Letter

The onset of phenological plant response to climate warming

Introduction

The industrial era, which began in the 18th century, led to an increase in greenhouse gases in the atmosphere which have driven anthropogenic climate warming. Paleoclimate records suggest that this warming began just before the mid-19th century (around the 1830s; Abram *et al.*, 2016) and has continued unabated to the present day. The key question that arises is, when did this warming become significant enough to start impacting organisms? Neglecting this question risks falling into the shifting baseline syndrome (Soga & Gaston, 2018), that is, the erroneous perception that recent anthropogenically warmed climates represent 'natural' baseline conditions.

There is ample evidence of the effects of climate change on plants and animals (Parmesan, 2006; Dijkstra *et al.*, 2011). However, it is not easy to pinpoint the starting point for these impacts, nor distinguish them from natural dynamics, nor from the impacts of other anthropogenic changes (such as land use, pollution, and invasive species). Sustained phenological shifts are among the clearest evidence of climatic change effects on organisms (Cleland *et al.*, 2007). Plant phenology (e.g. time of flowering, leaf unfolding, and leaf coloring) is usually strongly tied to temperature cues (Sparks & Carey, 1995; Allen *et al.*, 2014; Piao *et al.*, 2019) and so changes in phenology can reflect the timing of significant climate impacts. In addition, phenological changes in plants are likely to have cascading effects on interacting species (e.g. insects and birds), and so have an impact beyond the phenological change of the plants themselves (Renner & Zohner, 2018).

Most studies on plant phenological changes consistent with climate warming suggest changes during the second half of the 20th century (Menzel *et al.*, 2001; Walther *et al.*, 2002; Fu *et al.*, 2014; Renner & Zohner, 2018; Zeng *et al.*, 2025), despite global warming starting much earlier (Abram *et al.*, 2016). This is due to the lack of longer-term data, which is obscuring our understanding of the real overall effect of global warming. Old herbarium specimens for some specific species may provide long-term information on flowering (Calinger *et al.*, 2013; Speed *et al.*, 2022); however, old records are scarce and often represent disparate populations and habitats, complicating the establishment of robust long-term time series needed to accurately identify the onset of phenological shifts.

Here, we use long-term phenological data for the Japanese mountain cherry tree (*Prunus jamasakura*; Rosaceae) in Kyoto to identify the starting point of a consistent and sustained phenological change. The full-flowering date of this cherry tree has been recorded since the 9th century (Aono & Kazui, 2008; Aono & Saito, 2010), which makes it possible to distinguish phenological changes caused by anthropogenic climate change from natural variability in climate and phenology. Furthermore, the phenology of this species is known to be temperature-sensitive (Aono & Kazui, 2008); both warm and cool temperatures are believed to be important for flowering (Allen *et al.*, 2014). In addition, the peak flowering time in this species is relatively brief, lasting only 2–4 d (Primack *et al.*, 2009), making this species appropriate for depicting flowering changes.

Materials and Methods

Data

The day of the year (DOY) with peak cherry tree blossom in Kyoto, Japan, from 812 to 2024 (Aono & Kazui, 2008; Aono & Saito, 2010) was extracted from https://ourworldindata.org (Supporting Information Dataset S1). Monthly temperatures were obtained for the Kyoto Meteorological Station (ID 47759, World Meteorological Station) from the Japan Meteorological Agency (https://www.data.jma.go.jp). To validate the results, we also used three additional stations from smaller Japanese cities that have temperature data since the late 1800s (Table S1; Dataset S2).

Change-point analysis

We first tested the null hypothesis that the flowering day remained constant using the sequential F-test. Given that we rejected this hypothesis, we dated the breakpoint in the time series of the flowering day. We considered one-change-point analysis (single breakepoint) to depict the most important change, which is likely to be related to anthropogenic warming. We used three methods to date the breakpoint (Notes S1): (1) dating the structural change in the regression model, that is, computing the optimal breakpoint using the 'strucchange' library (Zeileis *et al.*, 2002, 2003); (2) fitting a piecewise linear model and computing the confidence interval by bootstrap using the 'SiZer' library (Sonderegger *et al.*, 2009); and (3) fitting regression models with segmented relationships using the 'segmented' library (Muggeo, 2003). Methods 2 and 3 are conceptually similar (based on regression analysis) but use different approaches for estimating the confidence interval; method 1 is based on testing deviation from stability. We then related the peak flowering time (DOY) with the monthly temperature previous to flowering for each year (for years after the breakpoint) using linear regression analysis. Given that some phenological processes are related not only to spring (our expectation) but also to autumn temperatures (Beil *et al.*, 2021), the effect of temperatures during each month on the flowering dates was tested separately to define

