diggle, 2002; Zuur *et al.*, 2009; West *et al.*, 2015) to build all models and selected the best models with optimal fixed structures following three steps. First, we started by fitting a model where the fixed component contained as many explanatory variables as possible to make sure the response variable is well explained (i.e. a beyond optimal or loaded model). Second, we selected an optimal structure for fixed effects in the model, as we used the same random structure in all models. We used the Akaike information criterion (AIC;

Akaike, 1998) as the selection criterion; smaller AIC values indicate better model fits. We tested the covariance of the fixed components to select appropriate fixed variables. Maximum likelihood (ML) estimation was used to estimate the coefficients of fixed components. Finally, we reported the best model using restricted ML estimation. Data were analyzed using R software 3.6 (R Core Team, 2020) with R packages LME4 (Bates *et al.*, 2015) and LMERTEST (Kuznetsova *et al.*, 2017).

To further investigate the species-specific change in frost risk driven by change in population density under different environmental conditions across counties, we predicted the frost risk to flowers for the species with potential frost risk based on the 30 yr normal (1981–2010) mean spring temperature and spring precipitation, and the averaged climate anomalies in each county. In the predictions, population density in each county increased from 1 to 24 000 km⁻², so the predicted frost risk was only driven by increased population density. From the model predictions of frost risk of flowering, we calculated the change in frost risk along with increased human population density in each county, representing the net effect from urbanization on frost risk.

Results

Phenological responses to climate

Both long-term averages and anomalies of spring mean temperature and total precipitation were consistently identified as significant effects on plant flowering and fruiting dates in all models. The best models overall for predicting plant reproductive phenology included long-term average climate and anomalies of spring mean temperature and total precipitation, and an interaction between winter mean temperature anomaly and spring precipitation anomaly as fixed effects. Higher spring and winter temperatures, and lower spring precipitation advanced flowering and fruiting times (Table 1; Fig. 2).

In the models, long-term average climate explained the geographic variation in phenology, while climate anomalies explained the inter-annual variation in phenology. In the urbanization models, an increase of 1 standard deviation in long-term average of spring mean temperature (i.e. 7°C) advanced flowering by 14.8 ± 0.4 d and fruiting by 14.1 ± 0.5 d across all species (Table 1). An increase of 1 standard deviation in long-term average of spring precipitation (i.e. 39 mm) delayed flowering by 0.9 ± 0.3 d on average (Table 1). An increase of 1 standard deviation in spring mean temperature anomaly (i.e. 2°C) advanced flowering by 1.3 ± 0.2 d and fruiting by 1.6 ± 0.3 d across all species (Table 1). An increase of 1 standard deviation in spring precipitation anomaly (i.e. 30% of the long-term average) delayed flowering by 0.5 ± 0.1 d and fruiting by 0.7 ± 0.2 d on average (Table 1). Our models also indicated a negative interaction between spring precipitation and winter temperature anomalies for flowering and fruiting phenology. Increased spring precipitation was associated with advancement in flowering during warmer winters, but delayed flowering during colder winters. Models for peak flowering and fruiting phenology demonstrated similar patterns (Table S2).

Table 1 Coefficient values of variables in the best non-urbanization and urbanization models for flowering and fruiting dates.

Variable name	Non-urbanization Coefficient (±SE)	Urbanization Coefficient (±SE)
Flowering date		
LT_tm_sp	-15.4 ± 0.4***	-14.8 ± 0.4***
LT_ppt_sp	1.5 ± 0.3***	0.9 ± 0.3*
Tm_sp_anm	-1.3 ± 0.2***	-1.3 ± 0.2***
ppt_sp_anm	0.4 ± 0.1**	0.5 ± 0.1**
Tm_wn_anm:ppt_sp_anm	-0.8 ± 0.2***	-0.9 ± 0.2***
Pop_den:LT_tm_sp	N/T	1.6 ± 0.3***
Pop_den:LT_ppt_sp	N/T	-1.6 ± 0.3***
Fruiting date		
LT_tm_sp	-14.1 ± 0.5***	-14.1 ± 0.5***
LT_ppt_sp	1.4 ± 0.4***	N/I
Tm_sp_anm	-1.5 ± 0.3***	-1.6 ± 0.3***
ppt_sp_anm	0.7 ± 0.2**	0.7 ± 0.2**
Tm_wn_anm:ppt_sp_anm	-1.0 ± 0.2***	-1.0 ± 0.2***
Pop_den	N/T	1.2 ± 0.3***
Pop_den:LT_ppt_sp	N/T	-1.7 ± 0.3***

