## Letter

# Consistent, linear phenological shifts across a century of observations in South Korea

Shifts in the timing of spring flowering events are recognized as one of the clearest and most sensitive ecological indicators of climate change (Pau *et al.*, 2011). Numerous efforts are under way to track yearly variation in flowering phenology (Crimmins *et al.*, 2017; Templ *et al.*, 2018), but most ongoing studies began in the last few decades and so lack data on phenology before the onset of anthropogenic climate change. Such studies typically calculate phenological sensitivity as the linear relationship between flowering time and temperature, but there is emerging uncertainty as to whether plants may be reaching the limit of their ability to track temperature (Iler *et al.*, 2013; Wolkovich *et al.*, 2021). If they are reaching this limit, we would expect to see either nonlinearities (e.g. asymptotes) in phenological sensitivity (Pope *et al.*, 2013) or increased variability (or a lack of predictability) in comparison with what were once tight, strong relationships (Pearse *et al.*, 2017). Indeed, some have suggested that drivers such as winter chilling and photoperiod will become more prominent in cueing flowering as spring temperatures become less limiting (Cook *et al.*, 2012). To gain an understanding of whether climate change is resulting in different patterns of phenological response, we need to compare recent shifts to historical baseline data from before the onset of rapid anthropogenic climate change.

The Korean Meteorological Agency (KMA) has been recording data on spring flowering time (date of first flower) for seven woody plant species – pear (*Pyrus communis*), Yoshino cherry (*Prunus yedoensis*), Korean forsythia (*Forsythia koreana*), black locust (*Robinia pseudoacacia*), peach (*Prunus persica*), Korean azalea (*Rhododendron mucronulatum*), and Japanese apricot (*Prunus mume*) – for 100 yr as of 2022, making it, to our knowledge, the longest continuously running phenological monitoring effort in Asia (Ibáñez *et al.*, 2010; Fig. 1). This centennial study offers a unique opportunity to compare phenological trends before and after the onset of rapid climate change. The extremity of recent phenology is stark: during this 10th decade of study, the record for the highest average annual temperature was broken six times and, in 2021 alone, species at nine of the 72 sites exhibited the earliest flowering phenology ever recorded. Overall, species flowered an average 4.1 d earlier for every 1°C of warming, and as much as 5.5 d earlier in the case of apricots (Fig. 2; but see also Supporting Information Figs S2, S3; model results given in Notes S1). Spring temperature explained the highest amount of variation in flowering, at least twice as much as any other factor, with significant contributions from latitude and whether the site was coastal or

inland. Partitioning variation in temperature and rainfall across locations, on average through time across all locations, and across years within sites (*sensu* Daru *et al.*, 2019), made no impact on these findings (see Notes S2 and the Materials and Methods section). However, these analyses did reveal that variation among sites was the dominant driver of variation in phenology, followed by variation through time across South Korea – leaving site-specific variation as the weakest driver of phenology. But this still leaves open the question as to whether spring temperature sensitivity has changed over time in response to accelerated warming.

We evaluated these data with two criteria that could indicate shifting sensitivity to spring temperature: nonlinearity in trends and increased interannual variability around the mean trend. Regarding linearity, we found that while models were best fit by quadratic and cubic phenology-to-temperature functions for most species, their gains in predictive ability were small, suggesting a high degree of fidelity with linear functions. Averaged across all species, quadratic and cubic models explained < 2% more variation than linear models. At most, the error associated with the sensitivity prediction was reduced by only 0.03 d (for forsythia). We found no evidence that an exponential decay response curve was more appropriate than a simple linear fit for any species. Thus, we find little evidence to suggest that the capacity for flowering phenology to respond to spring temperature is saturating in this system (all models given in Notes S3). There are, of course, hard physiological limits to many aspects of plant physiology, and as such there is no reason to suppose that these species will be able to track shifting
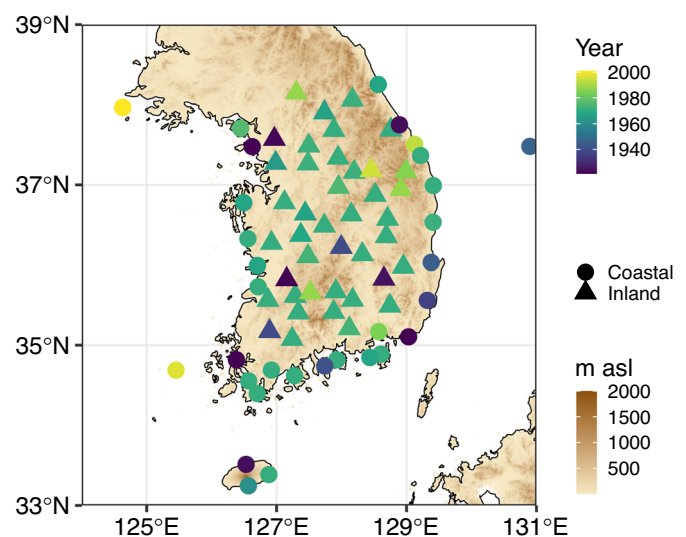