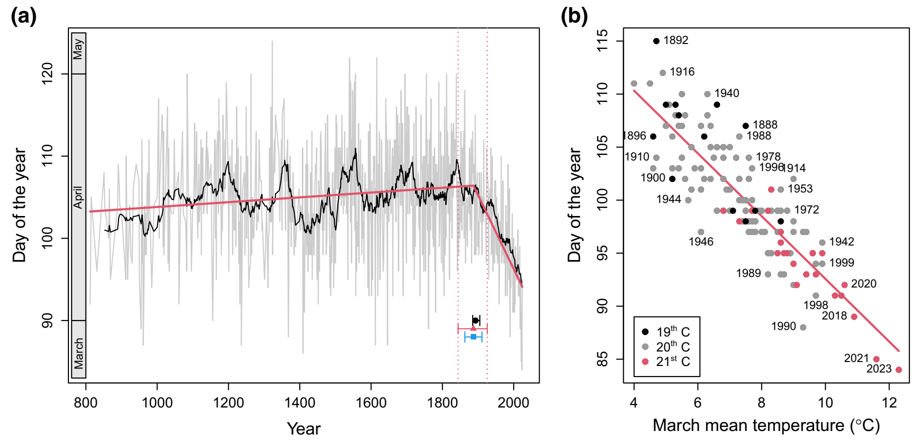

Fig. 1 Phenology changes for the Japanese cherry tree (*Prunus jamasakura*) in Kyoto. (a) Day of the year of the flowering peak for the period between 812 and 2024. The black line is the 20-yr moving average; the red line is the piecewise linear model (slopes: 0.00293 and −0.09268; P = 0.0002 and < 0.0001; R^2 = 0.015 and 0.417, respectively) with the confidence interval of the breakpoint indicated by vertical dotted lines. [Correction added on 20 June 2025, after first online publication: details of the moving average in the preceding sentence have been updated.] Horizontal segments between the dotted lines indicate the confidence interval of the three methods used to detect the breakpoint (black (top), structural change; red (middle), piecewise model; blue (bottom), segmented model). (b) Relation between March mean air temperature (°C) in Kyoto and the day of the year of the Japanese cherry tree peak flowering for the period between 1890 and 2024 (i.e. after the breakpoint). The red line is the linear fit (y = 121.84–2.93x; P < 0.00001; R^2 = 0.75); the color of the symbols relates to the century (19th, 20th, 21st, in black, gray, and red, respectively); some of the years are indicated as reference.

the most influential period; we considered the months from April of the flowering year to April of the previous year.

The climate-flowering analysis was first performed for the Kyoto Meteorological Station and then repeated for additional smaller cities where the urban heat effect was likely much smaller (Table S1). All analyses were performed using the R software (R Core Team, 2024).

Results and Discussion: 134 years of climate warming response

The peak of flowering in the cherry tree was not constant during the period 814–2024 (sequential F-test; sup.F = 78.56, P < 0.001). The three methods used to detect the year with a significant change-point in the time series yielded similar results (year and confidence interval): 1893 (CI = 1885–1905 based on structural changes); 1887 (CI = 1855–1925 based on piecewise linear model); and 1887 (CI = 1863–1911 based on segmented regression). That is, the onset of the climate warming effect on the Japanese cherry tree occurred around 1890, in Japan's Meiji Era (1868–1912). During the 1078 yr before 1890, peak flowering occurred, on average, on 16 April (mean DOY = 105.2, SD = 6.37, median = 105). After 1890, a sustained and significant advance in flowering was observed over the next 134 yr (Fig. 1a), with the earliest recorded flowering on 26 March (DOY = 84) in 2023. This represents an average advance of 0.9 d per decade (slope: −0.0927; Fig. 1a). This may seem a slow phenologic change compared with estimates for other plants (up to 5 d per decade; Renner & Zohner, 2018, Zeng *et al.*, 2025); however, the value depends on the length of the time series as the climate is constantly changing. If we only consider changes from 2000 (or from 2005), the estimated advance is 3 (or 4.8) d per decade. That is, we do not find evidence of a temporal attenuation in the phenological response to warming, as has been reported in experimental studies (Lu *et al.*, 2025). The slight (but significant) positive trend (i.e. delayed flowering) during the period 812–1887 aligns with the pre-industrial cooling trend in terrestrial records over the past millennium (McGregor *et al.*, 2015; Sigl *et al.*, 2015). After 1890, flowering time was strongly correlated with the mean temperature for March (−2.9 d per 1°C; Fig. 1b; Table S2; Aono & Kazui, 2008), confirming that the advance is primarily driven by increasing spring temperatures (Figs S1, S2), that is, when flowers develop.

