Spring understory herbs flower later in intensively managed forests

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Abstract. Many organisms respond to anthropogenic environmental change through shifts in their phenology. In plants, flowering is largely driven by temperature, and therefore affected by climate change. However, on smaller scales climatic conditions are also influenced by other factors, including habitat structure. A group of plants with a particularly distinct phenology are the understory herbs in temperate European forests. In these forests, management alters tree species composition (often replacing deciduous with coniferous species) and homogenizes stand structure, and as a consequence changes light conditions and microclimate. Forest management should thus also affect the phenology of understory herbs. To test this, we recorded the flowering phenology of 16 early-flowering herbs on 100 forest plots varying in management intensity, from near-natural to intensely managed forests, in central and southern Germany. We found that in forest stands with a high management intensity, such as Norway spruce plantations, the plants flowered on average about 2 weeks later than in unmanaged forests. This was largely because management also affected microclimate (e.g., spring temperatures of 5.9°C in managed coniferous, 6.7 in managed deciduous, and 7.0°C in unmanaged deciduous plots), which in turn affected phenology, with plants flowering later on colder and moister forest stands (+4.5 d per −1°C and 2.7 d per 10% humidity increase). Among forest characteristics, the percentage of conifers had the greatest influence on microclimate, but also the age, overall crown projection area, structural complexity and spatial distribution of the forest stands. Our study indicates that forest management alters plant phenology, with potential far-reaching consequences for the ecology and evolution of understorey communities. More generally, our study demonstrates that besides climate change other drivers of environmental change, too, can influence the phenology of organisms.

Key words: climate change; forest structure; global change; land-use change; microclimate; phenological shifts; structural equation modeling; temperature.

INTRODUCTION

Phenology is the study of the timing of recurrent biological events, the biotic and abiotic drivers of this timing, and its variation within and among species (Lieth 1974). It includes the seasonal timing of key life events, such as animal migration or reproduction, or the leaf-out, flowering, and fruiting of plants, which are important for individual fitness. In plants, many phenological events are triggered by abiotic environmental factors, especially temperature, and are therefore sensitive to climate change (Walther et al. 2002, Schwartz et al. 2006, Tang et al. 2016, Chuine and Regniere 2017). Long-term observational studies have found earlier leaf-out and changes in the start of flowering associated with climate change across the world (Fitter and Fitter 2002, Schwartz et al. 2006). Spring-flowering plants seem to be particularly responsive to climate change and often show the largest phenological shifts (Fitter and Fitter 2002, Chmielewski et al. 2004, Pau et al. 2011, Renner and Zohner 2018).

Plants play a key role in many ecosystems, and they interact with many other species. Therefore shifts in plant phenology can have significant consequences for pollinators, food webs, and agricultural yields, as well as many ecosystem functions and services such as productivity and carbon cycling (Reilly et al. 1996, Chmielewski et al. 2004, Cleland et al. 2007, Tang et al. 2016). Understanding the drivers of phenology variation is thus important to predict future states of species abundance and distribution, biogeochemistry and ecosystem productivity, as well as ecosystem services such as pollination (Durant et al. 2005, Memmott et al. 2007, Chuine 2010, Richardson et al. 2010, 2013, McKinney et al. 2006).
2012, Haye et al. 2013, Kharouba et al. 2018), and it should also help to inform environmental conservation (Cerdeira Morellato et al. 2016) and to develop adaptive management strategies in a changing world (Walther 2010, Bellard et al. 2012, Enquist et al. 2014, Pacifici et al. 2015).

However, our mechanistic understanding of the impact of environmental change on plant phenology is still limited (Richardson et al. 2012). In particular, besides climate warming, the influences of other global change drivers—such as land-use change—on plant phenology have received little attention. Climatic cues that have been shown to influence phenology can be influenced by topography or forest cover at small spatial scales (Geiger et al. 2003). As a consequence, microclimates can differ from regional climate patterns and affect the timing of phenological events on small spatial scales (Hwang et al. 2011, Ward et al. 2018). Forest understory microclimates are often buffered against extreme heat or cold and macroclimatic warming (De Frenne et al. 2013, 2019, Zellweger et al. 2019). Valdés et al. (2015) showed that in European forests plant diversity depends more on forest habitat features than on landscape structure or microclimate. Within forests, differences in stand structure affect the microclimate and light availability (Chen et al. 1999, Baker et al. 2014, Ehbrecth et al. 2019) and is thus likely to impact flowering phenology of understory herbs. Forest stand structure can be defined as the distribution of trees in space and their variability in size, arrangement, consistency, and time (Schall et al. 2018). Stand structure can, for example, be characterized by the main tree species, the ages of trees, the mean and variation in diameter at breast height, the basal area covered, or their crown projection area (Schall et al. 2018). Furthermore, stand structural complexity indices (SCI; see, e.g., Zenner and Hibbs 2000) can combine several structural attributes (Gossner et al. 2014, del Río et al. 2016) or take the spatial distribution of trees into account (Penttinen et al. 1992, Ehbrecth et al. 2017). Zellweger et al. (2019) showed that changes in canopy cover and composition change understory temperature in temperate forest across Europe.

Changes in forest management alter stand structure in temperate forests and, as a consequence, microclimate conditions. Although thinnings and selection cuttings lead to only small increases of radiation at the forest floor (Aussenac 2000, Hale 2003), clear-cuttings radically reduce the canopy cover and thus result in drastic and persistent changes of the microclimate. In deciduous forests, there is a time window during spring when the leaf-out of trees is not yet completed that allows early spring-blooming species to take full advantage of the available sunlight, moisture, and nutrients of the forest floor (Lapointe 2001). Planting of evergreen coniferous trees—such as Norway spruce (Picea abies (L.) H. Karst), one of the most economically important tree species in Europe (Spiecker 2003)—reduces the light availability during early spring and changes microclimatic conditions. Furthermore, Ehbrecth et al. (2017) showed that structural complexity was higher in even-aged, mature European beech stands and uneven-aged, single-tree selection systems than in coniferous stands. Actually, structural complexity of coniferous stands increased linearly with increasing proportion of broad-leaved tree species such as European beech (Juchheim et al. 2020). More generally, all management changes that alter tree species composition and stand structure are likely to also affect the phenology of forest understory herbs through changes in radiation, microclimate or other factors. Because of their narrow and distinct flowering period, spring-flowering forest herbs should thus be particularly susceptible to management changes, and therefore they are a particularly relevant study system for exploring forest management effects on plant phenology.