**Fig. 1** Korea Meteorological Agency weather station locations used in this study, with point color indicating the year of first observation. Background colors indicate elevation (m above sea level (asl)). Sites that were designated as 'coastal' are plotted as circles, and 'inland' sites are plotted as triangles.
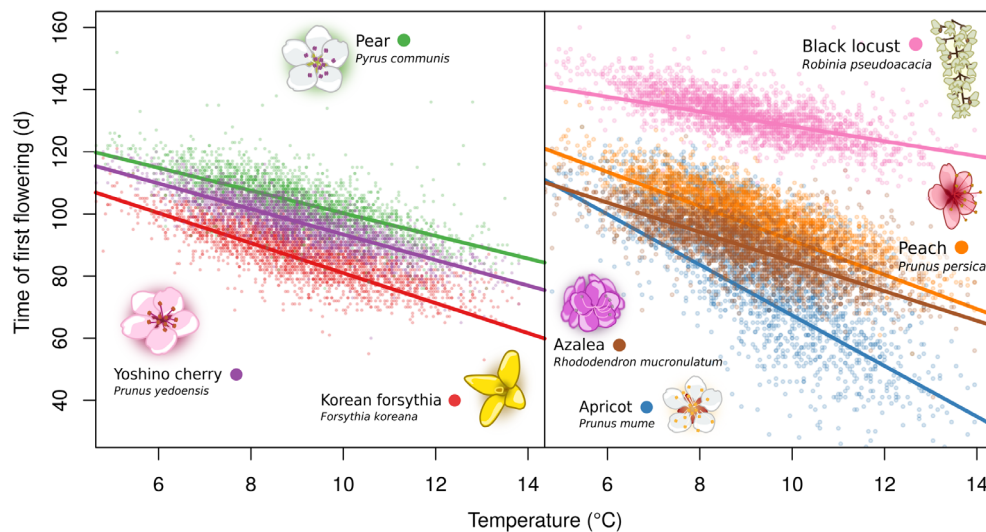
**Fig. 2** Date of first flower is consistently dominated by temperature across species. Points represent observations from the second half of the dataset (1971–2020), and the lines represent models fit to the first half of the dataset (1920–1970). All seven species' date of first flower is plotted against temperature (mean of February–March). Full model summary statistics are given in the Supporting Information, including direct comparisons of the predictive power of temperature vs other factors (Fig. S1). Notably, all species' responses are strongly, linearly correlated with temperature, opening earlier in warmer years.

climate forever, merely that they have not reached their limit of plasticity yet. We do also note that most species show a greater magnitude of response to yearly temperature post-2010 when climate change has been more intense. These trends are so small as to have limited impact on overall model fit (mean, additive increase in $r^2$ of 0.61% across all species; see Notes S4). This is notable given that we would expect species to respond more weakly to climate as they approached their response limits; we see, if anything, an increase in responsiveness.

We next quantified the degree to which interannual phenological variability changed over time. If climate change were disrupting the ability of species to track environmental variability through phenological plasticity, we might expect to see increases in interannual variability. This could occur if flowering were to be decoupled from spring temperature through sensitivity saturation, with other factors becoming the dominant drivers (Meng *et al.*, 2021). We thus explicitly modeled changes in phenological variance over time as a function of spring temperatures to test for changes in predictability. All but one species (cherry) tended to become, if anything, slightly less variable in their interannual phenology over time. Of these, four (forsythia, apricot, black locust, and rhododendron) showed strong evidence (Bayesian $P > 95\%$ for estimated slope of $\sigma^2$) that this reduction in variance over time was statistically significant, though we note that these variance reductions are very small when compared to the magnitudes of mean shifts (the greatest shift is in plums, which also have the greatest variance overall; see Notes S5). Further, five of the seven species (excepting cherry and pear) showed extremely modest (albeit statistically significant) evidence of reductions in variance in warmer years (model results given in Notes S6), suggesting that the reductions in variance over time are not simply a product of shifting temperature variance. These findings indicate that interannual phenological variation has not become more variable and any increase is so small as to be biologically irrelevant.