Values indicate changes in flowering/fruiting in days when each variable changed by 1 SD. LT_ppt_sp, long-term average of spring precipitation; LT_tm_sp, long-term average of spring temperature; N/I, not included in models; N/T, not tested; pop_den, human population density; ppt_sp_anm, spring precipitation proportional anomaly; Tm_sp_anm, spring temperature anomaly; Tm_wn_anm, winter temperature anomaly. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Random slopes in all best models suggested that phenological sensitivities of flowering and fruiting to inter-annual variation in spring and winter temperatures are species specific. The species-specific responses of flowering and fruiting dates to spring temperature anomalies were linearly related to species-specific intercepts in all models (e.g. in urbanization models, flowering: $r = 0.47$, $P < 0.001$; fruiting: $r = 0.49$, $P < 0.001$; Fig. 3 top row), suggesting species that flower or fruit earlier tend to advance their phenology to greater degrees in response to higher spring temperatures than species that did so later in the year. However, phenological sensitivities to winter temperature anomalies did not differ significantly among early and late flowering species in terms of flowering time ($r = -0.07$, $P = 0.36$, urbanization model), nor fruiting time ($r = -0.0003$, $P = 0.99$, urbanization model; Fig. 3 bottom row). In addition, the degree of variation in phenological responses to the inter-annual changes in climatic conditions was similar across all phenophases (Table S3).

Urbanization and plant reproductive phenology

The inclusion of population density improved model fit (i.e. the best urbanization models had lower AIC values than non-urbanization models; Table S4). The best urbanization models suggested that both flowering and fruiting phenology were mainly affected by population density via interactions with long-term average climatic factors (Fig. 4). Flowering phenology advanced with increasing population density under colder and wetter spring conditions (Fig. 4a,b). Fruiting also tended to advance with increasing population density in wetter spring

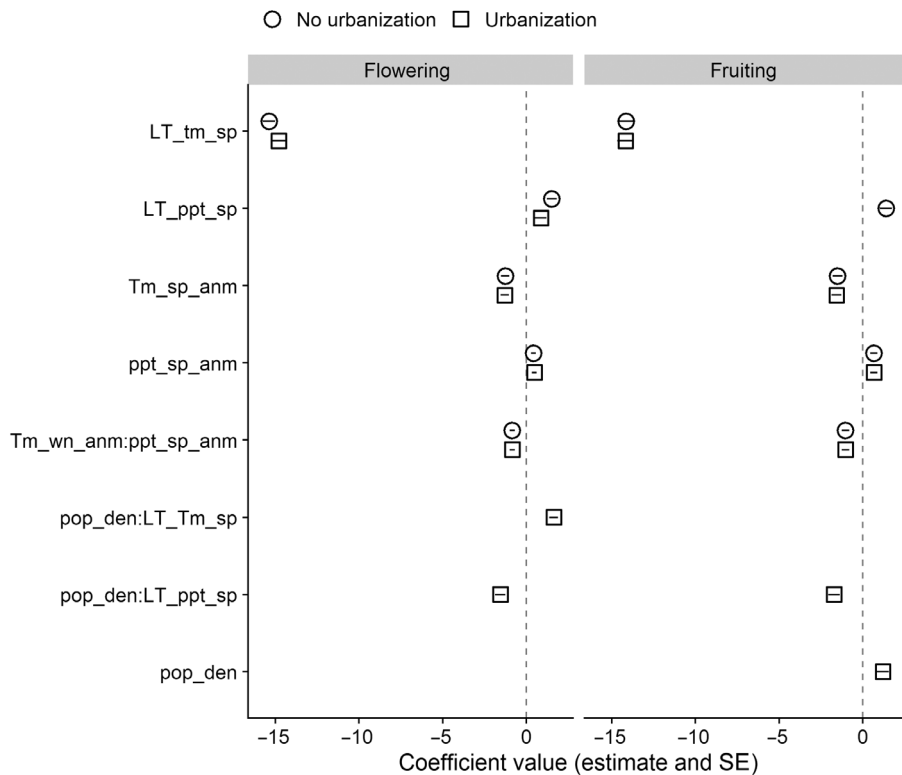


Fig. 2 Coefficients of all significant fixed effects variables in two models (circle: non-urbanization model; square: urbanization model) for two phenophases (i.e. flowering and fruiting dates). Symbols indicate coefficient estimate values, and lines represent SE of coefficients. LT_ppt_sp, long-term average of spring precipitation; LT_tm_sp, long-term average of spring temperature; pop_den, population density; ppt_sp_anm, spring precipitation proportional anomaly; Tm_sp_anm, spring temperature anomaly; Tm_wn_anm, winter temperature anomaly.

