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Forest wildflowers bloom earlier as Europe warms: lessons from herbaria and spatial modelling

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Summary

- Today plants often flower earlier due to climate warming. Herbarium specimens are excellent witnesses of such long-term changes. However, the magnitude of phenological shifts may vary geographically, and the data are often clustered. Therefore, large-scale analyses of herbarium data are prone to pseudoreplication and geographical biases.
- We studied over 6000 herbarium specimens of 20 spring-flowering forest understory herbs from Europe to understand how their phenology had changed during the last century. We estimated phenology trends with or without taking spatial autocorrelation into account.
- On average plants now flowered over 6 d earlier than at the beginning of the last century. These changes were strongly associated with warmer spring temperatures. Flowering time advanced 3.6 d per 1°C warming. Spatial modelling showed that, in some parts of Europe, plants flowered earlier or later than expected. Without accounting for this, the estimates of phenological shifts were biased and model fits were poor.
- Our study indicates that forest wildflowers in Europe strongly advanced their phenology in response to climate change. However, these phenological shifts differ geographically. This shows that it is crucial to combine the analysis of herbarium data with spatial modelling when testing for long-term phenology trends across large spatial scales.

Introduction

Since the industrial revolution, anthropogenic global change threatens species and ecosystems. Climate warming, in particular, can cause shifts in the timing of annual life-history events of plants and animals (Root *et al.*, 2003; Menzel *et al.*, 2006; Cleland *et al.*, 2007). Such phenological changes, including earlier leaf-out or flowering of plants, are some of the most striking large-scale biological responses to ongoing climate change (Cleland *et al.*, 2007). To understand why and how phenology shifts, it is critical to infer which attributes of the environment are the triggers (cues) or proximate causes (drivers) of life cycle events. As their phenology links plants to their environments, changes in the phenology can affect the local persistence and biotic interactions of plants (Inouye, 2008; Willis *et al.*, 2008; Wheeler *et al.*, 2015; Cerdeira Morellato *et al.*, 2016). For instance, Willis *et al.* (2008) found that plant species whose flowering time poorly tracked temperature variation declined in abundance during the last century. Conversely if leaf-out or flowering advances too much, the risk of late-frost damage can increase (Wipf *et al.*, 2006; Inouye, 2008; Zohner *et al.*, 2020). Unequal shifts of interacting organisms in trophic interactions can result in phenological 'mismatches', for example when the timing of the activity of consumers aligns less well with the availability of their resources, or when the phenology of plants and pollinators shift differently (Renner & Zohner, 2018; Visser & Gienapp, 2019). Such mismatches can have severe demographic and evolutionary consequences (reviewed e.g. in Renner & Zohner, 2018; Visser & Gienapp, 2019). Changes in plant phenology can even influence ecosystem functions such as productivity or carbon cycling (Menzel *et al.*, 2006; Cleland *et al.*, 2007; Piao *et al.*, 2019).

When studying phenological changes over time, we should keep in mind that phenology, and magnitudes of phenological responses to climate change, not only vary among species but also vary across space. At smaller scales, that is within regions or local sites, phenology can vary because of microclimatic differences (Hwang *et al.*, 2011; Ward *et al.*, 2018; Willems *et al.*, 2021) and, at larger scales, that is across broad regions, both (baseline) phenology as well as phenological responses are expected to vary because of macroclimatic variation, because the magnitudes of climatic changes differ geographically (Klein Tank *et al.*, 2002; IPPC, 2019) and because phenological sensitivities to cues such as temperature may differ between regions (Riihimäki & Savolainen, 2004; Ibáñez *et al.*, 2010; Zohner & Renner, 2014; Prevéy *et al.*, 2017; Kopp *et al.*, 2020; Zohner *et al.*, 2020). Robust studies on phenology and climate change therefore require a larger scale perspective, with spatial variation and autocorrelation explicitly taken into account. However, many previous studies on plant phenological responses to climate change have had a limited geographical scope (Pau *et al.*, 2011).

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In this context, herbaria offer unique opportunities, because they allow tracking phenology at large temporal as well as spatial scales. Herbarium specimens are usually collected when plants flower, and most herbarium sheets provide collection dates and locations (Fig. 1). With many herbaria dating back to some 200 yr, and hundreds of millions of specimens worldwide, herbaria are a tremendous treasure for studying phenology changes both long term and large scale. Previous studies have indeed found strong patterns of long-term phenology changes in herbarium data (Primack *et al.*, 2004; Miller-Rushing *et al.*, 2006; Davis *et al.*, 2015; Willis *et al.*, 2017; Lang *et al.*, 2019; Park *et al.*, 2019; reviewed by Jones & Daehler, 2018), and they have also demonstrated that phenology trends estimated from herbarium data are comparable to those from field observations (Davis *et al.*, 2015; Jones & Daehler, 2018; Miller *et al.*, 2021). However, almost all previous studies have been carried out in the USA, and there has been little work so far on herbaria and plant phenology in Europe (but please refer to Robbirt *et al.*, 2011; Diskin *et al.*, 2012; Molnar *et al.*, 2012). Most previous studies also did not consider geographic variation in phenology and spatial correlation of herbarium samples (but please refer to Matthews & Mazer, 2016; Park *et al.*, 2019; Kopp *et al.*, 2020).

In Europe, climatic conditions vary substantially across the ranges of many plant species, especially from north to south, and not only the overall timing of phenological events but also phenological responses (i.e. sensitivities to cues or drivers) may differ across this latitudinal gradient. For a similar climatic gradient in the eastern USA, Park *et al.* (2019) found that long-term phenological responses estimated from herbarium specimens substantially differed among climatic zones, with greater mean climate sensitivities, as well as greater among-species variability in sensitivities, in the warm and mixed-temperate climatic regions than in the cool-temperate northeast and the Appalachians. Similarly, for the Pacific Northwest region of North America, Kopp *et al.* (2020) found that sensitivity to temperature was greater at low elevations and in the maritime (western) regions.

Another problem with large-scale herbarium data is that they are often, for historical reasons, strongly clustered, that is specimens are more frequently collected where collectors live, and around academic institutions (Daru *et al.*, 2017). However, when modelling across a spatial range, standard methods such as linear regression ignore the spatial dependency between sampling locations and treat all data points as independent. This assumption is very likely to be not correct, as the proximity of spatial locations is usually related to their environmental similarity (Tobler, 1970), and, as explained above, this is certainly true for climatic conditions. Ignoring spatial dependency, therefore, results in pseudoreplication and it can strongly bias model results.