This is in keeping with studies with greater taxonomic and geographic effects on phenology but more limited temporal extent (Stemkovski *et al.*, 2023).

Combined, these two lines of evidence suggest that phenological sensitivity of woody plants in Asia has not significantly changed over the past century. Indeed, it suggests that had scientists in 1971 used the first 50 yr of data to predict phenology in 2021, their predictions would have been highly accurate. To quantify this, we modeled the degree to which predictability has changed since the onset of climate change by comparing the predictive accuracy of models trained with the first 50 yr and the most recent 50 yr of data. A simple linear model containing only one term – average spring temperature – when fit to data from 1921 to 1971, predicts the observed phenology from 1972 to 2021 with an average error of 7.3 d across all species (lowest RMSE is 4.4 d for cherries and highest 13.1 d for apricots). On the contrary, the same model, when fit using the most recent 50 yr, had only slightly higher accuracy for all species, with an average error of 6.6 d: a 6.4% improvement. Thus, scientists in 1971 could have made very good predictions of shifts in phenology that would have been accurate for the next 50 yr (full model results given in Notes S7). Of course, we must temper this observation by remembering that this dataset, while almost unprecedented in temporal scale, is of only seven species – all of which are trees and shrubs – and so we caution against generalizing our findings to other taxa. We note, however, that other studies of more taxa (790 plants, 168 birds, and 79 insects; Stemkovski *et al.*, 2023) and that extends back further in time (1852–2007, albeit not measured each year; Willis *et al.*, 2008) find similar patterns. Datasets exist with longer time periods that could be used for additional tests but, we caution, they are not as standardized, making it difficult to accurately test constancy of responses through time (Christidis *et al.*, 2022).

These results provide three critical insights for modern climate change research. The first is confirmatory but sometimes

overlooked: historic records form an important baseline against which contemporary change must be measured to avoid the problem of shifting baselines (Pearse *et al.*, 2017). Second, while climate is shifting in unprecedented ways that are challenging to model and forecast, the biological responses to these changes may still be linear and predictable based on existing data. Third, we stress that even these linear phenological responses may still have complex, nonlinear, and multifaceted ecological consequences. All species adjust their phenology in response to temperature variation, but their sensitivities differ from one another (note the variation in slopes in Fig. 2). For every 1°C of warming, black locust flowering advances by 3.3 d, but apricot advances by 5.5 d. Even subtle, linear differences in species sensitivities have the potential to fundamentally reorder phenological relationships and vulnerability to frost and drought and profoundly affect ecological interactions and function. This may occur long before species reach hard physiological limits on flowering plasticity. Still, our results suggest that currently-available data hold the key to predicting the future consequences of shifts in flowering phenology.

## Materials and Methods

We analyzed changes in predictability of flowering time in seven species from a 100-yr dataset collected by the Korea Meteorological Administration. We describe the data processing and collection briefly due to its long record period and because it is given in more detail elsewhere, and describe the analyses in full detail. All reproducible analysis codes are released in the Notes S8; the data were not collected by us and are housed with the Korea Meteorological Agency (KMA) but are also available in Notes S9.

### Data collection

We used data gathered by the Weather Service of the Republic of Korea on the first flowering date of *Forsythia koreana* (Korean forsythia), *Prunus mume* (Japanese apricot), *Pyrus communis* (pear), *Prunus × yedoensis* (Yoshino cherry), *Prunus persica* (peach), *Robinia pseudoacacia* (black locust), and *Rhododendron mucronulatum* (Korean rhododendron) at 74 weather stations distributed across the country, with some weather stations starting in 1921 (data available from Korea Meteorological Administration, https://data.kma.go.kr/data/seasonObs/seasonObsDataList.do?pgmNo=648; Fig. 1; Ibáñez *et al.*, 2010). Monitoring at other weather stations started later, and not all stations have operated continuously. Temperatures have risen across the country over the study period, with greater temperature increases in areas with larger human populations (Primack *et al.*, 2009). These data have been extensively used to investigate how species are changing their phenology over time and in response to annual variation in temperature (Lee *et al.*, 2011; Ellwood *et al.*, 2012; Kim *et al.*, 2021). However, we emphasize that while our dataset spans a large number of sites and years, it is of only seven species and all of those species are trees and shrubs (and not, for example, understory plants, or even animals). This taxonomic and functional-grouping limitation is important and should be borne in mind when considering the broader implications of this study.