Here, we hypothesized that forest management would change forest structure and thereby microclimatic conditions and, as a consequence, flowering phenology. To investigate this, we studied the phenology of 16 early-flowering forest herb species on 100 forest plots of different management type and intensity. The studied forest plots ranged from protected unmanaged forests and extensively managed selection system forests to managed deciduous age-class forests (from young thickets to mature timber plots) and intensively managed Norway spruce plantations. For each study plot, we obtained detailed phenology, forest structure and microclimate data. We first looked at the overall effect that management intensity had on phenology, and we then analyzed the effects of different individual microclimatic and forest structural traits on phenology. Finally, we used structural equation modelling to get a better understanding of the possible underlying causal relations, and to disentangle direct and indirect effects of forest characteristics and microclimatic variation on plant phenology. We expect unmanaged, old, and structurally complex deciduous forests to have sheltered, warmer microclimatic conditions during spring than age-class forests (especially young thickets which have a drastically reduced crown projection area of remaining mature trees) or the highly managed and homogenous spruce plantations. Thus, we generally expected understory plant species to flower later on more disturbed and more intensively managed forests. Specifically, we asked the following questions: (1) Does forest management intensity affect plant phenology? (2) Which forest characteristics are the strongest drivers of phenological variation? (3) To what extent does forest management affect phenology through changing microclimate?

**Methods**

**Study system**

Most forests in Central Europe have a rather low tree diversity and are dominated by only few deciduous tree
species (Schulze et al. 2016). Therefore, variation in stand composition is to a substantial degree related to the effects of forest management (Schall et al. 2018). We studied the forest plots of the Biodiversity Exploratories project (www.biodiversity-exploratories.de) in Germany, a large-scale platform for ecological research that includes a broad range of forests plots of different management types and intensities (Fischer et al. 2010). We focused on 100 forest plots (100 × 100 m) located in equal parts in two of the three regions of the Biodiversity Exploratories, the Schwäbische Alb in Southwest Germany (longitude 9.39°, latitude 48.44°) and the Hainich-Dün in Central Germany (longitude 10.47°, latitude 51.16°). The elevation at sea level (a.s.l.) ranges from 285 to 550 m in the Hainich-Dün area to 460–860 m on the Schwäbische Alb. Further details on the characteristics of the regions are provided in Fischer et al. (2010). The forests in the study areas are dominated by native deciduous trees, mainly European beech (Fagus sylvatica L.). However, decades ago some forests were been converted to plantations of Norway spruce (P. abies), a coniferous species originally restricted to montane and subalpine regions, but cultivated for timber in the lowlands for the last 250 yr (see Fig. 1 and Schall et al. 2018). The studied plots included (more intensively managed) even-aged deciduous forests at a range of developmental stages, but also uneven-aged and unmanaged deciduous plots, as well as managed even-aged stands of coniferous spruce forests of different age-classes (see Appendix S1: Table S6 and Schall et al. 2018). On all but three plots the main tree species was either beech or spruce, and we therefore grouped all beech plots together with the three other hardwood-dominated plots as deciduous forest plots (N = 83 plots) for the subsequent analyses.

![Fig. 1. Impressions from the study plots. Top: beech plot at the Hainich-Dün. Bottom: spruce plot at the Schwäbische Alb. Both photos were made in April 2017](image-url)
whereas plots dominated by Norway spruce were labelled as coniferous forest plots ($N = 17$ plots).

**Phenological monitoring**

From March to June 2017, we monitored the phenology of 20 early-flowering herbs in the understories of our study plots (Appendix S1: Table S1). The monitored species included all common spring-flowering herbs in the plots. For all further analyses, we only considered the 16 species that were flowering on at least 10 plots (see Fig. 2). Most of the studied species (12 out of 16) grew on both deciduous and coniferous forest plots. We visited all 100 forest plots once per week and monitored the phenology of all plants within a 3-m-wide strip outside the $20 \times 20$ m core area of each plot, corresponding to an area of $224$ m$^2$ within each 1-ha plot. For each species in each plot, we recorded flowering start as the day of the year with the first fully open flower, and flowering end as the time when no fully open flowers could be found anymore. To be able to determine flowering peaks, we counted the number of open inflorescences or,
if plants were abundant on a plot, we estimated the percentages of flowering individuals. We then defined the day of the year with the highest number or percentage of open inflorescences as the day of flowering peak. If there were 2 d with equal maximum flowering, we used their median as the time of peak flowering. If it was apparent during a weekly visit of a plot that a start, peak, or end of flowering had been well between the present and past visit, we dated this record back between the two visits, resulting in an effective half-weekly resolution of our data. For an overview of the overall and species specific number of plots and data points per region and forest type see Appendix S1: Table S2.

Forest characteristics

The structure of the studied forests is strongly influenced by management, and it can be characterized by differing forest attributes. The required data have been collected in two forest inventories that were conducted on the forest plots of the Biodiversity Exploratories at single-tree level for all living trees with a diameter at breast height ≥7 cm. We used the data from the most recent inventory (2014–2016). Specifically, we used the following individual variables: main tree species (deciduous vs. coniferous), the mean age of the main tree species, the richness and diversity (inverse Simpson’s index) of tree species, crown projection area of mature trees, the share of conifers based on crown projection, stand density, the mean diameter at breast height and its standard deviation, and the basal area covered with trees. Furthermore, we used Morisita’s index of dispersion as well as Clapham’s variance mean ratio as measures of horizontal heterogeneity (for both <1: regular, >1: clumping; 1: random; 20 × 20 m raster cells), and Zenner’s structural complexity index based on tree height as a proxy for vertical structural complexity (Zenner 1998). We selected these variables because they characterize stand structure, and we expected them to have an influence on microclimatic conditions as well as on light availability and other abiotic and biotic factors.

In addition to these individual forest variables, we also used a synthetic index for silvicultural management intensity (SMI) developed by Schall and Ammer (2013). This index combines data on tree species, stand age and stand biomass into a quantitative measure of forest management intensity. The main idea of the SMI index is that it has a component related to tree density (SMI₅) based on the discrepancy between potential and actual basal area, that is, how far away a forest stand is from equilibrium biomass, and a component related to “risk” (SMIₓ) based on stand age and tree species, which determine the susceptibility of a stand to natural disturbances and thus the need to manage such stands more intensively. A recent study by Gossner et al. (2014) demonstrated that SMI is indeed strongly negatively correlated with other estimates of forest “naturalness.” For more details on the SMI index please see Schall and Ammer (2013), and for an overview of all forest characteristics used in our study see Table 1.