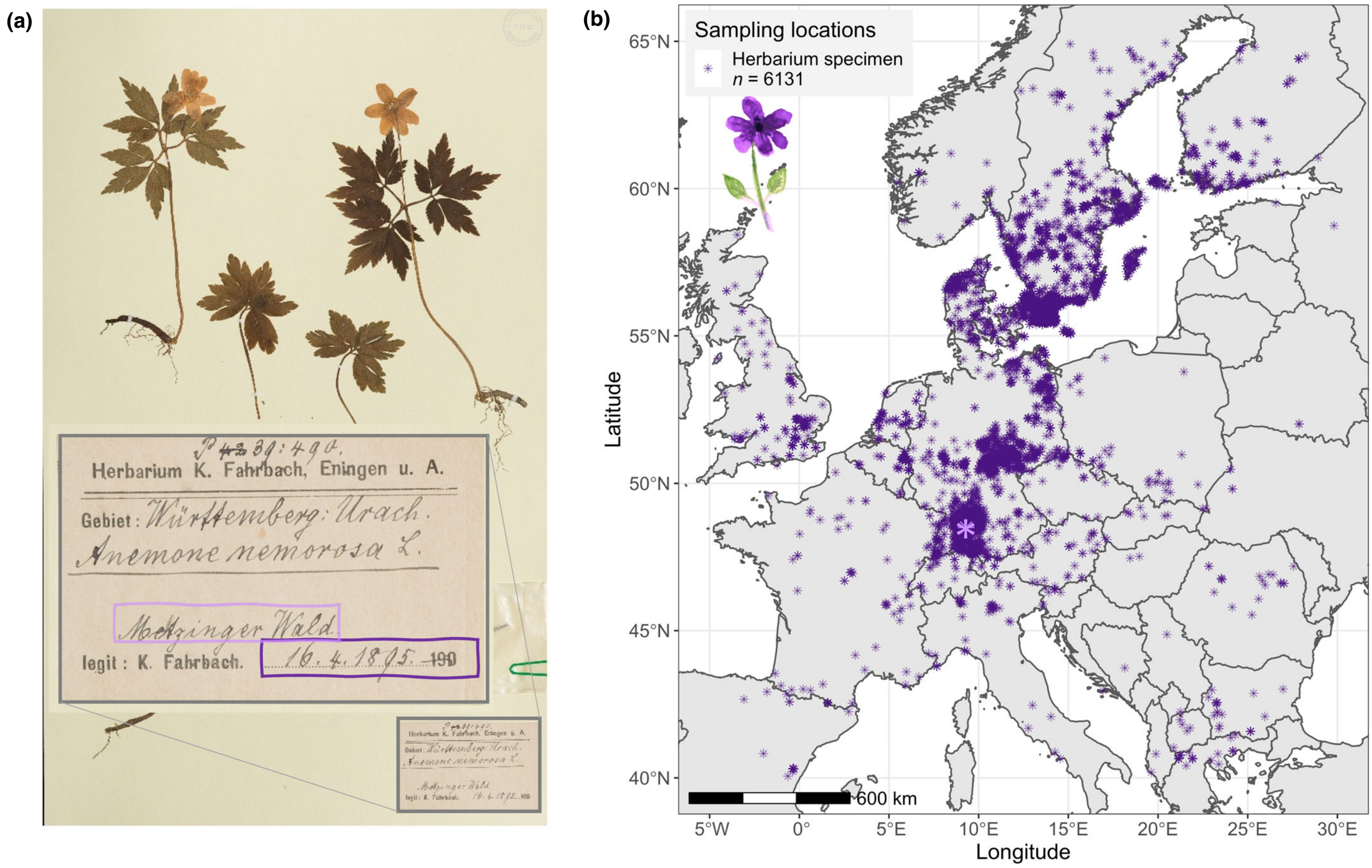

Fig. 1 (a) Example of an herbarium specimen, with the collection date and location on the herbarium label. This *Anemone nemorosa* was flowering on 16 April (day of the year (DOY) = 107) in 1895, and it was collected in the Metzinger Wald forest close to Tübingen (lighter purple point in the map). (b) Sampling locations of the 6131 herbarium specimens included in our analyses.

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The solution to this, spatial modelling with explicit incorporation of spatial structure and therefore spatial autocorrelation, is computationally challenging, and it has therefore hardly been used in analyses of herbarium data. However, recent advances in statistical methods now allow modelling of these spatial data, for example using stochastic partial differential equations (SPDE) and integrated nested Laplace approximations (INLA), as implemented in the R package R-INLA (Rue *et al.*, 2017; Bakka *et al.*, 2018). It is therefore possible to take the next step in herbarium studies and analyse large-scale phenology in relation to climate change in a spatially explicit framework.

Here, we analysed long-term and large-scale trends in the flowering time of 20 common forest understory wildflowers, and their relationships with climate change, across Europe, using over a century of herbarium data. We focused on early-flowering understory plants, because they have a very distinct phenology, with a critical time window for flowering before the leaf-out of deciduous trees. Because of this, they may be particularly sensitive to climate change and phenology shifts. Forest understory plants may also be exposed differently to climate change because climate warming is buffered under forest canopies (De Frenne *et al.*, 2019). In our analyses, we used R-INLA (Rue *et al.*, 2009, 2017; Bakka *et al.*, 2018) to account for spatial clustering and autocorrelation of climate and phenology data. We asked two main questions: (1) Did forest understory plants advance their flowering phenology during the last *c.* 100 yr? (2) If yes, are these phenological shifts associated with climate change in Europe? We answered both questions with or without accounting for spatial correlation in the statistical models, and therefore also addressed the question of how important doing this was for the results and conclusions of our study.

Materials and Methods

Phenological data

We mined three large German herbaria and the Global Biodiversity Information Facility (GBIF) for all European specimens of 20 common spring-flowering forest understory herbs (please refer to Supporting Information Table S1). The three herbaria were at the University of Tübingen (herbarium code TUB), University of Jena (JE) and at the State Museum of Natural History in Stuttgart (STU). Our criteria for including herbarium specimens were that: (1) they had flowers, and that open flowers represented at least 50% of the reproductive structures, (2) they had an exact collection date and (3) information on the sampling location that we could use to estimate GPS coordinates, and (4) they were collected in Europe. In addition, we obtained all digital specimens of the same 20 species from GBIF (2020) that were from Europe and also had (1) an exact collection date and (2) GPS coordinates of the sampling location, using the RGBIF package (Chamberlain & Boettiger, 2017) in R (R Core Team, 2018). This resulted in an initial 3930 specimens from the three herbaria and 3511 specimens from GBIF, with the collection years ranging from 1807 to 2017. However, as reliable, gridded climate data were not available before 1901 we decided to restrict our analyses to data from 1901 onwards. Moreover, because there were only very few specimens from outside of these limits, we truncated our data to 40° to 65° northern latitude and −5° to 30° longitude, covering a broad geographic area in mainly central and northern Europe, but also western and south-eastern Europe (Fig. 1a). We further discarded all specimens with dates outside the normal flowering range of our 20 study species (before day of the year (DOY) 50 and after DOY 200), because we suspected these to be recording mistakes. Also, the GBIF data contained unusually many specimens from 1 May and 1 June (DOYs 121 and 152, respectively), which strongly indicated that they were from specimens without exact collection dates that were arbitrarily assigned to the first day of a month, and we excluded these data from our analyses. Lastly, we discarded six datapoints for which the assigned elevation value was below −10 m. Our final set of phenology data contained 6131 herbarium specimens, with 46–600 records per species (Table S1).

Climate and elevation data

For associating plant phenology variation with long-term temporal and spatial variation in climate, we used gridded estimates of historic monthly air temperature (°C) and precipitation (mm) that were available for 1901–2017 and with a 0.5° × 0.5° grid resolution from the Climate Research Unit (CRU, https://crudata.uea.ac.uk; Harris *et al.*, 2020; version *cru_ts4.04*). We used these data to calculate mean winter (December to February) and spring (March to May) temperatures, as well as annual precipitation values for each year and grid cell. Each herbarium specimen was then assigned to a specific set of values of these three climate variables, based on its collection year and the geographic grid cell it was located in, using custom-made scripts in PYTHON (Van Rossum & Drake, 2009). We also estimated the elevation above sea level (asl) of each herbarium specimen using the RASTER package in R (Hijmans & van Etten, 2020).