Observations were made on plants growing in phenological gardens on the grounds of each weather station. All plants used in this study were obtained from stock maintained and distributed by the Weather Service of the Republic of Korea to maintain genetic uniformity. When plants died or were not healthy, they were replaced by new plants. To minimize the effects of plant aging, the plants in the phenological garden have been replaced at regular intervals of between 15 and 25 yr throughout the study. Surface air temperature data have been available continuously from as early as October 1907 (city of Seoul), and records at some stations were missing during the Korean War of 1950–1953. The phenological observations were made by weather station employees according to precise written instructions that have remained constant for the entire study. First flowering was recorded when at least three flowers were open on a plant.

### Statistical analysis

Our analysis was split into five main components: (1) quantifying the drivers of phenological change; (2) assessing changes in forecast skill in recent decades; (3) testing for nonlinearity in phenological responses; (4) estimating the predictability of phenology over time and in warmer years; and (5) partitioning responses into among-site, among-year, and individuals' plastic *in situ* adaptation/responses. (1) We chose six predictor variables to explain interannual variation in first flowering phenology: spring temperatures (mean over February and March), spring precipitation (mean over February and March), regional population (https://jumin.mois.go.kr/index.jsp#), elevation, latitude, and whether the station was inland or coastal (as defined by our knowledge of the region and detailed in Notes S10). Coastal sites are port cities at sea level with an oceanic influence on climate (never > 15 km from the ocean). Inland sites are at higher elevations, not at port cities, and with a climate not strongly influenced by the ocean. We used means over February and March after exploratory analysis revealed that these were the most strongly predictive regions and also to match previous work (e.g. Primack *et al.*, 2009). While temperature sensitivity is often calculated using degree-day models, we follow similar studies interested in variance shifts through time (notably Stemkovski *et al.*, 2023, who further justify this approach) in order to ensure comparability among studies. All continuous predictor variables were centered to have means of 0 and SDs of 0.5 to allow for the estimation of standardized effect size and important across continuous and discrete variables (Gelman, 2008). The day-of-year (DOY) of first flowering was modeled using linear mixed effects models for each species separately, with the predictor variables modeled as additive fixed effects, and station as a hierarchical effect with variable intercepts to account for site-specific differences and pseudo-replication (Goodrich *et al.*, 2020). We extracted slope coefficients (fixed effects) from these models to compare the relative importance of the phenology predictors to one another and across species, and median $r^2$ values from across the posterior distribution to estimate the absolute improvement in model fit of various model terms.
(2) In quantifying the drivers of phenology as described previously, we found support for temperature as the dominant

driver of phenology in this system. As a first test of whether phenological responses to temperature have changed fundamentally over the course of the study, we quantified how surprising phenological patterns in the second half of the dataset (after the onset of climate change; 1972–2021) are compared to what was observed in the first half (preclimate change; 1921–1971). We did this by assessing the improvement in forecast skill (Dietze, 2017) that was achieved by the second half of the dataset. For each species, we quantified forecast skill improvement as the percent change of the root-mean-square error (RMSE) of a linear model of DOY as a function of temperature trained on the 1921–1971 data and evaluated on the 1972–2021 data and the RMSE of the same model trained and evaluated on the 1972–2021 data. To obtain one metric of forecast skill improvement, we also calculated the mean of the RMSE estimates across all species.

(**3**) To assess evidence of nonlinearities in species' responses to temperature, we contrasted models where temperature was modeled in various nonlinear ways, using the mean squared error and AIC of the models as decision criteria. To be both conservative and also maximize the comparability of models (since some nonlinear modeling approaches struggle to fit models with as many terms as are present in our models above), we first fit linear (not mixed effects) models to all explanatory variables in part 1 above, excluding temperature. We then modeled the residuals of these models against: (a) temperature; (b) temperature and its quadratic; (c) temperature and its cubic; and (d) temperature as a saturating exponential decay. Finally, we repeated our models from part (1) but with an interaction term between whether a sample was observed in the years after 2010 and the temperature and precipitation terms already incorporated in that model. This tests whether this more recent period, during which the impacts of climate change have been more pronounced, is causing a shift in how individual species are responding.

