URBANIZATION

Phenology and the city

Temperature differences between cities and the countryside have been regarded as useful surrogates for ecological responses to climate warming. However, research reveals mismatch between the phenological responses to spatial and temporal temperature gradients as well as complex interactions between urbanization and climate.

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How do urban environments affect the timing of leaf-out and flowering in plants, and can we use urban areas as a proxy for ecosystem responses to future climate warming? These questions are addressed in two independent contributions published in *Nature Ecology & Evolution*[1,2]. Using different approaches, Wohlfahrt et al.[1] and Li et al.[2] reveal that the effect of urbanization on plant phenology depends on the local climate and that spatial urbanization gradients cannot be used as a surrogate for temporal variation in plant phenology, suggesting that in addition to the urban heat island effect in which cities experience warmer temperatures than their surrounding countryside[3], unknown factors drive phenological differences between urban areas and the countryside.

The timing of phenological events, such as spring leaf-out and flowering, is a key indicator of the ecological impact of climate change[4]. Changes in plant phenology affect ecosystem functioning by altering plant productivity, species interactions and geographic distributions[5–7]. Ultimately, these changes exert strong feedbacks on the climate system[8]. Yet, the combined effects of increasing air temperature and other anthropogenic pressures — such as air and light pollution, habitat fragmentation and limited water supply — on plant phenology are understudied. As a result, how plant phenology will respond to anthropogenic climate change remains highly uncertain.