Statistical analyses

Our statistical analyses generally had a two-step logic, relating to the two main questions of our study. We first tested for overall phenological shifts, that is temporal trends in flowering time, across our 20 study species, using a simpler statistical model (model A), and we then tested for phenology–climate associations with a more complex model B (details below). Both models were run with and without accounting for spatial correlation.

To test for temporal trends in flowering time (model A) we modelled flowering phenology during the last 120 yr as a function of the year of collection, while accounting for the effects of elevation and species. Model A was specified as:

$$Y_{ij} \sim \text{Intercept} + \beta_{ij}\chi_{ij} + S_i + T_i \cdot \text{Year}_{ij} + U_i + \epsilon_{ij}$$

where Y_{ij} is the day of flowering of herbarium specimen i of species j, χ_{ij} is a vector containing all covariates (model A: collection year and elevation) as linear fixed effects, β_{ij} is the vector of estimated parameters (regression slopes), $S_{(i)} \sim N\left(0, \sigma^2_{\text{species}}\right)$ is the species random intercept, $T_{(i)} \sim N\left(0, \sigma^2_{\text{species}}\right)$ the species random slope, both with a Gaussian distribution, and $\epsilon_{ij} \sim N(0, \sigma^2)$ the residuals. The species random intercept allows species to differ in their mean flowering times, and the species random slope means that temporal trends can be species specific, for example because species respond differently to climate change. $U_{(ij)} \sim N(0, \Omega)$ represents the spatial structure (as described in the following paragraphs) that is additionally included as a random effect in the models accounting for spatial correlation. In model A, the slope of the linear relationship between the collection dates (= DOY of flowering) of specimens and their collection year is the formal test for long-term phenological shifts.

To test for phenology–climate associations (model B) we additionally included spring temperature, winter temperature and precipitation, plus the interactions between spring temperature (usually considered a key driver of spring phenology) and all other variables into the model described above. We kept year in the model to be able to test for an interaction between year and spring temperature, which could indicate temporal changes in temperature sensitivities, for example if selective pressures were shifting population phenotypes (please refer to Table 1 for more detailed explanations of the variables, and their expected effects on phenology). χ_{ij} again included all these covariates and β_{ij} are their respective effects, that is regression slopes. We therefore modified the model equation to:

$$Y_{ij} \sim \text{Intercept} + \beta_{ij}\chi_{ij} + S_i + T_i \cdot \text{SpringTemp}_{ij} + U_i + \epsilon_{ij}$$

In model B the slopes of the linear relationships between the collection dates (= DOY of flowering) of specimens and the temperature or precipitation at the corresponding location and year estimate the sensitivities of phenology to climate changes. Here, the species random slopes are the species-specific shifts with temperature ($T_{(i)}$), accounting for the fact that some species might be more temperature sensitive than others. As for model A, we

Table 1 All explanatory variables (fixed and random effects) that were included in our analyses, together with the reasonings for including them, and their expected effects on plant phenology.

Variable	Why did we include it?	What do we expect?
Elevation	Climate conditions, including snow-melt patterns, vary with altitude, which should influence flowering patterns (Inouye, 2008; Bucher & Römermann, 2020).	Plants flower later at higher altitudes.
Year	Long-term trends of rising temperatures should result in corresponding long-term trends in plant phenology.	Plants advanced their flowering during the last century.
Spring temperature	Temperature drives plant phenology (Tang *et al*., 2016; Piao *et al*., 2019). For early flowering understory plants, spring temperature should be particularly relevant.	Plants flower earlier with warmer temperatures.
Winter temperature	To start leaf-out or flowering in spring, some plant species depend on a preceding chilling period (vernalisation) indicating that winter has passed (Tang *et al*., 2016; Piao *et al*., 2019).	Unclear, if winter chilling requirements are still meet, plants will flower earlier with warmer temperatures if not later.
Precipitation	As plant growth depends on water availability, precipitation could also influence plant phenology (Peñuelas *et al*., 2004; Matthews & Mazer, 2016).	Precipitation effect alone unclear; maybe temperature-dependent.
Spring temperature × Winter temperature	If plants experience insufficient chilling in warm winters they can be less sensitive to warm spring temperatures (Tang *et al*., 2016).	We expect a negative interaction, with plants flowering earliest when winters are sufficiently cold but springs are warm.
Spring temperature × Precipitation	AS plant growth depends on both temperature and precipitation, phenology may be driven by the interaction of the two. Matthews & Mazer (2016) showed that (in western North America) phenological responses to warming were strongest where precipitation was high.	We expect a positive interaction, with plants flowering earliest where both temperature and precipitation are increasing.
Spring temperature × Elevation	Previous studies suggested, that that plants at high elevation are more sensitive to temperature changes (Čufar *et al*., 2012; Chapman, 2013; Liu *et al*., 2014; but please refer to Vitasse *et al*., 2010; Dai *et al*., 2014).	We expect a positive interaction, with greater temperature sensitivity at higher elevations.
Spring temperature × Year	If plants have evolved in response to climate change, then sensitivity to spring temperature might have changed over the years.	We expect an interaction between temperature and collection year.
Spatially dependent random intercept (U_{ij})	Environmental conditions are variable and correlated across space. Plants that are closer to each other experience more similar conditions, and may also show more similar phenological responses (Park *et al*., 2019).	We expect substantial geographic variation, and that this will influence model estimates for other covariates.
Species (random intercept and slope) (S_i, T_i)	Flowering time, as well as its sensitivity to climate, differs between plant species.	There is variation in mean phenology (intercept) and phenological responses (slopes) of the study species.

Model A included elevation, year and the two random factors, model B also the climate variables, and the interactions of spring temperature with the other covariates.

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also fitted model B with and without including the spatial structure U_{ij}.

To estimate spatial dependency, we used INLA, an approximate Bayesian technique and faster alternative to MCMC methods for fitting Bayesian models (Bakka *et al.*, 2018). A key challenge with spatial models is that the Gaussian random field, the most common tool for capturing spatial dependency, is hard to use with large data. R-INLA solves this problem through SPDEs that allowed the modelling of Gaussian random fields fast and efficiently, and handling of complex spatial data (Lindgren *et al.*, 2011). The SPDE is the mathematical solution to the Matérn covariance function describing the statistical covariance between values at two different points. The covariance matrix of the Gaussian field is approximated as a Gaussian Markov Random Field (GMRF) using a Matérn covariance structure (Bakka *et al.*, 2018). The GMRF models spatial dependence by defining a neighbourhood structure on a mesh that divides the study area (in our case Europe) into nonoverlapping triangles (Fig. S1). The data points (in our case sampling locations of herbarium specimens) are then assigned to the adjacent nodes of the mesh according to their proximities (or to only one if they fall directly onto one). This creates an observation matrix for estimating the GMRF (Bivand *et al.*, 2015; Cosandey-Godin *et al.*, 2015). The mesh can have different shapes and sizes, and we used the default constrained Delaunay triangulation (a particular way to divide an area into triangles) together with vague priors that have little effect on the posterior distributions of the fixed effects. To select the mesh size, we compared models with different meshes and chose the finest mesh (with a maximum triangle edge length of 20 km and a minimum edge length of 5 km) as it resulted in the lowest deviance information criterion/widely applicable information criterion (DIC/WAIC) values. The derived GMRF is then represented by the term U_{ij} in the model above, a smooth spatial effect that links observations to spatial locations, with the covariance structure Ω estimated via the Matérn correlation. The term U_{ij} is therefore spatially variable and captures spatial patterns not already modelled by the fixed covariates, ensuring that the residuals $\varepsilon_{\mathrm{ij}}$ are independent. We compared the results of models with and without including U_{ij}.