(**4**) To test for changes in phenological dispersion over time and in warmer years, we follow Pearse *et al.* (2017) in fitting models which explicitly estimated heteroskedasticity by modeling variance as a function of time and annual temperature. Specifically, we fit Bayesian hierarchical models using *brms* (Bürkner, 2017) with the equivalent formulation as in part (1), where the average response ($\mu$) of DOY varies additively as a function of the explanatory, and each station has a hierarchically drawn estimate for its mean. We then modeled, in two separate models, the variance in response ($\sigma^2$) as a function of time and temperature and the same hierarchical intercept structure to account for variance differences by station. We note that this modeling formulation is conservative because temperature always appears in the $\mu$ term, and inclusion of the hierarchical term in both the $\mu$ and $\sigma^2$ formulas accounts for changes in station coverage. We used a Gaussian identity link function for the $\sigma^2$ coefficients in order to report variance changes in units of d yr$^{-1}$ and d °C$^{-1}$. Models were run for four chains and 2000 iterations each using default noninformative priors and were checked for convergence.

(**5**) Additionally, we investigate whether the responses we see through time can be partitioned into variation associated with broader environmental adaptation (per site), overall annual climate change (constant across all sites), and year-to-year variation at each site within the context of this variation. In doing this, we follow Daru *et al.* (2019) and estimate the mean temperature/precipitation at each site, the annual trend in temperature/rainfall through time across all sites, and finally the difference in temperature/rainfall at each site in each year from the previous two summed together. We then fit these additional terms in a model following the procedure outlined in (3). We present these results in Notes S2 and note that, in all cases bar the models where the explanatory variables were not normalized, we find that the site-level terms are greater (and thus more important; see argument above) than the annual terms, which are themselves greater than the site-level variation. We suggest the unstandardized terms are not the best choice for interpretation, since standardization helps address co-linearity issues which may occur in such time-series data, but regardless note that the pattern is present in unscaled data for all species except black locust and acacia regardless.

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## Competing interests

None declared.

## Author contributions

WDP, RBP, and SDL planned research. WDP, MS, and BRL carried out statistical analysis. All authors contributed to the writing of the manuscript.

## ORCID

Benjamin R. Lee https://orcid.org/0000-0002-5256-0515
Sang Don Lee https://orcid.org/0000-0002-3282-873X
William D. Pearse https://orcid.org/0000-0002-6241-3164
Richard B. Primack https://orcid.org/0000-0002-3748-9853
Michael Stemkovski https://orcid.org/0000-0002-9854-887X

## Data availability

All reproducible analysis codes are released in the Supporting Information; the data are housed with the Korean Meteorological Agency and are also released in the Supporting Information.

**William D. Pearse[1]** , **Michael Stemkovski[2]** ,
**Benjamin R. Lee[3,4,5]** , **Richard B. Primack[6]** and
**Sang Don Lee[7]\***

[1]Department of Life Sciences, Imperial College London, Ascot, SL5 7PY, UK;

[2]Department of Biology & Ecology Center, Utah State University, 5305 Old Main Hill, Logan, UT 84322, USA;
[3]Section of Botany, Carnegie Museum of Natural History, 4400 Forbes Ave, Pittsburgh, PA 15213, USA;
[4]Department of Biological Sciences, University of Pittsburgh, 4249 Fifth Ave, Pittsburgh, PA 15260, USA;
[5]Holden Arboretum, 9550 Sperry Rd. Kirtland, OH 44094, USA;
[6]Biology Department, Boston University, 5 Cummington Mall, Boston, MA 02215, USA;
[7]Department of Environmental Science and Engineering, Ewha Womans University, Seoul 03760, Korea
(*Author for correspondence: email lsd@ewha.ac.kr)

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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** Standardized effect sizes of the drivers of interannual variation in flowering phenology.

**Fig. S2** One hundred years of first flowering dates in seven species across the Korean Peninsula and islands.

**Fig. S3** One hundred years of mean temperature and precipitation data across the sites within the Korean Peninsula and islands.

**Notes S1** Outputs from models of all species against all explanatory variables, both scaled (to estimate the relative importance of variables) and unscaled.

**Notes S2** Outputs from models partitioning variation in temperature and precipitation among sites, time, and within-site variation.

**Notes S3** Outputs from linear and nonlinear models to assess support for saturation/nonlinearity of species' functional responses to temperature.

**Notes S4** Outputs from models testing for differences in species' responses post-2010.

**Notes S5** Outputs from Bayesian hierarchical models with variance terms accounting for correlated changes in variation with year.

**Notes S6** Outputs from Bayesian hierarchical models with variance terms allowing for correlated changes in variation with temperature.

**Notes S7** Forecast and hindcast predictions from models, along with within-sample model results.

**Notes S8** Compressed archive of all analysis codes.

**Notes S9** Raw data provided to us by the Korean Meteorological Agency.

**Notes S10** Information about sites.

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