climates (Fig. 4c). However, population density tended to delay flowering and fruiting in warmer, drier spring climates. Specifically, increased population density advanced the flowering date when long-term mean spring temperature was lower than *c.* 7.4°C, whereas it delayed flowering date when long-term average winter temperature was higher than 7.4°C. Increased population density advanced the flowering date when long-term average spring precipitation was lower than *c.* 295 mm, whereas it delayed the flowering date when long-term average spring precipitation was higher than 295 mm. Fruiting showed similar responses to human population density mediated by long-term average spring precipitation. Overall, increased population density advanced the fruiting dates when long-term average spring precipitation was lower than *c.* 293 mm, whereas it delayed the fruiting date when long-term average spring precipitation was higher than 293 mm (Fig. 4c). Similar effects from interactions between population density and climatic factors were found for both peak flower and peak fruit dates (Fig. S1).

Urbanization and frost risk

There were 133 species that had at least one flowering specimen collected before the last frost date in a given county and year, and thus were likely to experience frost during their flowering period. The frost risk model for these species included the same explanatory variables as the urbanization model of flowering dates for all 200 species (Table 2), and have relatively good performance in predictions out of sample (Fig. S2). The interaction terms in the model indicated that both long-term average of spring mean temperature and spring total precipitation mediated the effect of human population density on frost risk. We found that frost risk

decreased with increasing population density in areas with warm and dry spring conditions, while frost risk increased in areas with cold and wet spring conditions (Fig. 5). Geographically, population density generally had a positive effect on frost risk in regions across the western and northeastern edges of the eastern US, and a negative effect in the southeastern US (Fig. 6).

Discussion

Shifts in plant reproductive phenology are one of the clearest indicators of the effects of climatic change. Temperature influences flowering phenology in many plants (Rathcke & Lacey, 1985) and warming has often been associated with earlier flowering (Menzel *et al.*, 2006; Cleland *et al.*, 2007; Körner & Basler, 2010; Dunnell & Travers, 2011). Similar phenomena have been observed for plants growing in or near urban areas as a result of the urban heat-island effect, and it has been suggested that rural-to-urban gradients may serve as a space-for-time substitute for forecasting the phenological effects of climate change (Roetzer *et al.*, 2000; White *et al.*, 2002). However, our results demonstrate that effects of urbanization and climate are more complex and context dependent and do not necessarily coincide in obvious or consistent ways. Thus, our results suggest that models for exploring phenological response to urbanization that focus solely on its interaction with temperature are likely overly simplistic.

Urbanization advances plant reproductive phenology in colder regions

Human population density did not have a uniform effect on plant reproductive phenology. Rather, phenological responses to