To avoid biased parameter estimates because of unequal scales, we fitted covariates in the following forms: year expressed in decades, spring precipitation in mm 10^{-1}, elevation in hundred metres (100 m) and spring and winter temperature in degree Celsius (°C) We also mean-centred all covariates, because this estimated the regression slopes of each covariate with all other covariates at their mean values (rather than zero; Dalal & Zickar, 2012), which greatly helped to interpret the results of the regression analyses.

For both models we checked whether the residuals were normally distributed, plotted the distribution of residuals against fitted values and explanatory variables to check for heterogeneity or other patterns in the variances, and we plotted the observed vs fitted data to evaluate model fit and performance (Zuur *et al.*, 2017). All statistical analyses were performed in R v.3.6.2 (R Core Team, 2018) using the R-INLA package (http://www.r-inla.org, please refer to also: Rue *et al.*, 2009; Lindgren *et al.*, 2011; Bakka *et al.*, 2018).

Results

Model validation and spatial correlation

The herbarium data analysed in our study covered a broad geographical range in Europe, but their spatial distribution was heterogenous (Fig. 1) and, in addition, the flowering time data were spatially correlated up to a distance of *c.* 200 km and 100 km in models A and B, respectively (Fig. S2). If this spatial correlation was not included in the analyses, then the model residuals were clearly nonrandom in space, especially in model A (Fig. S3), and there were other violations of model assumptions, in particular nonrandom distribution of residuals in relation to several covariates (Figs S4, S5). Including spatial correlation solved these problems. Moreover, models that included spatial correlation also generally had a better fit (please refer to Fig. S6 for a comparison of DIC values and regression parameter estimates of model B with and without spatial correlation), and the fitted values were closer to the observed values ($r = 0.78$ vs 0.57 for Model A and $r = 0.82$ vs 0.70 for Model B; Fig. S7). Overall, residual variation was reduced when spatial correlation was accounted for (Fig. S8). Therefore, models that explicitly incorporate spatial correlation between data points are not only more statistically sound, but they are also stronger and more informative. In the next sections, we show that taking spatial correlation into account also substantially affects the model estimates answering the main questions of our study.

Temporal shifts in plant phenology

Overall, the herbarium data indicated that the studied 20 forest understory plants significantly advanced their flowering time during the last century (Fig. 2a,b; Table 2). The estimated advancement of flowering time was −0.56 d per decade (credible interval: −0.74 to −0.39; please refer to Table 2) according to model A with accounting for spatial correlation, and these responses were different from zero (posterior probability > 0.95) for all 20 species. For species-specific residuals please refer to Fig. S9 and, for a summary of all hyperparameters, please refer to Table S2. The observed phenology shifts corresponded with increasingly warmer spring temperatures during the last century (Fig. 2c). If model A ignored spatial correlation, it severely overestimated the overall magnitude of phenology shifts, with an estimated −1.34 d per decade (CI: −1.69 to −0.98; Table S3; Fig. 2b), that is it estimated an average shift of *c.* 2 wk during the last century, more than twice as much as in model A with spatial correlation. One reason for this discrepancy was that datapoints from northern vs southern Europe were unevenly distributed in time, with more earlier data from the north, and an overrepresentation of southern data during the last decades (Fig. 2c). When spatial information is ignored in model A, this latitudinal bias therefore distorts the estimated shift over time. The opposite is true for the relationship with elevation: in model A with spatial correlation plants flower later at higher altitudes (2.44 d/100 m; 95% CI 1.98–2.89; Table 2; Fig. 2b), but when spatial correlation is ignored there is no relationship between elevation and