Microclimate and other environmental data

In addition to the data on forest structure, there is detailed information on local microclimate available for all plots in the Biodiversity Exploratories (Fischer et al. 2010). On every plot, air temperature is measured at 10 cm above ground as well as several depths below ground using a multilayer temperature sensor (Meier-NT GmbH, Zwönitz, Germany), air temperature, and air humidity at 2 m above ground using a Mela KPCI/S-ME sensor (MELA Sensortechnik GmbH, Mohlsdorf-Teichwolfframsdorf, Germany), and soil moisture at 10 cm below ground using a Delta-T ML2X soil humidity probe (Delta-T Devices Ltd., Cambridge, UK). All data were taken at hourly intervals and stored on an ADL-MX data logger system (Meier-NT GmbH, Zwönitz, Germany). To be able to test for relationships between microclimate, forest management, and phenology, we compiled data for two different potentially relevant time periods, the spring months during which our phenology monitoring took place, and the preceding winter months. For the spring months (February–May 2017), we calculated the average air temperature at 10 cm and 2 m above ground, the growing days (=days with mean temperatures between 10°C and 30°C), the growth sum (=sum of mean day temperatures > 5°C [-5]), the warm sum (=sum of mean day temperatures with >10°C [-10]), mean relative air humidity (measured at 2 m), as well as mean soil moisture and soil temperature (both measured at 10-cm depth). For the winter months (October 2016–January 2017), we also calculated the mean air temperature (measured at 2-m height and 10-cm height), the number of cold days (=days with a temperature minimum <0°C), the cold sum (=sum of mean day temperatures <0°C), the number of cool days (=days with a temperature maximum <10°C), the number of ice days (=days with a temperature maximum <0°C), mean relative air humidity (measured at 2 m), as well as mean soil moisture and soil temperature (both measured at 10-cm depth).

In addition to the microclimate data, we also included several geographical variables that we expected to influence abiotic conditions at the stand level, such as region and a slope variable—calculated by multiplying inclination (in degrees; average over the plot area) by 1 for south-, −1 for north-, and 0.5 for east- and west-facing slopes, to be able to distinguish slopes in the four cardinal directions which are known to differ in their microclimatic conditions (Dahlgren et al. 2007). Elevation above sea level is confounded with region and therefore not included as an explanatory variable. For an overview of all explanatory variables, see Table 1.
Our data analyses following a three-step logic. First, to get an overview of the overall effect forest management intensity had on flowering time we employed a linear mixed effect model, pooling all data, with silvicultural management intensity (SMI) as the explanatory variable and species as random factor. Second, we used univariate linear regression to test the effects of forest management intensity, as well as individual forest characteristics and microclimatic variables on flowering time for each species separately. Third, we selected a subset of these variables for structural equation modeling, to understand the relationships between forest characteristics and microclimate, and disentangle direct and indirect effects on plant phenology. Prior to the data analyses, we checked all variables for outliers, and if outliers clearly resulted from measurement errors, we removed them from our data set. Such outliers were generally very rare; we removed only a few data points from three different plots. For the statistical analyses we excluded 4 (out of the original 20 species, see Appendix S1: Table S1) species that were flowering on less than 10 plots (Adoxa moschatellina L., Euphorbia amygdaloides L., Polygonatum verticillatum L., and Pulmonaria obscura Dumort).

### Table 1. Overview of all explanatory variables used in our study

| Variable | Explanation |
|----------|-------------|
| **Geographic variables** | |
| **Slope** | Inclination multiplied by 1 for south-, –1 for north-, and 0.5 for east- and west-facing slopes |
| **Region** | Schwäbische Alb vs. Hainich-Dün |
| **Forest variables** | |
| **Age (yr)** | Mean age of the main tree species |
| **Basal area (m²/ha)** | Total basal area covered by trees |
| **Clapham’s variance mean ratio** | A measure of horizontal dispersion, <1: regular, ≈1: random, >1: clumping |
| **Crown projection area (m²/ha)** | Cumulative crown projection area of trees |
| **Coniferous basal area (%)** | Percentage of conifers based on basal area |
| **Coniferous crown projection (%)** | Share of conifers based on crown projection area |
| **Diameter at breast height (cm)** | Mean diameter at breast height |
| **Standard deviation of DBH (cm)** | Standard deviation of the diameters at breast height of trees |
| **Main tree species** | Main tree species: deciduous vs. coniferous |
| **Morisita’s index of dispersion** | Horizontal dispersion, <1: regular, ≈1: random, >1: clumping |
| **Silvicultural management intensity (SMI)** | Synthetic index of forest management intensity developed by Schall and Ammer (2013), 0 = lowest to 1 = highest |
| **Species diversity** | Species richness = number of tree species |
| **Species diversity 2D** | Tree species diversity based on abundance = inverse Simpson’s index |
| **Stand density (trees/ha)** | Total number of trees |
| **Structural complexity (m²/m²)** | Zenner’s structural complexity index based on tree height. A proxy for vertical structural complexity |
| **Microclimatic variables Spring (Feb–May)** | |
| **Air temperature 2 m (°C)** | Air temperature measured at 2 m above ground |
| **Air temperature 10 cm (°C)** | Air temperature measured at 10 cm above ground |
| **Growing days** | Number of days with temperatures between 10°C and 30°C |
| **Growth sum** | Sum of mean day temperatures > 5°C (–5) |
| **Warm sum** | Sum of mean day temperatures > 10°C (–10) |
| **Soil temperature (°C)** | Soil temperature at 10 cm below surface |
| **Relative air humidity (%)** | Mean relative air humidity measured 2 m above ground |
| **Soil moisture (%)** | Soil moisture at 10 cm below surface |
| **Microclimatic variables winter (Oct–Jan)** | |
| **Air temperature 2 m (°C)** | Air temperature measured 2 m above ground |
| **Air temperature 10 cm (°C)** | Air temperature measured 10 cm above ground |
| **Ice days** | Number of days with a temperature maximum <0°C |
| **Cold days** | Number of days with a temperature minimum <0°C |
| **Cold sum** | The sum of days with a mean day temperature <0°C |
| **Cool days** | Number of days with a temperature maximum <10°C |
| **Soil temperature (°C)** | Soil temperature at 10 cm below surface |
| **Soil moisture (%)** | Soil moisture at 10 cm below surface |
| **Relative air humidity (%)** | Mean relative air humidity measured 2 m above ground |

**Note:** Variables in bold were included in the structural equation model (SEM).
Using linear regression analyses, we calculated $R^2$ values, standardized regression coefficients and $P$-values (corrected for multiple testing using false discovery rate [FDR]) for the relationships between each forest trait and microclimatic variable and the phenology of each studied species. We used these results to make an informed preselection of variables for the subsequent structural equation modeling (see Results), because the microclimatic variables included several temperature proxies with high levels of collinearity. All data analyses were conducted using R (R Development Core Team 2018). Standardized regression coefficients were derived using the Quantsr package (Fletcher 2012).