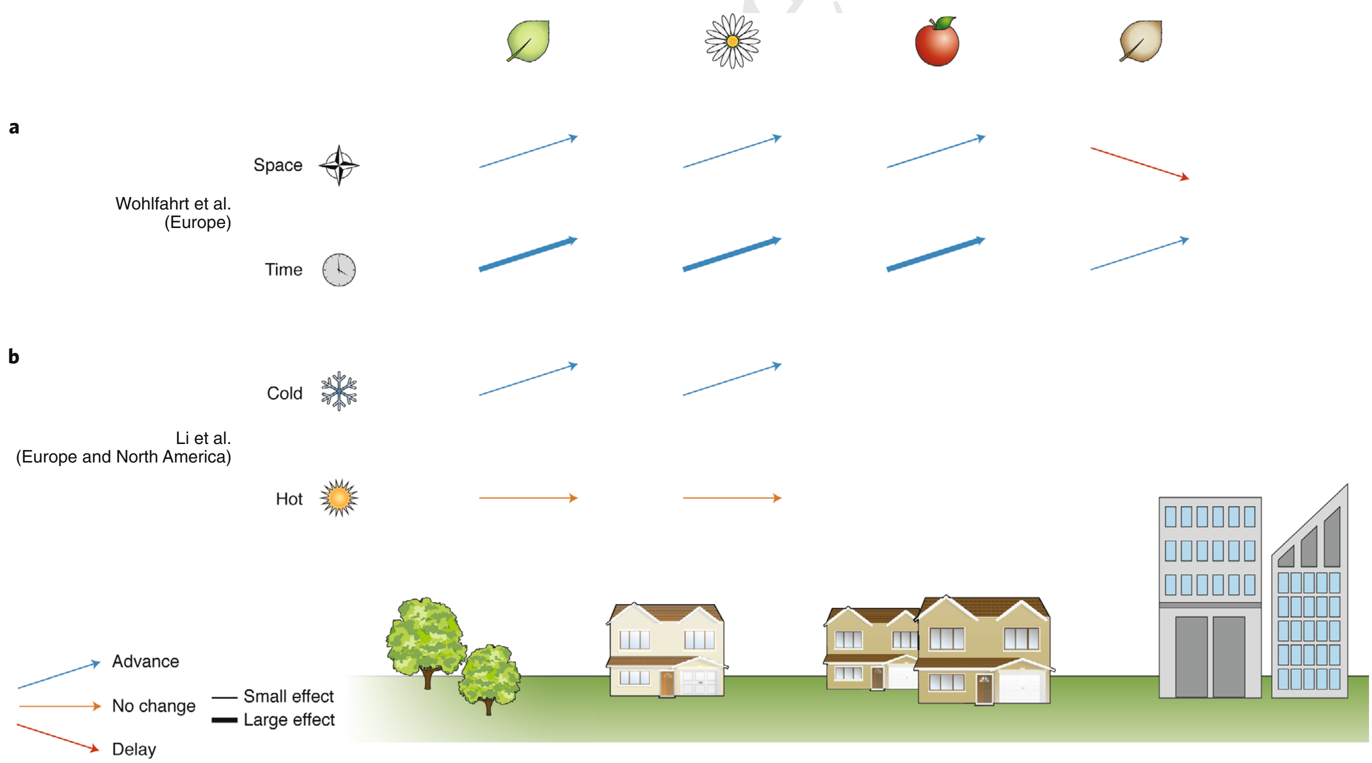

Fig. 1 | The effect of urbanization on plant phenology. a, Wohlfahrt et al.[1] compared the effect of temperature on the timing of spring leaf-out, flowering, fruiting and autumn leaf senescence based on urban and temporal gradients. For leaf-out, flowering and fruiting, the temperature effect created by urbanization was consistently smaller than the temperature effect observed over time; for leaf senescence, the effect reversed, with later senescence inferred from urban warming gradients and earlier senescence observed from temporal warming gradients. **b**, Li et al.[2] compared the effect of urbanization on the timing of spring leaf-out and flowering between warm and cold regions. Urbanization advanced phenology in cold regions but had no effect in warmer regions, revealing that complex interactions between temperature and urbanization govern the phenological responses to environmental change. Arrows pointing up indicate phenological advances, arrows pointing down indicate delays, straight arrows indicate no effect and arrow sizes indicate effect sizes.

Urban areas provide a powerful setting in which to study ecological responses to temperature, and because spatial data are often easier to collect than temporal data, 'space for time' substitutions are frequently used to assess the effects of climate change on ecosystems. However, this approach might not be useful where spatial and temporal variations in ecosystem functioning are driven by different mechanisms. To test this, Wohlfahrt et al.[1] explored whether phenological responses to temperature gradients between cities and the surrounding countryside — created by the urban heat island effect — can be used as proxies for temporal changes in plant phenology. The authors used about seven million observations on the timing of spring leaf-out, flowering and autumn senescence in European plants to create robust statistical models of plant sensitivity to urban and temporal warming. Their main finding is that spatial temperature gradients have a much smaller effect on plant phenology than do temporal temperature gradients (Fig. 1a), leading the authors to conclude that space-for-time substitutions are not suitable to study the effects of climate change on plant phenology.

Li et al.[2] further addressed the impact of urbanization on plant phenology by asking whether effects aside from urban warming contribute to the phenological differences between urban areas and the surrounding countryside. In contrast to Wohlfahrt et al., they disregarded temporal variation in phenology, instead testing for interactions between local temperature and urbanization status on leaf-out and flowering times based on more than 22 million individual observations from central Europe and North America. Their main finding is that the effect of urbanization on plant phenology depends on local temperature, with urbanization advancing phenology in cold regions, but lacking effect in warmer areas (Fig. 1b). An important aspect of their work is the attempt to isolate temperature effects associated with urbanization, which interestingly indicated that factors apart from the urban heat island effect contribute to the phenological differences between urban areas and the surrounding countryside.

These studies offer valuable insights into the mechanisms governing the seasonal activity of plants, and both harness the power of long-term citizen science datasets from central Europe and the United States that are openly accessible[9–11]. These data provide an outstanding documentation of the seasonal growth and reproductive development of common plants across large spatial and temporal gradients. However, both studies lack mechanistic explanations for their results. Wohlfahrt et al.[1] convincingly show discrepancies in the direction and magnitude of the temperature sensitivity of plants inferred from urban and temporal gradients. Yet, the factors driving this mismatch remain uncharacterized. They speculate that this is due to other confounding factors affecting plant phenology such as genetic variation, biotic interactions, soil modifications, and air and light pollution, but cannot yet say for sure. Similarly, by showing that the effect of urbanization increases towards colder areas, Li et al.[2] characterize an important, novel pattern, but cannot explain this. They hypothesize that the observed pattern is either due to differences in plants' temperature responses or caused by a declining urban heat island effect in warmer regions. Given these uncertainties, the mechanisms responsible for the observed correlations remain unknown, obscuring the causal links between the environmental factors associated with urbanization and plant phenology.

Nevertheless, in combination, both studies provide compelling evidence that factors apart from the urban heat island effect influence the timing of key ecological events, such as spring leaf unfolding and flowering, in cities. Indeed, Li and colleagues' results[2] might at least partly explain why urbanization gradients are a poor proxy for temporal warming trends. If factors apart from temperature drive phenological differences between urban areas and the countryside, this might well explain why responses to temperature increases under climate change cannot be extrapolated from urbanization gradients.

The two contributions open an important avenue of research on ecological changes in response to anthropogenic influences on the environment. Future studies that build on these findings should aim at disentangling the mechanisms that drive the changes in plant phenology in response to urbanization gradients. Ultimately, the new findings demonstrate that we are still far from a predictive understanding of the environmental determinants of plant phenology. However, innovative, resourceful studies such as these bring us closer towards that goal. ❐

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Competing interests

The author declares no competing interests.

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