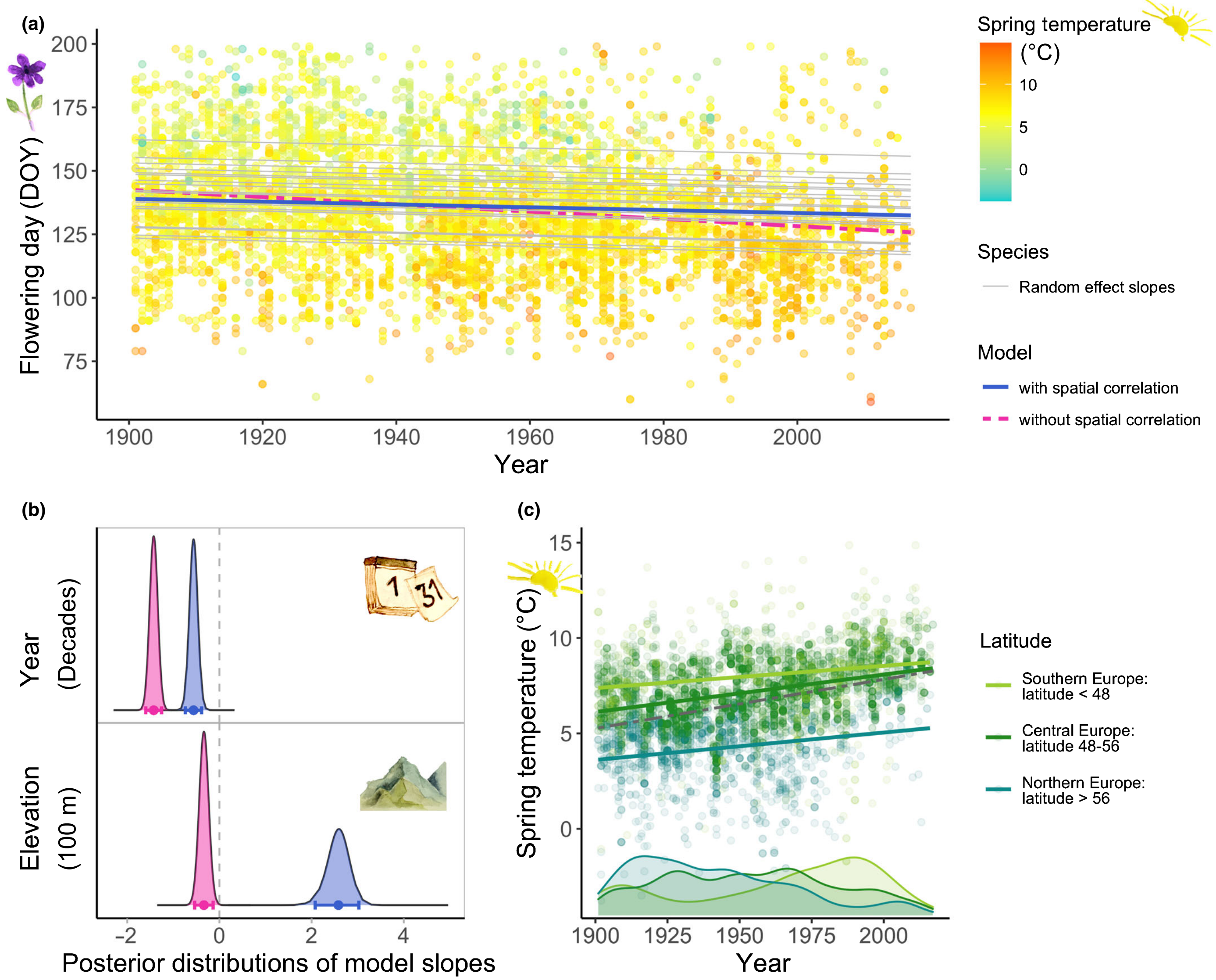

Fig. 2 Temporal trends of flowering time and spring temperature over the last century, and the results of model A. (a) Shifts of flowering time since 1901 estimated by model A with spatial correlation (solid blue line) and without spatial correlation (dashed magenta line). With spatial correlation, plants advanced their flowering on average by *c.* 6 d, and the responses were different from zero (posterior probability > 0.95) for all 20 species (thin grey lines). In the model without spatial correlation the estimated phenology shift is more than twice as large. (b) Differences in parameter estimates (posterior probability distributions) for model for model A without (magenta) and with (blue) spatial correlation. (c) Long-term trends in spring temperature in the locations of the studied herbarium specimens, separately for southern, central and northern European data. The histograms at the bottom show the temporal distributions of these data. The dashed black trend line shows the mean across all regions.

flowering time (Table S3; Fig. 2b). Even with including spatial correlation, and after the effects of the covariates year and elevation have been accounted for, there is still strong spatial variation in flowering time in model A, with plants from northern and eastern Europe flowering up to *c.* 60 d later than plants from central and southern Europe (Fig. 5).

Relationships with climate change

Across the European sampling locations included in our study, spring temperatures increased during the last century (Fig. 2c), and the phenology of the plants was related to these climatic changes. Overall, plants flowered *c.* 3.6 d earlier per +1°C (for a summary of all hyperparameters, see Tables 2, S3; Figs 3, 4). If spatial correlation was not included in model B, the strength of this relationship was overestimated with 5.4 d per +1°C (Figs 3, 4). The general temperature–phenology relationship was consistent across the 20 studied species, with negative slopes credibly different from zero (posterior probability > 0.95) for all (Fig. 3).

In addition to the relationship with spring temperature, there was a significant, albeit weaker, relationship with winter temperature, but no relationship with precipitation, in the model B with spatial correlation (Table 2; Fig. 4). There were further relationships of phenology with elevation and the year of sampling (Table 2; Fig. 4). The direction of these results – later flowering at higher altitudes and earlier flowering in more recent specimens

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Table 2 Model estimates (slopes), with standard deviations and 95% credible intervals, for all variables included in models A and B with spatial autocorrelation.

	Estimate	SD	95% CI
Model A			
Intercept	136.09	4.07	128.02, 144.03
Years (decades)	−0.56	0.09	−0.74, −0.39
Elevation (100 m)	2.57	0.24	2.08, 3.02
Model B			
Intercept	138.62	2.52	133.57, 143.48
Spring temperature (°C)	−3.61	0.22	−4.04, −3.18
Winter temperature (°C)	−1.05	0.13	−1.31, −0.79
Precipitation (mm/10)	0.07	0.15	−0.23, 0.37
Elevation (100 m)	1.42	0.21	1.00, 1.84
Year (decade)	−0.22	0.09	−0.40, −0.04
Spring temperature × Year	0.05	0.04	−0.03, 0.13
Spring temperature × Elevation	0.06	0.05	−0.04, 0.16
Spring temperature × Precipitation	−0.04	0.06	−0.16, 0.07
Spring temperature × Winter temperature	−0.06	0.03	−0.12, 0.01

– was as in model A, only with smaller effect sizes. This is because both the year of sampling and elevation are systematically related to temperature, so the larger effects in model A are partly temperature effects. None of the interaction terms between spring temperature and the other covariates were significant (Table 2). Ignoring the spatial locations of specimens also substantially affected these parameter estimates: in model B without spatial correlation the relationship with elevation was underestimated, whereas the relationship with winter temperature was lost, and there was now a relationship with precipitation, and several significant interactions between covariates (Table S5; Fig. 4).

As in model A, there was significant spatial variation in flowering time after the covariates and their interactions had been accounted for (Fig. 5, right panel). Although the residual spatial correlation was clearly much less and more small scale than in model A, there were still several regions with clustering of positive or negative residuals, showing the importance of incorporating spatial correlation also in model B.

Discussion

Herbaria are unique archives for studying long-term responses of plant phenology to anthropogenic climate change. Here, we studied herbarium specimens of 20 early-flowering forest herbs across Europe and show that these plants advanced their flowering during the last century, most likely in response to increasing spring temperatures. However, our analysis showed that phenology did not advance the same everywhere in Europe. The herbarium data we used were substantially autocorrelated in space – even after accounting for elevation, climate and year – and the inclusion of this spatial structure in our statistical models significantly improved the model fit and parameter estimates. One reason for this is that herbarium specimens are not evenly distributed in space and time (Daru *et al.*, 2017). This is particularly critical when spatial and temporal heterogeneity are confounded, that is some regions are more or less well sampled during particular time periods than others. For instance, in our study there were generally more data points from northern Europe for the first half of the 20th century and more data points from southern Europe for the second half of the century (please refer to Fig. 2c). Given this spatio-temporal variation, we discuss only the results from models that accounted for spatial correlation.

Temporal shifts in plant phenology

We found that forest understory herbs from central Europe advanced their flowering by an average of 6 d during the last century (−0.6 d per decade). Previous herbarium studies conducted in the temperate zone estimated flowering time shifts between −0.4 and −1.5 d per decade (Primack *et al.*, 2004; Miller-Rushing *et al.*, 2006; Molnar *et al.*, 2012; Panchen *et al.*, 2012; Bertin, 2015; Bertin *et al.*, 2017). All of these studies were geographically very restricted and, except for one study from Hungary (Molnar *et al.*, 2012), all came from the northeastern USA. There have been other longer-term studies on phenology trends in Europe, but these were based on field observations, and they did not go back further than the 1970s. The trends reported in these observational studies tend to be stronger (−2.5 to −4.5 d per decade; Fitter & Fitter, 2002; Menzel *et al.*, 2006), indicating that phenological changes may have accelerated during the last decades in response to more rapid climate changes (European Environmental Agency, 2020).