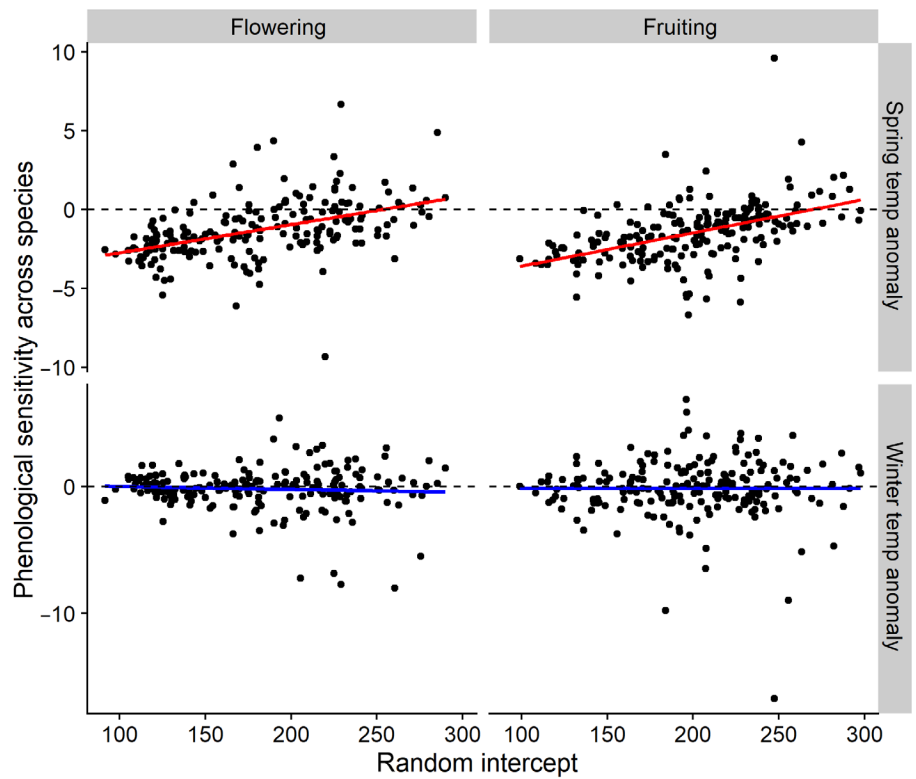


Fig. 3 Phenological sensitivities to spring and winter mean temperature anomalies along the random intercepts among species (i.e. a measure of relative phenology) estimated by urbanization models for flowering (left column) and fruiting (right column) dates. Phenological sensitivity is represented by the shifts in flowering and fruiting time per 1 SD change in temperature anomalies. Each dot represents one species. Colored solid lines are fitted linear regression lines. Red lines represent statistically significant linear relationships ($P < 0.05$). Blue lines represent non-significant correlations ($P > 0.05$).

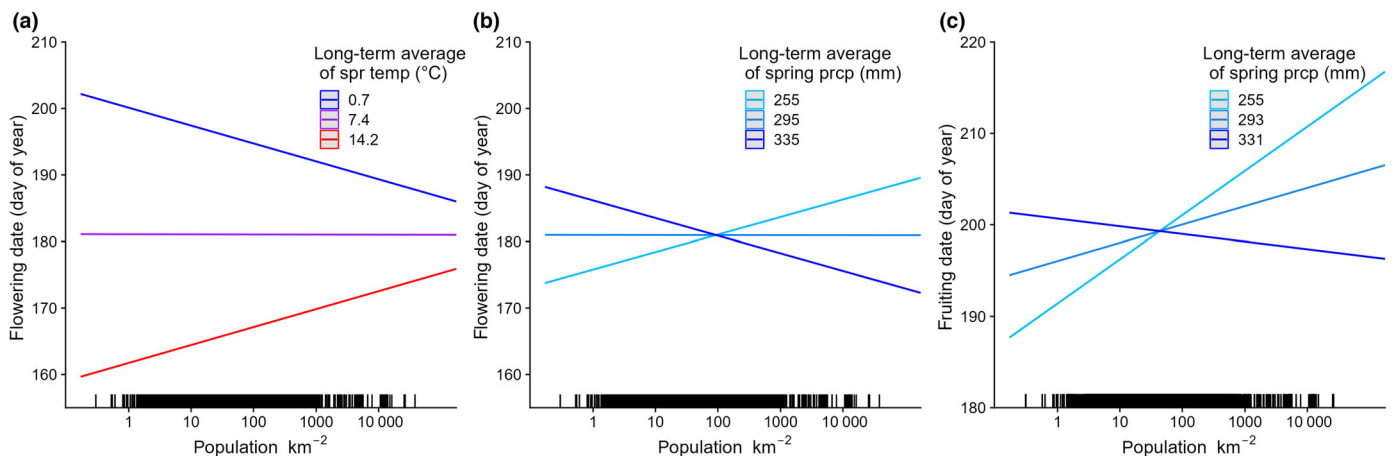


Fig. 4 Effect plots of interactions between population density and long-term average climate on flowering and fruiting dates. Flowering date: (a) long-term average spring mean temperature, (b) long-term average spring total precipitation; fruiting date: (c) long-term average spring mean temperature. Three levels of temperature and precipitation were used to represent three scenarios (i.e. cold, average, warm for temperature, and dry, average and wet for precipitation) based on the mean and SD values of the climatic factors used. Data density plots on the x-axis represent the distribution of observed population density values.

population density varied in direction and magnitude depending on temperature. With increased population density, both flowering and fruiting phenology tended to: advance in areas with low spring temperatures (e.g. New Hampshire); and be delayed in areas with higher spring temperatures (e.g. Florida). This result is consistent with previous studies that examined the influence of the urban heat-island effect on plant spring phenology (Meng *et al.*, 2020; Li *et al.*, 2021). The urban heat-island effect may facilitate the necessary thermal accumulation for initiating earlier

plant growth and reproduction in cold regions, but may simultaneously reduce the chilling accumulation required for plants to break dormancy in warm regions (Chen *et al.*, 2017; Martínez-Lüscher *et al.*, 2017; Vitasse *et al.*, 2018) and increase drought stress, thus delaying flowering and fruiting.