Next, we conducted confirmatory path analysis across all species based on piecewise fitting of component hierarchical linear mixed-effects models (Shipley 2009, Lefcheck 2016). Path analysis or structural equation modeling is a powerful, multivariate technique used increasingly in ecology to evaluate complex multivariate causal relationships, particularly with observational data that often includes substantial collinearity. Structural equation models (SEMs) differ from many other modeling approaches as they test the direct and indirect effects in preassumed causal relationships (Fan et al. 2016). In our analysis we used the piecewiseSEM package (Lefcheck 2016). In piecewiseSEM, each set of relationships is estimated independently (or “locally”). For each response variable, the process decomposes the network into the corresponding simple or multiple linear regressions, which are evaluated separately, and then recombined afterwards to draw conclusions about the full model (Lefcheck 2016). The relationships between variables can then be visualized through path diagrams where arrows denote which variables are influencing (and are influenced by) other variables.

Prior to our path analyses we checked for additivity and linearity of individual variables. We used correlation matrices (Appendix S1: Fig. S1) and variance inflation factors (with a cut-off value of 4) to check for collinearity among the explanatory variables, to avoid inclusion of highly correlated variables, and we used simple regression plots to confirm linearity. Furthermore, to check the statistical assumptions of linear models—normality and homogeneity of residuals—we visually inspected histograms of the standardized residuals, Q-Q-plots and residual scatter plots, as well as calculations of skewness and kurtosis. The skewness and kurtosis values were all within the guidelines set by Kline (2015) and also below the more conservative threshold set by Ryu (2011).

The subset of forest characteristics that we included in the SEM, after checking for collinearity, were: crown projection area, variance mean ratio, structural complexity index, the diameter at breast height and its standard deviation, and the percentage of coniferous trees. We selected diameter at breast height as an explanatory variable over tree age and density because it was the best proxy for the developmental stage of a forest. After the exclusion of highly correlated variables and based on the simple linear regressions results (considering average $r^2$ values and standardized regression coefficients), mean spring air temperature and spring relative air humidity (both measured at 2 m above ground) were the only microclimatic variables we included in the SEM. Because other geographical or environmental factors might also influence plant phenology, we additionally included slope as well as region as explanatory variables in the SEM. In the submodel with flowering peak as a response variable and forest characteristics and microclimatic variables as explanatory variables, we included species identity as a random variable. To test whether the forest characteristics influence the local microclimate, we set both spring air temperature and spring relative humidity also as response variables, while using the forest characteristics as well as other geographical factors as explanatory variables. The complete data set included 687 data points, but since 45 rows had missing values for at least one of the variables, we analyzed the full SEM with 642 data points.

We evaluated the overall path model using Shipley’s test of directed separation (Shipley 2009), which yields a Fisher’s $C$ statistic comparable to a $\chi^2$ value. A $P$ value above 0.05 indicates that a model can adequately reproduce the hypothesized causal network. Fisher’s $C$ is then used to calculate Akaike’s information criterion (AIC), or a corrected AIC for small sample sizes (AICc), to compare model fits. We calculated both marginal and conditional $R^2$ values, where the former describes the proportion of variance explained by only fixed factors, whereas the latter describes the variance explained by fixed and random factors. Starting with a full model based on a priori knowledge of interactions that included all the above-mentioned variables, we used a backwards stepwise elimination process based on AICc to remove nonsignificant pathways. Additionally, we used d-separation tests to evaluate whether any nonhypothesized independent paths were significant, and whether the models could be improved by including any of the missing paths.

**Results**

The onset of flowering in our study species ranged from mid-March (Mercurialis perennis L., Primula elatior (L.) Hill, Anemone nemorosa L.) to the beginning of May (Galium odoratum (L.) Scop., Arum maculatum L., P. verticillatum (L.) All.). Similarly, the peak flowering time of the different species ranged from the end of March until the end of May. For some species, the flowering period ended already in mid-May, whereas others continued to flower until mid-June. Besides these species differences in mean onset and peak and end of flowering, we also found large differences among species in their levels of among-plot variation. Some species had very narrow ranges, for example, the flowering peak of $G.$ odoratum varied only by 10 d across the 79 studied plots, whereas for $A.$ nemorosa ($n = 87$) and $M.$ perennis...
(n = 71) the flowering peaks differed by up to 42 and 46 d, respectively. Of the studied species 75% (12 out of 16) flowered on both deciduous and coniferous forest plots (Appendix S1: Table S2). The average peak flowering time of those four species that grew on deciduous plots only (day of the year = 118.3) did not differ significantly from those that grew on both deciduous and coniferous plots (day of the year = 119.9). For an overview of mean flowering start, peak, and end, as well as the respective N of all species, see Appendix S1: Tables S1 and S2.

**Impact of forest management on phenology**

Across all studied species, forest understory herb species growing on plots with a high silvicultural management intensity had a significantly delayed start, peak and end of their flowering periods (Fig. 3: Flowering start: regression coefficient /SE \( \beta = 11.45 \pm 2.00 \), conditional \( R^2 = 0.86 \), P-value < 0.001. Flowering peak: regression coefficient \( \beta = 18.14 \pm 1.78 \), conditional \( R^2 = 0.87 \), P-value < 0.001. Flowering end: regression coefficient \( \beta = 19.60 \pm 1.90 \), conditional \( R^2 = 0.78 \), P-value < 0.001.). For detailed results of the corresponding linear mixed effect models see Appendix S1: Table S3). On plots with the highest management intensity, the average peak of flowering was over two weeks later than on plots with the lowest management intensity (average days of year of 128, 119, and 113 in managed spruce forests, managed beech forests, and unmanaged beech forests, respectively). Generally, plants flowered later on plots dominated by coniferous trees than on deciduous forest plots (Figs. 3 and 4). These general patterns were also reflected at the level of individual species: in all but one of the studied species, there was a positive (albeit not always significant) relationship between silvicultural management intensity and peak flowering (Table 2), with some of the strongest effects observed in *P. elatior*, *A. nemorosa*, and *G. odoratum*. For detailed regression results, see Table 2 and Appendix S1: Tables S4 and S5.