Relationships with climate warming

The long-term changes in plant phenology we detected are likely to be responses to climate change, in particular rising spring temperatures. For each 1°C of temperature increase, the herbarium specimens were on average collected −3.6 d earlier. In Europe, land temperatures have increased *c.* 1.5°C since 1900 (Luterbacher *et al.*, 2004; Harris *et al.*, 2014; European Environmental Agency, 2020), so the magnitude of overall phenological changes we observed is similar to what would be expected based on climate change and the observed temperature sensitivities (1.5°C × 3.6 d/°C = 5.4 d, vs our observed average shift of *c.* 6 d). Previous herbarium studies from the temperate zone estimated similar flowering-time advancements of −2.4 to −6.3 d per 1°C temperature increase (Primack *et al.*, 2004; Miller-Rushing *et al.*, 2006; Panchen *et al.*, 2012; Calinger *et al.*, 2013; Hart *et al.*, 2014; Bertin, 2015; Davis *et al.*, 2015; Bertin *et al.*, 2017). Again, most of these studies were from the northeastern USA, and they were often geographically very restricted. Two previous herbarium studies from Europe found stronger shifts of −6 to −13 d per 1°C (Robbirt *et al.*, 2011; Diskin *et al.*, 2012), but both were based on single species in rather restricted geographic areas. More robust European data found a similar average advancement of plant phenology of 2.5 d per 1°C temperature increase (Menzel *et al.*, 2006). A long-term field observation in the UK found advances of −1.7 to −6.0 d per 1°C across 385 plant species (Fitter & Fitter, 2002). In a field monitoring study of a subset of 16

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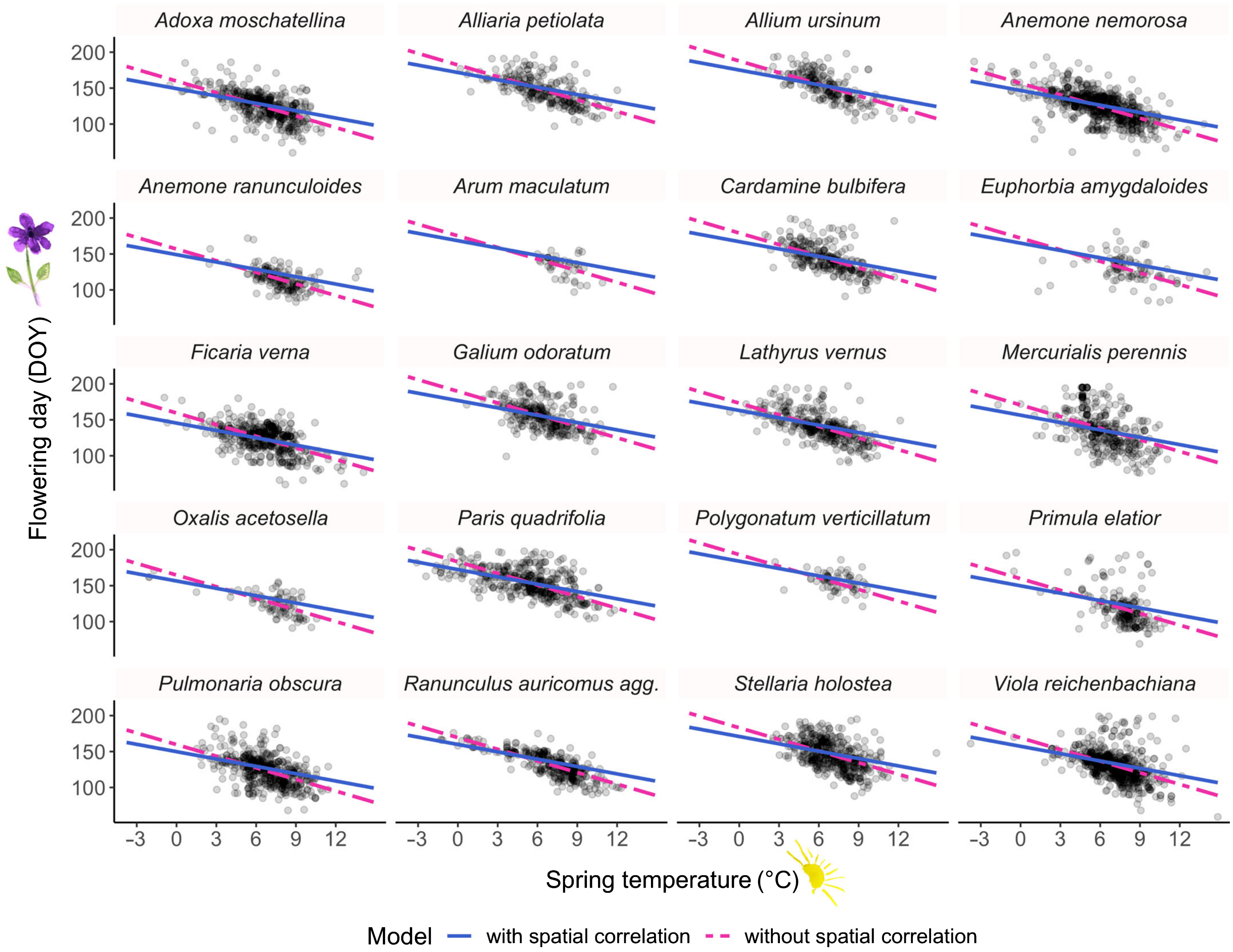

Fig. 3 Relationships between the spring (March–May) temperature in the year of collection and the date of collection (= flowering day) of European herbarium specimens of 20 early-flowering forest understory plants. The blue and magenta lines indicate slope estimates from statistical models with and without taking spatial autocorrelation into account, respectively.

of our study's species, we recently showed that flowering time was −4.5 d earlier per 1°C temperature increase of the local microclimate (Willems *et al.*, 2021). So the overall pattern of 3–4 d earlier phenology per degree of warming appears quite robust across a range of species and temperate regions, and our study strongly indicates that this large-scale biological response to anthropogenic climate change has also been taking place in Europe during the last century. That the plants in our study also flowered earlier with warmer winter temperatures suggests that their potential chilling requirements (indicating that winter has passed) are however still fulfilled. However, this might change if winter temperatures keep rising.

Other drivers of phenology variation

While temperature may be a key driver of phenology, it is not the only one, and often does not explain all observed phenology variation (Marchin *et al.*, 2015; Piao *et al.*, 2019). We found that, across the study area, plants flowered later at higher elevation, and this pattern remained significant even if temperature was included as explanatory variable. Therefore, the later flowering at higher elevations must be more than a temperature effect, and it indicates that phenology advances are slower at higher altitudes, maybe because plants at higher elevation are less sensitive to temperature changes (Vitasse *et al.*, 2010; Dai *et al.*, 2014). Conversely, the residual spatial variation in our model B indicates that, in some mountainous regions (especially the Alps), plants flowered earlier than expected (after accounting for all covariates) and therefore, by contrast, might be more sensitive to temperature changes (Chapman, 2013; Liu *et al.*, 2014). A solution for this apparent contradiction could be that the relationship between elevation and phenology is nonlinear, or confounded with other environmental variables. Previous studies that related phenology to altitude found mixed results, from slower to faster phenology changes at high elevations (Defila & Clot, 2005; Ziello *et al.*, 2009; Čufar *et al.*, 2012; Kopp *et al.*, 2020).