Despite the focus on spring temperature in studies of temperate (and especially eastern US) plant phenology, our results suggest that the effects of human population density on flowering and fruiting phenology may also be mediated by winter

Table 2 Scaled coefficient values with SE of variables in the best models for the frost risk of flowering (last frost date – flowering date).

Variable name	Coefficient (\pm SE)
LT_tm_sp	$-13.0 \pm 0.3^{***}$
LT_ppt_sp	$2.9 \pm 0.3^{***}$
Tm_sp_anm	$0.6 \pm 0.2^*$
Tm_wn_anm:ppt_sp_anm	$0.5 \pm 0.2^*$
Pop_den:LT_tm_sp	$-0.6 \pm 0.2^{**}$
Pop_den:LT_ppt_sp	$1.2 \pm 0.3^{***}$

LT_ppt_sp, long-term average of spring precipitation; LT_tm_sp, long-term average of spring temperature; pop_den, population density; ppt_sp_anm, spring precipitation proportional anomaly; Tm_sp_anm, spring temperature anomaly; Tm_wn_anm, winter temperature anomaly. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

temperature. It is possible that this pattern could be attributed to chilling requirements for plants to break dormancy, grow, and reproduce. Critical chilling accumulation usually happens during the time period when daily temperature is between $c. -3^{\circ}\text{C}$ and 10°C , which tends to be during winter and early spring (NeSmith & Bridges, 1992; Chuine, 2000; Luedeling *et al.*, 2009; Rinne *et al.*, 2011). Thus, in warmer conditions, increased urbanization may result in extending the time necessary to fulfill these requirements, leading to delayed flowering and fruiting (Yu *et al.*, 2010; Chen *et al.*, 2017). It has also been suggested that urbanization affects plant phenology by raising minimum temperatures more than mean or maximum temperatures (Kalnay & Cai, 2003; Neil *et al.*, 2010; Argüeso *et al.*, 2014; Cai

et al., 2017), and this effect is likely to be more pronounced during winter months. As temperatures vary across the landscape, urbanization effects on plant reproductive phenology can vary spatially across environmental gradients within species' ranges as well. For instance, our models show that *Arisaema triphyllum* (L.) Schott (Jack-in-the-pulpit) and *Sisyrinchium atlanticum* E.P.Bicknell (Eastern Blue-eyed Grass) both advance their flowering to greater degrees in response to urbanization in the colder, northern parts of their ranges (Fig. S3).

The temperature-dependent urbanization effects on plant phenology we observed are consistent with prior studies (e.g. Li *et al.*, 2019). Both our results and others (e.g. Li *et al.*, 2019) suggest that urbanization advances plant phenology in colder regions where plants tend to be less phenologically sensitive to temperature (Menzel *et al.*, 2006; Sherry *et al.*, 2007; Wolkovich *et al.*, 2012; Park *et al.*, 2019; Love & Mazer, 2021; Xie *et al.*, 2022). This suggests that: urbanization-driven phenological shifts are not only a result of increases in temperature; and urbanization affects long-term temperature more so than it does the degree of inter-annual variation in temperature. In contrast to previous studies, our partitioning of the phenological effects of long-term and inter-annual climatic variation allowed us to identify significant interactions between urbanization and long-term temperature (and precipitation, as discussed later). Urbanization is often accompanied by long-lasting changes in the environment (e.g. construction of impervious surfaces), which can alter local climates. Furthermore, phenological responses to climate have been shown to evolve rapidly in some species (Franks & Weis, 2009), including invasive ones in new environments