The observed phenological shifts are indeed likely explained by the rising spring temperatures in Kyoto (Fig. S1) and globally. However, other factors could potentially contribute. One is the industrialization and the urban heat effect; however, their impact on the late 19th century, when the breakpoint occurred, was likely minimal; its effect is confined to recent decades (Aono & Kazui, 2008). The fact that the relation between the flowering time and March temperature is maintained when using meteorological stations from smaller cities suggests that the urban effect is unlikely to bias our results. Changes in tree management practices (e.g. pruning and irrigation) may also modify flowering, although they may introduce noise rather than a systematic trend. Tree mortality and new plantations could also influence phenology, specially if there is an artificial selection for early-blooming individuals. In fact, we do not know whether all trees are simultaneously advancing their flowering time, or alternatively, there are early- and late-blooming genotypes with different sensitivity to warming (Goeckeritz *et al.*, 2024). To what extent warming has other phenological implications different from the time of peak flowering (e.g. flowering duration, pollination, fruiting) also deserves further research (Hegland *et al.*, 2009). In any case, the abrupt change in flowering around 1890 (Fig. 1) is unlikely to be strongly influenced by those factors; given the high sensitivity of the flowering time to temperature, anthropogenic global warming is the most plausible explanation.

Climate warming is not uniform across the globe (Abram *et al.*, 2016; IPCC, 2023) and different species may exhibit varying responses and sensitivities to climate (Renner & Zohner, 2018; Horbach *et al.*, 2023). Woody species and spring flowering species tend to advance their flowering time in response to warming faster than herbs or summer flowering species (Calinger *et al.*, 2013; Zeng *et al.*, 2025), suggesting that the Japanese cherry tree may be a good indicator of the onset of the global warming response for many other species. Species' sensitivity to photoperiod also contributes to shaping the phenology of woody plants; for example, species that are less sensitive to photoperiod changes may be more responsive to spring warming (Fu *et al.*, 2019). In short, the Japanese cherry tree is unlikely to be the species most sensitive to global warming. That is, we provide evidence that climate change has been impacting our biota since at least the late 19th century – *c.* 50 yr after human activities began altering the climate (Abram *et al.*, 2016). During this 50-yr time lag, the magnitude of warming may have been insufficient to trigger a noticeable phenological shift in this species. If the Japanese cherry has been affected by climate warming for *c.* 137 yr, many other species of plants and animals may have been similarly affected.

The lack of long-term data limits our ability to establish references for the functioning of ecosystems before the industrial era. This poses significant challenges to fully understanding the real effects of climate change. In other words, climate change may be impacting our biosphere more than we may realize. Our analysis of long-term data using breakpoint models strengthens our ability to establish baseline conditions before the industrial era. It is important to search for more unambiguous evidence of climate change effects to reduce the shifting baseline syndrome in climate change research (Pausas, 2024).

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Competing interests

None declared.

Author contributions

All work has been performed by JGP.

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Data availability

All data used have been downloaded from public websites (https://ourworldindata.org, and https://www.data.jma.go.jp) and are provided in the Supporting Information (Datasets S1 and S2).

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Supporting Information

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

Dataset S1 Day of the year of the flowering peak of the cherry tree in Kyoto, Japan, from 812 to 2024.

Dataset S2 Monthly temperature for the four meteorological stations considered.

Fig. S1 Recent changes in air temperature in Kyoto.

Fig. S2 Recent changes in mean March temperature in the four meteorological stations considered.

Table S1 Details of the meteorological stations considered.

Table S2 Relation between monthly temperature and flowering peak day of the year.

Notes S1 Numerical methods for detecting the breakpoint using the R software.

Key words: climate change, flowering time, global warming, phenology, shifting baseline.

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