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**Fig. 3.** The relationships between silvicultural management intensity and flowering start, peak, and end, respectively, across all 16 species and 100 plots. Each point represents a plot by species combination. Silvicultural management intensity is a synthetic index mainly based on tree species, tree density, and stand age, with values from 0 (lowest management intensity) to 1 (highest management intensity). The shape and color of the symbols code for main tree species and mean spring temperature (see legend). The fitted regression lines are derived from a linear mixed model with species as random factor. Species-specific slopes are shown in gray.
Although the strongest impact of management intensity on phenology can be attributed to the percentage of conifers, that is, spruce plantations, there are other aspects of forest management that also have effects on phenology and microclimate. Even if analyses are restricted to deciduous-dominated plots only, higher management intensity is still connected with significantly colder spring temperatures ($F$ value = 7.221, df = 80, $P$ = 0.009, regression coefficient = $-0.85$) and 75% of the studied species still show a tendency to flower later on plots with higher management intensity.

Because forest management affects many aspects of forest structure simultaneously (see Appendix S1: Table S6), we used linear regressions to understand which specific forest characteristics were most related to variation in plant phenology. We found the strongest statistical associations with flowering peak for the percentage of the crown projection area of mature trees and the basal area that is taken up by coniferous trees (with an average standardized regression coefficient of 0.41 and 0.40, mean $R^2 = 0.20$ and 0.21, and maximum $R^2 = 0.67$ and 0.67, respectively; Table 2). The higher the percentage of coniferous trees was, the later the understory herbs tended to flower (see also Fig. 3). Furthermore, plants flowered later in younger forest stands (average standardized regression coefficient $-0.26$, with a mean $R^2 = 0.11$, maximum $R^2 = 0.30$) and those with a low structural complexity (average standardized regression coefficient $-0.19$, with a mean $R^2 = 0.15$ and a maximum $R^2 = 0.89$). Table 2 gives an overview of the standardized regression coefficients of all forest characteristics, and the corresponding $R^2$ values and unstandardized regression coefficients are provided in Appendix S1: Tables S4 and S5. 

**Impact of microclimate on phenology**

We found that microclimatic conditions varied substantially between different forest plots, and that this was partly related to forest management (Fig. 3 and Table 2 and Appendix S1: Table S7). For instance, on managed forest plots the mean spring temperatures were significantly lower than on unmanaged forest plots (5.9°C on managed coniferous, 6.7 on managed deciduous, and 7.0°C on unmanaged deciduous plots, $F_{2,96} = 32.82$, $P < 0.001$), for all pairwise comparisons between the three categories, and the patterns were also very similar for the two regions. Microclimate, in turn,
Table 2. Relationships between forest characteristics and microclimate (last two columns), and the peak flowering of different plant species

| Species                  | N   | Age  | Slope | BA   | Con BA | Con CPA | CPA  | Dbh  | Dbh SD  | Density | Div  | Div 2D | Morisita | SCI  | SMI  | VMR  | Ta    | rH  |
|--------------------------|-----|------|-------|------|--------|---------|------|------|---------|---------|------|--------|----------|------|------|------|-------|-----|
| Alliaria petiolata        | 20  | -0.41| -0.08 | 0.10 | 0.42   | 0.41    | 0.06 | -0.04| -0.27   | 0.23    | 0.32 | 0.26   | -0.19    | -0.27| 0.41 | -0.16| -0.64 | 0.26|
| Allium ursinum           | 16  | -0.52| 0.13  | -0.43| -0.39  | -0.10  | -0.29| 0.19 | 0.24    | 0.55    | -0.14| -0.33  | 0.26      | 0.15 | 0.06 | 0.17 |       |     |
| Anemone nemorosa†        | 87  | -0.37| 0.01  | 0.46 | 0.82   | 0.82    | 0.08 | 0.16 | -0.22  | -0.04  | -0.14| -0.17  | -0.13    | -0.34| 0.54 | -0.13| -0.63 | 0.37|
| Anemone ranunculoides     | 42  | 0.11 | -0.41 | 0.00 | 0.32   | 0.34    | 0.08 | -0.19| -0.20  | 0.28    | 0.20 | 0.03   | 0.08      | -0.07| 0.07 | 0.22 | -0.11 | 0.01|
| Arum maculatum           | 0.55| -0.63| -0.10 | 0.19 | 0.18   | 0.06    | -0.36| -0.35| 0.57    | 0.11    | 0.06 | 0.06   | 0.22      | 0.22 | 0.12 | 0.29 | 0.07  |     |
| Cardamine bulbifera†      | 62  | -0.22| -0.33 | 0.48 | 0.58   | 0.59    | 0.11 | 0.31 | -0.01  | -0.22  | -0.31| -0.35  | -0.21     | 0.32 | -0.37| -0.65| 0.56  |     |
| Ficaria vernix†           | 37  | -0.31| -0.02 | 0.01 | 0.37   | 0.38    | -0.16| 0.01 | -0.18  | 0.08    | -0.03| -0.06  | -0.18     | -0.36| 0.45 | -0.16| 0.34  |     |
| Galium odoratum†          | 79  | -0.39| -0.24 | 0.36 | 0.60   | 0.61    | 0.08 | 0.14 | -0.19  | 0.03    | -0.21| -0.21  | -0.17     | -0.42| 0.49 | -0.19| -0.72| 0.36|
| Lathyrus vernus†          | 32  | -0.14| 0.28  | 0.13 | 0.50   | 0.51    | -0.28| 0.09 | -0.17  | -0.22  | -0.28| -0.40  | -0.10     | -0.37| 0.42 | 0.12 | 0.52  | 0.53|
| Mercurialis perennis†     | 71  | -0.39| -0.23 | 0.19 | 0.53   | 0.53    | -0.08| 0.07 | -0.27  | 0.02    | -0.06| -0.08  | -0.22     | -0.32| 0.48 | -0.15| -0.61| 0.45|
| Oxalis acetosella†        | 39  | -0.16| 0.12  | 0.05 | 0.28   | 0.29    | -0.24| 0.02 | -0.08  | 0.03    | -0.21| -0.13  | -0.13     | -0.18| 0.30 | -0.11| -0.49| 0.38|
| Paris quadrifolia†        | 22  | -0.14| 0.49  | 0.19 | 0.45   | 0.43    | -0.14| 0.24 | -0.06  | 0.12    | 0.24 | 0.04   | 0.02      | -0.40| 0.41 | 0.02 | -0.12| 0.07|
| Primula elatior†          | 28  | -0.26| 0.09  | 0.46 | 0.63   | 0.63    | -0.04| 0.24 | -0.10  | -0.09  | -0.25| -0.19  | -0.13     | -0.21| 0.57 | -0.11| -0.52| 0.63|
| Ranunculus aquicomus      | 22  | -0.29| 0.24  | -0.25| 0.23   | 0.23    | -0.36| 0.11 | -0.20  | -0.10  | -0.22| -0.24  | -0.25     | -0.32| 0.26 | -0.15| -0.68| 0.06|
| Stellaria holostea†        | 24  | -0.38| -0.42 | 0.07 | 0.32   | 0.35    | 0.04 | -0.23| -0.42  | 0.21    | 0.27 | 0.05   | 0.08      | -0.19| 0.28 | 0.16 | -0.14| 0.07|
| Viola reichenbachiana†     | 55  | -0.24| -0.28 | 0.45 | 0.51   | 0.52    | 0.08 | 0.31 | 0.01   | -0.24  | -0.36| -0.41  | -0.24     | -0.20| 0.31 | -0.33| -0.57| 0.50|