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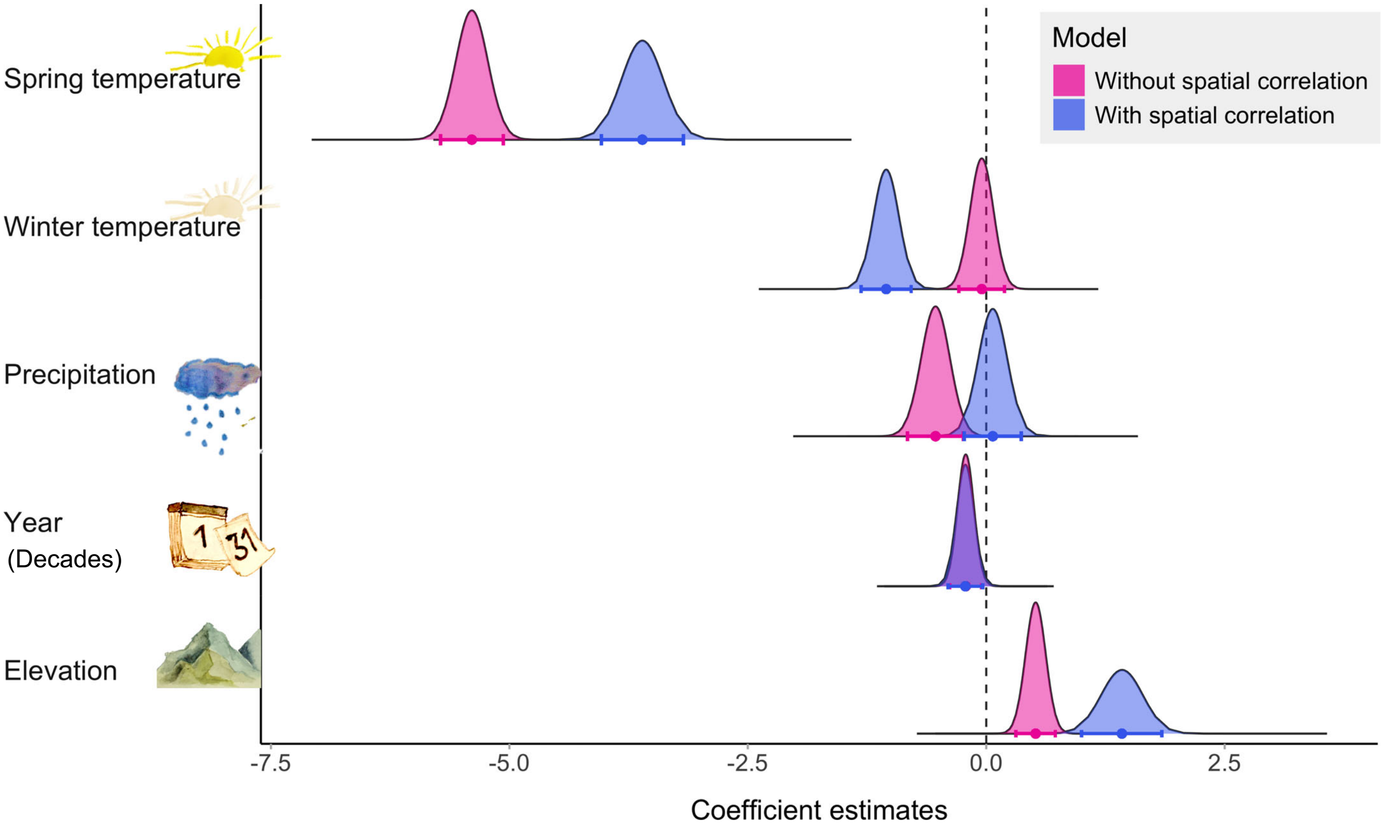

Fig. 4 Model coefficient estimates for relationships between different covariates (climate in the year of collection, year of collection, elevation of collection site) and the date of collection (= flowering time) of herbarium specimens of 20 forest wildflowers in Europe. The blue vs magenta curves show the differences between the parameter estimates (posterior probability distributions) from model B with and without taking spatial autocorrelation into account.

Clearly, the relationship between elevation and phenology changes is not well understood, and large-scale herbarium plus climate data that correct for spatial autocorrelation have the potential to shed more light on this.

In addition to temperature, another climate factor that could potentially influence plant phenology is precipitation. We had expected a significant interaction with temperature, with the strongest phenology advances for which both temperature and precipitation were increasing, but there was no evidence for precipitation effects in our data at all. Previous research found that changes in rainfall and water availability can influence phenology but with substantial geographical differences, for example in Mediterranean forests and shrublands (Peñuelas *et al.*, 2004). Another complication with precipitation effects is that if precipitation occurs as snow this may influence phenology in different ways than rainfall. Increased snowfall often delays plant growth and flowering (Park & Mazer, 2018), another potential explanation for why, overall, plants flowered later at higher elevations in our study. As global warming is expected to change snowmelt more severely at higher elevations, it might have quite different effects on species at higher altitudes than on those at lower elevation (Cornelius *et al.*, 2013), which in turn can cause problems for migrating or hibernating animal species across altitudinal gradients (Inouye *et al.*, 2000).

Spatial variation in phenology

Spatial autocorrelation has so far been largely ignored in herbarium-based studies of long-term phenology changes. However, it is important to take spatial variation into account not only because herbarium data are generally strongly spatially clustered, but also because neither phenology nor phenological responses to climate change are expected to be spatially homogenous across larger geographic scales. For previous studies that were geographically very restricted (Bertin, 1982; Primack *et al.*, 2004; Miller-Rushing *et al.*, 2006; Miller-Rushing & Primack, 2008; Bertin *et al.*, 2017) the problem may have been minor, but larger scale analyses will be required to take spatial variation into account. Recently, Park & Mazer (2018) studied phenological shifts across several climatic zones and Park *et al.* (2019) and Kopp *et al.* (2020) explicitly tested for geographic differences in phenological sensitivities in North America. To our knowledge, our study is the first herbarium-based study that modelled and mapped such spatial variation as a continuous variable in an analysis of large-scale phenology variation.

The most conspicuous pattern in the residual spatial variation of our data was that there appeared to be systematic differences in phenology associated with latitude, even when accounting for climatic variation. In particular, plants from central Europe