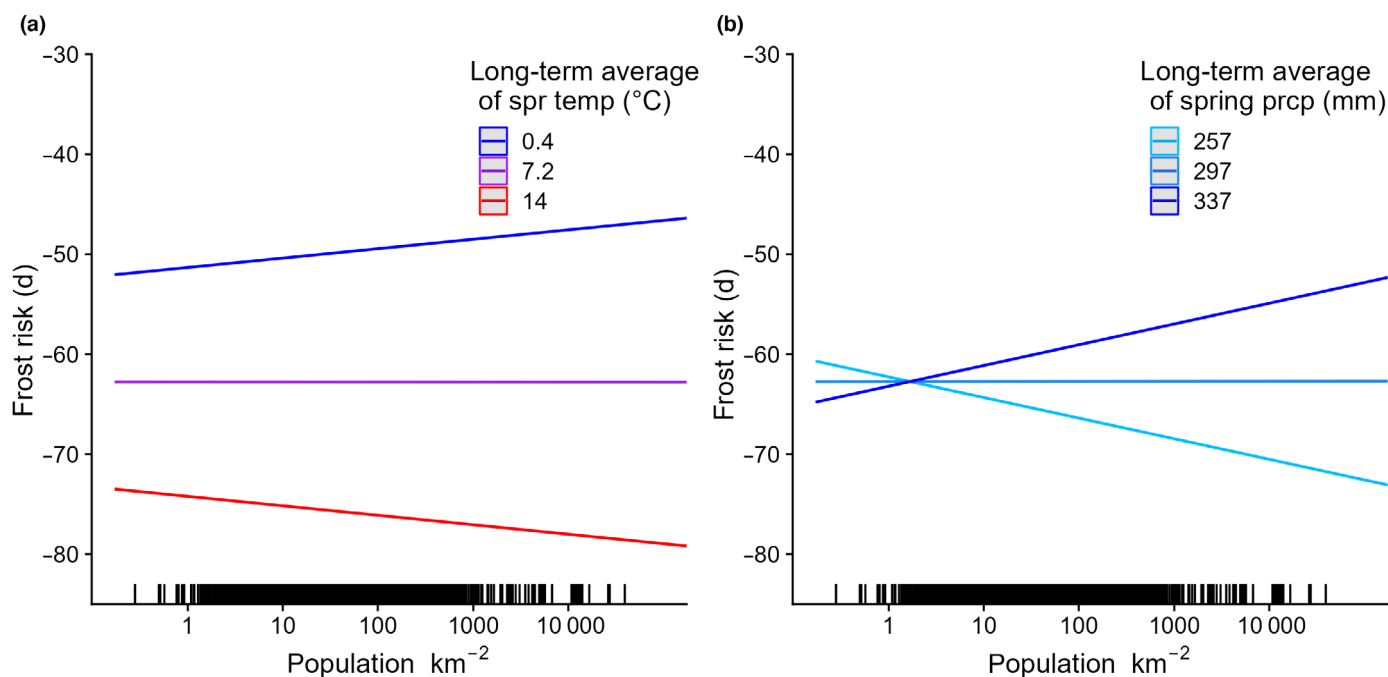


Fig. 5 Effect plots of interactions between population density and long-term average climate variables in the frost risk model: (a) long-term average spring mean temperature and (b) long-term average spring total precipitation. Three levels of temperature and precipitation are illustrated (i.e. cold, average, warm for temperature, and dry, average and wet for precipitation) based on the mean and SD values of the climatic factors used in the model. Data density plots on the x-axis represent the distribution of observed population density values.