Note: The values are standardized regression coefficients derived from linear regressions of flowering peak against the different forest trait and microclimate variables, with significant values in bold (corrected using FDR). Age = mean age of main tree species, dbh SD = standard deviation of dbh, density = stand density, Div = species richness of trees, Div 2D = inverse Simpson’s index for trees, Morisita = Morisita’s index of dispersion, SCI = Zenner’s structural complexity index, Slope = a combination of inclination and exposition, BA = basal area covered by trees, CPA = crown projection area, Con = Coniferous, dbh = diameter at breast height, SMI = silvicultural management intensity, VMR = Clapham’s variance mean ratio, Ta = air temperature, and rH = relative humidity, with both climate variables measured at 200 cm height during February–May 2017. See Table 1 for a more detailed explanation of the different explanatory variables, and Appendix S1: Tables S3–S6 for the corresponding R² values and unstandardized regression coefficients for all regressions. Species that covered the whole range of the different forest types. N = number of peak-flowering data points per species.
was significantly correlated with plant phenology. Higher spring and winter temperatures were generally associated with earlier flowering, whereas higher humidity was correlated with later flowering (Table 2 and Appendix S1: Tables S7–S9, Figure 4 and Appendix S1: Fig. S2). Of all tested microclimatic variables, mean spring temperature at 2 m height explained most of the variability in peak flowering across all species (mean $R^2 = 0.25$, maximum $R^2 = 0.52$, for $R^2$ values of all linear regression see: Appendix S1: Table S8). Per 1°C temperature increase, the plants reached the flowering peak on average 4.5 d earlier. At the level of individual species there was a significant negative relationship between spring temperature and peak flowering in 11 out of the 16 analyzed species, and for most of the other species there was a nonsignificant negative trend (Table 1, Fig. 4). The magnitudes of the responses varied substantially among species, ranging from a change of over 12 d per 1°C for *M. perennis* to only minor changes in flowering time of around 3 d per 1°C for *Cardamine bulbifera* L. For a comparison of all standardized and unstandardized regression coefficients of all microclimatic variables see Appendix S1: Tables S7 and S9. Of all moisture-related variables, relative humidity during spring was the best predictor of peak flowering (mean $R^2 = 0.15$, maximum $R^2 = 0.47$; see Appendix S1: Tables S7–S9 and Fig. S2) and was therefore also included in the SEM. On average, plants flowered 2.7 d later per 10% increase of relative humidity.

**Interactions among forest management, microclimate, and phenology**

The piecewise SEM confirmed that, on average, plants flowered earlier on warmer, south-facing, and less humid plots, and that most of the forest characteristics—percentage of coniferous trees, crown projection area of mature trees, variance mean ratio, and structural complexity index—had a significant influence on the forest microclimate (Fisher’s $C = 5.078$, df = 10, $P = 0.886$; see Fig. 5 and Appendix S1: Table S10). As expected, spring temperatures were lower on coniferous forest plots than on deciduous forest plots. Moreover, forest plots with a lower crown projection area of mature trees (also reflecting forest age) and structural complexity were also colder than plots with older and more

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**Fig. 5.** Results of the piecewise structural equation model (SEM) testing for direct and indirect relationships among forest characteristics, geographic parameters, microclimatic variables, and the timing of peak flowering of forest understory herbs. Arrows represent unidirectional relationships among variables; only significant paths ($P < 0.05$) are shown. Blue arrows are positive relationships, red arrows negative ones. The thickness of the arrows is proportional to the magnitudes of the standardized regression coefficient, which are also plotted on the arrows. The $R^2$ values for component models are also given for each response variable. In the model with flowering peak as a response variable, we included the species as random factor. The overall model is a good fit to the data: Fisher’s $C = 8.364$, df = 12, $P$-value = 0.756
heterogeneous and structurally complex forest stands. Further, plots with north-facing slopes were colder than south-facing ones. The relative humidity was higher in forest stands with a higher percentage of conifers, but lower crown projection area of mature trees and variance mean ratio (reflecting horizontal heterogeneity). Further, it was lower on warmer, south-facing plots. Plots located in the Hainich region were generally warmer and more humid and plants tended to flower earlier there than on the Schwäbische Alb (Fig. 5 and Appendix S1: Table S10). Furthermore, a high percentage of coniferous trees had an equally strong direct effect on the timing of flowering peak, with plants growing on forest stands dominated by Norway spruce flowering later than those in deciduous forests. All unstandardized and standardized estimates of the path coefficients, their degrees of freedom, standard errors, critical values, and $P$-values are listed in Appendix S1: Table S10. We reran the same SEM with data from deciduous plots only, but this analysis had very similar results, with even stronger effects of structural complexity and crown projection on temperature, except that the effect of horizontal heterogeneity and crown projection area of mature trees on relative humidity became nonsignificant (Appendix S1: Fig. S3 and Table S11).