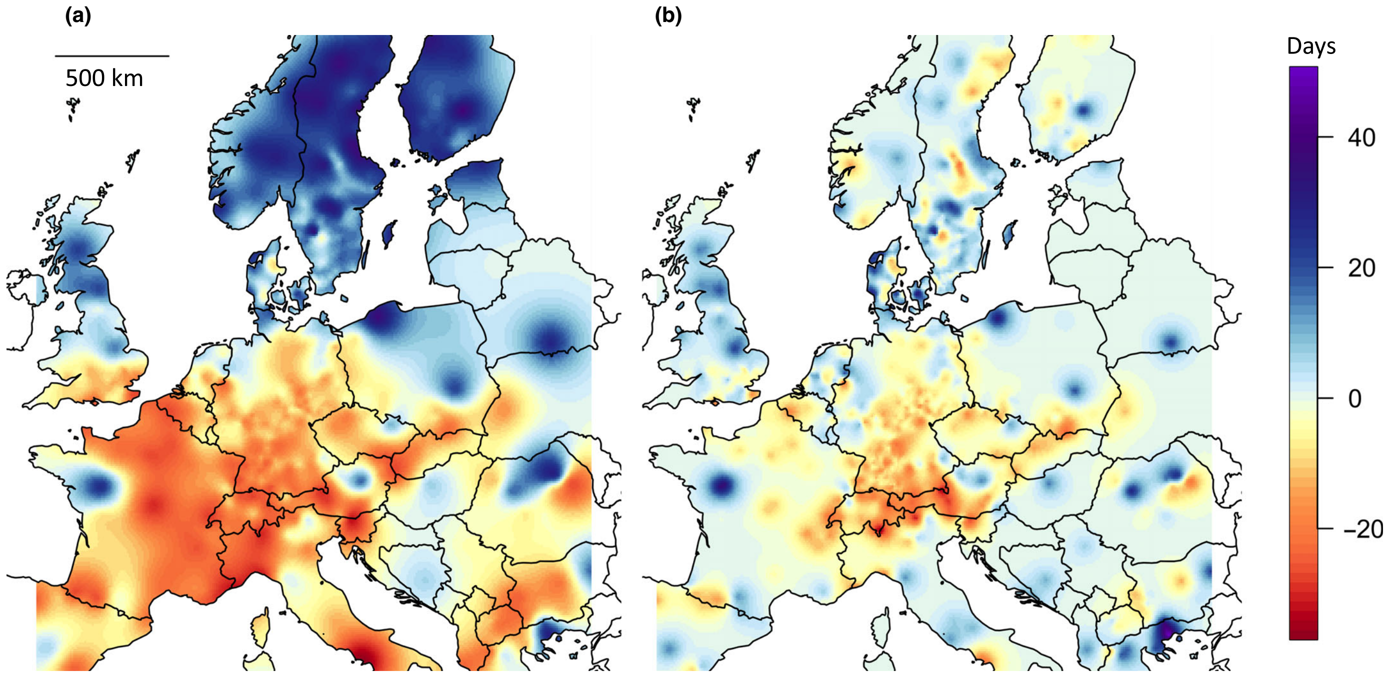

Fig. 5 Spatial variation in flowering time in model A (a) and model B (b) after the effects of the covariates (model A: year and elevation; model B: year, elevation, spring and winter temperature, and spring precipitation) have been accounted for. The values are numbers of days deviation from model predictions.

(especially around the Alps) flowered earlier than predicted by our model. Such deviations indicate that we were either missing an important driver, or that plant responses to some of the covariates in the model differed geographically. Previous studies often found phenology shifts at high latitudes to be stronger in absolute terms (Root *et al.*, 2005; Parmesan, 2007; Ge *et al.*, 2015) but weaker in relative terms (= per degree warming) than at low latitudes. This is usually explained by stronger temperature increases in northern regions (IPCC, 2014), but lower temperature sensitivity of northern populations (Dai *et al.*, 2014; Ge *et al.*, 2015; Shen *et al.*, 2015; Wang *et al.*, 2015a,b; Park *et al.*, 2019; but please refer to Pudas *et al.*, 2008; Wolkovich *et al.*, 2012; Dai *et al.*, 2014). The latter may be a (late frost) risk-avoiding adaptation to variable, less reliable climates, causing plants populations to rely more on photoperiod (Renner & Zohner, 2018). However, some studies also found that plants from (far) northern regions are more sensitive to temperature and require less warming to trigger leaf-out or flowering (Riihimäki & Savolainen, 2004; Pudas *et al.*, 2008; Liang & Schwartz, 2014; Prevéy *et al.*, 2017), ensuring that plants start growing as soon as growth conditions become good in early spring, which may be crucial in cold regions with short growing seasons. Consequently, phenological sensitivity to temperature might decrease from southern to mid-northern latitudes, but increase again in far-northern or high elevation regions. This could indeed explain the earlier-than-expected phenology that we observed in central Europe and the Alps. The missing consensus among studies about the association between latitude and phenology may be partially due to differences in spatial scale and because their relationship is complex, confounded with other environmental factors such as temperature and elevation, or nonlinear (Riihimäki & Savolainen, 2004; Chmura *et al.*, 2019; Kopp *et al.*, 2020). Such challenges can be tackled by analysing geographic patterns via a continuous spatial field (as we did here, using R-INLA) that explicitly maps differentiated geographic variability of phenology.

Conclusions

The flowering time of forest herbs in Europe has substantially advanced during the last century, and these advances are strongly associated with climate warming. While this may to some extent be considered good news, because plants so far were able to track climate change (Munguia-Rosas *et al.*, 2011), the observed phenological shifts will have further consequences for the species and their associated ecological communities. Our study demonstrates how herbarium specimens, together with spatial modelling, can be used to expand not only the temporal but also geographic and taxonomic scope of phenology research, and contribute to understanding global environmental change (Wolkovich *et al.*, 2014). Herbarium data from large geographic ranges are particularly powerful, but they also come with challenges, and we showed that accounting for spatial autocorrelation significantly improved model fits and parameter estimates. Phenology as well as phenological responses to climate change can vary substantially across large scales, and failing to account for this might draw a biased picture of how climate change affects plants and their associated communities and ecosystems. Future studies should more frequently employ spatial modelling when analysing large-scale phenology variation and its different drivers, ideally across multiple climatic regions.

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Author contributions

FMW, OB and JFS designed the study; FMW collected the herbarium data; FMW compiled and analysed all data; and FMW wrote the manuscript with all coauthors contributing to revisions.

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Data availability

The data set used in this paper is publicly available through the Biodiversity Exploratories Information System (https://www.bexis.uni-jena.de/): https://doi.org/10.25829/bexis.31230-10 for direct link to the data set. The GBIF data are from the Global Biodiversity Information Facility (GBIF.org; 17 July 2020; GBIF Download: https://doi.org/10.15468/dl.5ckxxb). The climate data are available from the Climate Research Unit (https://crudata.uea.ac.uk, version: cru_ts4.04).

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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 The mesh – based on refined Delaunay triangulation – used to estimate spatial autocorrelation of herbarium specimen data across Europe.

Fig. S2 The spatial correlation of flowering time data in models A and model B (after the effect of the covariates have been accounted for).

Fig. S3 Spatial patterns in the residuals of the model A and model B, without and with accounting for spatial correlation in the models.

Fig. S4 Residuals plotted against each covariate in model A without and with spatial correlation.

Fig. S5 Residuals of model A plotted against covariate that were not included in model A, without and with spatial correlation.

Fig. S6 DIC values and model estimates (regression coefficients) of model B without spatial correlation and with spatial correlation, using different mesh sizes.

Fig. S7 Observed vs fitted values for model A and model B, without and with spatial correlation.

Fig. S8 Residuals vs fitted values and histogram of the residuals of model A without and with spatial correlation.

Fig. S9 Residuals (of model A) for each species (that were included as a random factor) without and with spatial correlation.

Table S1 The 20 studied forest understories herbs, their respective families and the number of herbarium specimens of each species that were included in the analyses.

Table S2 Estimates, standard deviations and 95% credible intervals for the hyperparameter values in model A with spatial correlation.

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Table S3 Model estimates, standard deviations and 95% credible intervals for the parameters in model A without spatial correlation.

Table S4 Estimates, standard deviations and 95% credible intervals for the hyperparameter values in model B with spatial correlation.

Table S5 Estimates, standard deviation and 95% credible intervals for the parameters and hyperparameters in the model B version without spatial correlation.

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