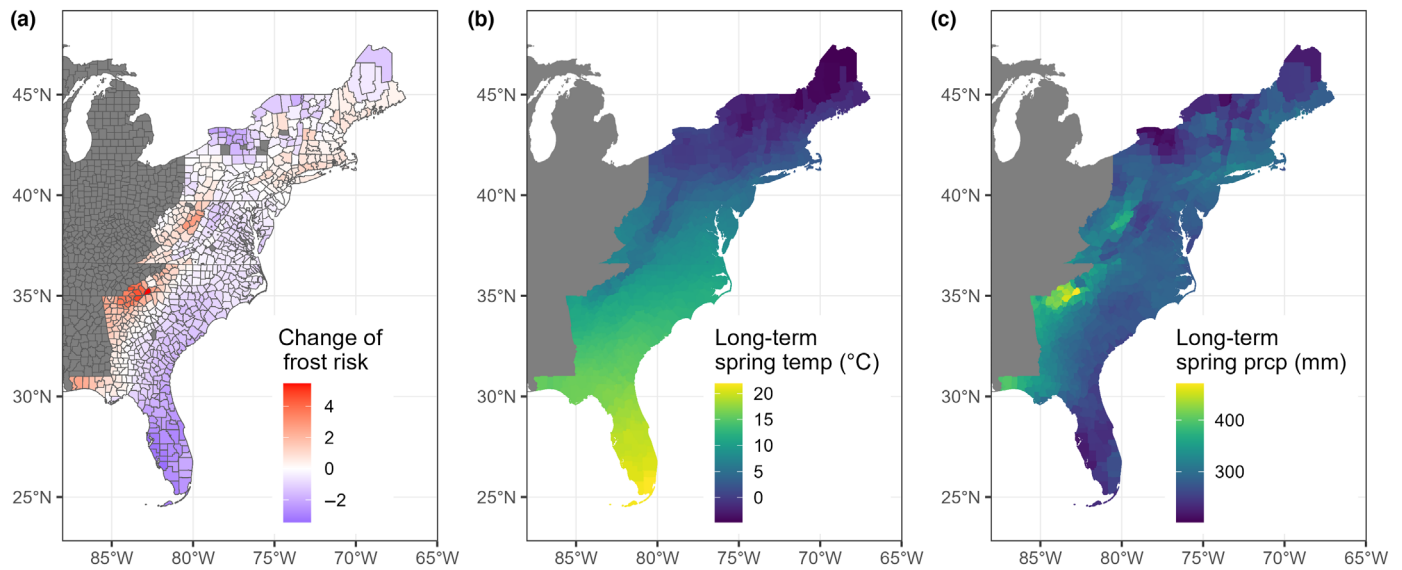


Fig. 6 Geographic distribution of population density effects on frost risk across 133 species in 764 counties. Estimates were based on 30-yr climate normal and anomalies from 1981 to 2010 for each county. (a) Predicted change in frost risk (unit is days per SD of log-transformed population density). Positive values (red) indicate that increases in population density increases frost risk, and negative values (blue) indicate that it decreases frost risk, (b) long-term mean spring temperature in each county, (c) long-term average of spring precipitation in each county.

(Colautti & Barrett, 2013). Thus, plant phenological responses to urbanization are likely mediated by adaptations to the local environment as represented by long-term climate averages and may be best assessed with data that can account for both spatial variation in phenological responses to climate, and temporal variation in urbanization.

Urbanization advances flowering phenology in wetter springs

To our knowledge, previous studies of the effect of urbanization on plant phenology have focused on the potential effects of temperature (i.e. the urban heat-island effect; Peñuelas *et al.*, 2004; Gim *et al.*, 2018; Li *et al.*, 2019; Meng *et al.*, 2020; Qiu *et al.*, 2020). However, our results suggest that precipitation also may mediate the effects of urbanization on plant reproductive phenology. Increased human population density was associated with advanced flowering phenology when spring precipitation levels were above average for the eastern US. By contrast, higher population density was associated with delayed flowering where springs were drier than average (Figs 2, S1; Tables 1, S2). Urbanization can reduce water availability by introducing impermeable surfaces, which increases surface run-off and reduces water infiltration into the ground (Li *et al.*, 2020). Furthermore, the heat island effect can increase evapotranspiration (Qiu *et al.*, 2017; Zipper *et al.*, 2017). Thus, in areas or years that receive less spring precipitation, plants may experience elevated levels of drought stress with increased urbanization, which may delay the development of flowers and fruits (Van Loon *et al.*, 2016; Lüttge & Buckeridge, 2020). On the other hand, increased precipitation could offset urbanization-induced drought stress and associated phenological delays, allowing plants to accelerate their development in response to the warmer

ambient temperatures that are also associated with increased urbanization (Moore & Lauenroth, 2017; Jin *et al.*, 2019; Pearson, 2019; Du *et al.*, 2020).

Increased precipitation generally had a positive (i.e. delaying) effect on flowering and fruiting phenology but its interaction with temperature (and population density) had a significant negative (i.e. advancing) effect on flowering and fruiting times. Though our results are congruent with recent studies that finding increased spring precipitation may delay flowering (Pearson, 2019; Du *et al.*, 2020), they also suggest that it can advance flowering phenology under warmer conditions (Fig. S4). As with the case of urbanization mentioned earlier, this may be because increased precipitation may mitigate the negative effects of drought stress associated with the occurrence of higher-than-average temperatures. Similar interactions between the effects of temperature and precipitation on plant phenology have been observed in case studies in the western US (Matthews & Mazer, 2016), semi-arid ecosystems (Lesica & Kittelson, 2010), prairies (Wolkovich *et al.*, 2013), and alpine meadows (Ganjurjav *et al.*, 2020). These findings suggest that multiple environmental factors and their interactions must be considered when estimating plant phenology, and that we must move beyond phenological models that only incorporate temperature variables, especially at larger spatial and taxonomic scales.