**Discussion**

Many organisms respond to anthropogenic environmental change through shifts in their timing of phenological events, and these changes can have important consequences for the ecology and evolution of ecological communities (Rudolf 2019). It is therefore key to understand the different potential drivers of phenological changes. Here, we disentangled direct and indirect effects that microclimate and forest management have on the phenology of forest understory herb species. We found that plants flowered later in intensely managed forests than in unmanaged forests. Much of this was because forest management affected microclimate, which in turn affected phenology, with plants flowering later on colder and moister forest stands. Our study thus demonstrates that besides climate change other drivers of environmental change, such as forest management, can influence the phenology of organisms.

**Impact of forest management and forest characteristics on phenology**

Although climate-related shifts of phenology are widely studied and accepted (e.g., Fitter and Fitter 2002, Parmesan and Yohe 2003, Cook et al. 2012, Wolkovich et al. 2012), the impacts of other global change drivers, such as land use, have received much less attention. However, land use can also influence life-history traits, such as phenology, and can even cause genetic differentiation in phenological traits (Völler et al. 2013; 2017). Our study demonstrated that understory herbs occurring on forest plots with a high silvicultural management intensity had a significantly delayed start, peak, and end of their flowering periods. On forest stands with the highest forest management intensity, the plants flowered on average about two weeks later than those growing in unmanaged forests. Among the different forest characteristics, the percentage of coniferous trees, the age of the trees, and the structural complexity of a forest stand were the strongest drivers of phenological variation. Plants generally flowered latest on plots dominated by coniferous trees that were relatively young and structurally less complex.

During the last years, there has been accumulating evidence for land-use effects on the phenology of plants and animals. Zhang et al. (2019) showed that land cover and land use change can lead to a delayed start of the growing season in intensively managed agricultural landscapes. Similarly, Altermatt (2012) showed that temperature-related phenological shifts of butterflies depend on their habitat, with delayed phenology in settlement habitats, even though such habitats are generally associated with higher temperatures. Moreover, Leong et al. (2016) found that bee phenology differed between urban and agricultural habitats, with seasonal patterns of abundance and species richness varying less in human-altered landscapes compared to more natural habitats. For plants it has been suggested that climate change and land-use change, alone and in combination, cause growing seasons to start earlier, with human-managed ecosystems greening up particularly faster than their natural counterparts (Wang et al. 2018).

One might argue that the prolongation of the flowering period through diverse forest management at the landscape scale may ultimately improve resource availability and heterogeneity for consumers such as bees. However, this is unlikely to be the case, because the abundances of many species (and thus total resource availability) appeared lower on the intensely managed plots we monitored (F. M. Willems, personal observation).

A challenge with the design of our study was that high management intensity was inevitably to some degree confounded with changes in the main tree species. Within our study regions, planting Norway Spruce is a measure of forest management, and there are no unmanaged coniferous forests. However, to tease apart management types from tree species identity, it would be scientifically ideal to compare managed with unmanaged spruce plots, if the latter existed. Therefore, comparing plant phenology also between unmanaged and managed coniferous forest (in other regions) would be a worthwhile focus for future research.

**Impact of microclimate on phenology**

Our studied forest plots differed not only in the management regime, but, as a consequence, in their microclimate. Both simple linear regressions and the SEMs confirmed that the flowering phenology of spring-
flowering understory herbs was affected by the microclimatic conditions, with higher spring (and winter) temperatures resulting in earlier flowering, and higher relative humidity associated with later flowering. The plants flowered on average 4.5 d earlier per +1°C temperature difference. This magnitude of change corresponds very well with the response of plants to interannual temperature variation observed in previous studies. For example, Heikinheimo and Lappalainen (1997) suggested that a springtime temperature increase of 1°C can result in flower buds bursting approximately 4 d earlier, based on phenological long-term data for 11 plant taxa (trees, shrubs, and forest understory herbs) in Finland. In Britain, the average first flowering of 385 plant species (trees, shrubs, and herbs) was advanced by 4.5 d in the 1990s compared to the previous four decades, and in relation to climate the effect size was also 4.3–6 d per 1°C increase in mean monthly temperature for spring flowering species (Fitter and Fitter 2002). Moreover, an analysis of a large phenological network data set showed that across Europe phenological shifts match the warming pattern in Europe (Menzel et al. 2006). Our data show that such climatic differences, and the associated very similar changes in phenology, can also occur on much smaller scales. However, microclimatic patterns can differ substantially from regional climate patterns (Hwang et al. 2011, Ward et al. 2018), and we therefore need to take them into account when projecting effects of climate change on phenology (De Frenne et al. 2013, Franklin et al. 2013). Especially in forests, these microclimate dynamics have a stronger impact than macroclimate warming on plant responses to climate change (Zellweger et al. 2020).

We also found that the magnitudes of the temperature-associated phenology changes varied substantially among species. This is consistent with several previous studies. Fitter and Fitter (2002), for example, found that annual plants are more likely to flower earlier than congeneric perennials, and insect-pollinated species more likely than wind-pollinated ones. Such differences in the phenological response might ultimately alter the diversity and composition of plant communities. Roberts et al. (2015) predicted that interspecific differences would change the order of spring phenology in temperate forests, which in turn would change hierarchies of light competition and thus potentially the composition of temperate forests. Furthermore, even if the majority of species flower earlier, some may still show nonsignificant trends or even delayed flowering. In a long-term study of 490 species, Cook et al. (2012) demonstrated that the interaction of fall/winter chilling (i.e., vernalization) and spring warming sensitivities explains much of the apparently paradoxical behavior of nonresponding species, or of species that show delayed spring events despite local warming. As both warmer spring and winter temperatures are correlated with earlier flowering in our study, the potential vernalization requirements are probably met for (most of) our plants.

High humidity delayed flowering on average by 2.7 d per 10% increase of relative humidity, and the phenological responses of plants to humidity changes were fairly consistent. The findings of previous studies were ambiguous. Although some suggested that humidity is crucial for plant phenology (Laube et al. 2014, Matthews and Mazer 2016), others found no evidence for a significant role of air humidity for plant phenology (Abu-Asab et al. 2001, Zipf and Primack 2017). Phenological responses to humidity generally seem to be more complex and species-dependent, and they may depend on interactions with other factors.