Urbanization can reduce or increase frost risk

Climate change has resulted in a general advancement of both the date of final frost and plant phenology in temperate regions (Schwartz & Reiter, 2000; Inouye, 2008; Beaubien & Hamann, 2011; Peterson & Abatzoglou, 2014; Ma *et al.*, 2019; Zohner, 2019; Park *et al.*, 2021). However, it has been suggested that the last frost date may advance more rapidly than plant

phenology (Zohner, 2019; Park *et al.*, 2021). We found that increased urbanization affects the frost risk to flowers to different degrees. Increased urbanization had a negative effect on frost risk in most areas of the eastern US. This result is consistent with a previous case study examining the effect of urbanization on frost risk of two shrub species (Gim *et al.*, 2018). However, our results demonstrate that urbanization also can increase frost risk under certain circumstances. Frost risk responds differently to increases in human population density across the landscape and can increase in colder and wetter areas (Fig. 6), likely due to the faster advancement of flowering date than the end of frost season. It is thus possible that increasing urbanization could result in increased frost damage to flowers in colder and wetter climates, reducing reproductive success, though it remains to be seen how the effects of urbanization may interact with those of global warming. Ecological impacts of changes in frost risk also could be mediated by additional factors, including variation in species' resistance to frost and microhabitat conditions. We note that frost risk in the context of our analyses is not the same as damage to buds, flowers, or fruits, and that focused field studies are needed to assess the extent of frost damage caused by urbanization-driven phenological shifts.

Conclusion

As our study examined phenological trends across large scales using specimens that were not collected for these purposes, the results may be affected by the gaps and biases known to occur in herbarium collections (Daru *et al.*, 2018). The species we sampled and their phenological responses are neither random nor fully representative of assemblages across regions. However, previous studies have shown that phenological trends derived from herbarium specimens are unlikely to be systematically biased and are compatible with direct observations from the field (Primack *et al.*, 2004; Davis *et al.*, 2015); such data have been used successfully to test hypotheses regarding phenological responses to climate and urbanization (Neil *et al.*, 2010; Park *et al.*, 2019). Finally, our analyses cannot determine the ultimate causes of these patterns, and further research into how urbanization modifies environmental cues that trigger phenological events is necessary. Nonetheless, our study represents one of the most comprehensive examinations of the effects of urbanization on plant phenology and expands our understanding of the complexity of the hypothesized impacts on phenology in urban systems. Specifically, we demonstrated that the likely effects of human population density (as a proxy for urbanization) on plant reproductive phenology and frost risk significantly depend on both temperature and precipitation. Moreover, our study demonstrates the extraordinary power of harnessing the phenological information embedded in tens of thousands of herbarium specimens collected well over a century, serving as yet another important application of the herbarium of the future and the 'global metaherbarium' (Davis, 2022). Though the specific physiological mechanisms underlying these patterns have yet to be elucidated, our study provides insight into the complex phenological impacts of urbanization and demonstrates that phenological predictions must take into account both climatic and human effects.

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Competing interests

None declared.

Author contributions

CCD proposed the initial idea for the study with subsequent development by DSP and AME; DSP, CCD, AME and YX designed the study; DSP and GML collected the data; YX, AME and DSP analyzed the data; DSP, AME, CCD and YX drafted the first version of the manuscript and all authors contributed significantly to subsequent revisions. DSP and YX contributed equally to this work.

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Data availability

All data, (links to) imagery, and model code are available from Zenodo (doi: [10.5281/zenodo.7714545](https://doi.org/10.5281/zenodo.7714545)) and GitHub (doi: [10.5281/zenodo.7717004](https://doi.org/10.5281/zenodo.7717004)).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Effect plot of interactions between population density and climatic factors for peak flower and peak fruit dates.

Fig. S2 Plot of observed frost risk of flowering and predicted frost risk by the frost risk model.

Fig. S3 Relationships between peak flower date and population density for two species (*Arisaema triphyllum* and *Sisyrinchium atlanticum*) in three regions (northeast, central-east, and south-east regions).

Fig. S4 Effect plot showing the interaction between mean winter temperature and spring precipitation and their effects on flowering date.

Table S1 Species used in this study with the information on growth habit, duration, native status, and number of observations for four phenophases.

Table S2 Scaled coefficient values with standard error of variables in the best non-urbanization and urbanization models for peak flower and peak fruit dates.

Table S3 Standard deviation of random intercepts at species and county levels, and random slopes of temperature anomalies at species level from the best urbanization models of four phenophases.

Table S4 Akaike information criterion values and their differences of the best non-urbanization and urbanization models of four phenophases.

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