**Interactions among forest management, microclimate, and phenology**

The SEM confirmed that variation in microclimatic conditions—spring temperature and relative humidity—was strongly influenced by several aspects of forest structure determined by forest management, with forest structure generally having stronger effect on temperature than on relative humidity. Our results confirm those of Nihlgard (1969) and Augusto et al. (2003), who showed that forests dominated by Norway spruce tended to be colder and moister than those dominated by European beech. As hypothesized, our results show that less spatially heterogeneous and structurally complex forest plots with a low crown projection area of mature trees are colder. This is in accordance with Zellweger et al. (2019), who also found that canopy cover increases daily absolute minimum temperatures during the spring. This may seem counterintuitive at first, because during the day plots with a lower crown projection area of mature trees should allow more light to penetrate the canopy and therefore be warmer. However, this trend reverses during the night, where plots with a low crown projection area are colder (see Appendix S1: Fig. S4), presumably because of a sheltering effect of large tree crowns, which reduce convection, mixing of air and infrared reflection (Geiger et al. 2003, von Arx et al. 2013). Because the night effect is stronger than that during the day, the net effect is a cooling under lower crown projection areas.

Planting of Norway spruce instead of European beech profoundly alters ecological properties of the forests in our study system. Besides their narrower crown-width-to-diameter-ratio in comparison to beech, spruce plantations differ from beech forests in many other characteristics such as stand density, size distribution, age, and horizontal/spatial and vertical patterns (Schall et al. 2018). One reason why forest stands dominated by conifers are colder is that particularly in early spring, when deciduous trees have not yet completed their leaf-out, they allow much less light to reach the forest floor and thus do not warm up to the same temperatures as deciduous forest stands during the day—but both cool down during the night (see Appendix S1: Fig. S3). De Frenne et al. (2013) argue that in Europe current conservation
actions are often directed toward restoring traditional management (e.g., coppicing in ancient forests), which results in canopy opening and thus potentially increased temperatures at the forest floor, and thereby could accelerate the increasing dominance of warm-adapted species.

In our study, the dominant tree species affected plant phenology not only indirectly, through altering microclimate, but also directly. This direct effect is almost as strong as the effect of temperature, and it must result from other abiotic or biotic factors that are affected by the dominant tree species in a forest. The two most likely candidate explanations are light and soil conditions. If not heavily thinned, evergreen, coniferous trees create much darker conditions on the forest floor during spring, which may be crucial for the development of the understory vegetation (Tinya et al. 2009). Moreover, coniferous forests are also known to differ in other biotic and abiotic traits—many soil properties, including soil moisture, pH, nutrients, and mycorrhizae (Messenger 1980, Ranger and Claude 1992, Augusto et al. 2003)—all of which could affect the phenology of understory plants. Wolf et al. (2017) showed that biotic interactions can affect the timing of flowering, with plants flowering earlier after (experimentally manipulated) biodiversity loss.

**Potential consequences of phenological shifts**

A phenology that is fine-tuned to environmental conditions is crucial for plants. Plants that fail to track seasonal temperatures or climatic long-term changes are prone to decline in abundance (Willis et al. 2008). As a consequence, microclimate warming in temperate forests can cause a shift in biological communities favoring warm-affinity species (i.e., thermophilization) (Zellweger et al. 2020). On the other hand, Schepens and Stöcklin (2013) showed that earlier flowering as a response to climatic changes can also be maladaptive and lead to a fitness decline due to a more rapid development and therefore lower flower numbers. Phenological shifts can alter reproduction and survival, leading to demographic changes (Miller-Rushing et al. 2010), and potentially favoring exotic species (Abu-Asab et al. 2001). For instance, Dreiss and Volin (2013) found that later leaf growth of deciduous trees can facilitate the establishment of invasive understory species. Furthermore, a review by Elzinga et al. (2007) argues that that biotic interaction with mutualists and antagonists, for example, pollinators or pollinator-transmitted fungi, can change plant phenological patterns. It is likely that the biotic and abiotic drivers that determine phenology vary between interacting groups of organisms (or species) such as plants, insects, or vertebrates (Parmesan and Yohe 2003, Voigt et al. 2003). Phenological shifts can alter species interactions and thereby influence the potential for persistence and coexistence of competing species and change biodiversity patterns in natural systems (Rudolf 2019). If overstory tree leaf-out advances more with increased spring temperature than understory wildflower phenology, those wildflowers must deal with a shorter period of high light before they are shaded by tree canopies. This can reduce their carbon budgets (Heberling et al. 2019). Further, asynchronous changes could potentially lead to mismatches between the phenology of interacting organisms (Stenseth and Mysterud 2002, Visser et al. 2004, Visser and Both 2005, McKinney et al. 2012, Kharouba et al. 2018), which could exacerbate the effects of climate change on organisms. Several studies found that spring warming can cause plants to flower earlier (Parmesan and Yohe 2003, Cleland et al. 2007) and create a phenological mismatch between plants and pollinators (Kudo and Ida 2013, Settele et al. 2016), with detrimental effects on plant reproduction (Forrest 2015) and pollinator fitness (Schenk et al. 2018). However, there is no consensus on how likely such mismatches are. Renner and Zohner (2018) argue that mismatches due to climate change are most likely in antagonistic interactions, whereas there is only limited evidence of phenological mismatches in mutualistic interactions. A literature review by Kharouba et al. (2018) suggests that a majority (57%) of interacting species changed their phenologies fairly synchronously, whereas 43% showed a trend toward asynchrony. Furthermore, because pollinator activities are low during early spring, due to cool temperatures, pollinator limitation is already common in spring-flowering forest species. Thus, climate change may have a particularly strong impact on bee-pollinated spring bloomers, because their reproductive success is highly susceptible to seasonal fluctuation (Kudo et al. 2008). Besides affecting the distribution and fitness of interacting species, changes in plant phenology can also affect ecosystem functions, such as productivity and carbon cycling, and they can therefore also affect yields in agriculture, horticulture, viticulture, and forestry (Menzel et al. 2006, Cleland et al. 2007).

**Conclusions**

Our study shows that plant phenology is affected by forest management. It thus contributes to the growing evidence that, besides climate change, other drivers of current environmental change, such as land use, influence phenology. Forest management interventions—for example, planting certain tree species, thinning, selective removal of target trees or even clearfellings—change many forest characteristics such as crown projection area, spatial dispersion of trees, and the structural complexity of a forest. Thus, forest management alters forest structure, and thereby changes the microclimatic conditions of a forest stand and its light conditions, and likely also changes other environmental factors that impact flowering phenology of understory herbs. These phenology changes in turn can have wide-ranging implications.
for forest ecosystems and their long-term composition, stability, and evolution.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2332/full

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