Title: Forest understorey flowering phenology responses to experimental warming and illumination

Authors: Eline Lorer*, Kris Verheyen, Haben Blondeel, Karen De Pauw, Pieter Sanczuk, Pieter De Frenne & Dries Landuyt

Affiliations:

Forest & Nature Lab, Department of Environment, Ghent University, Geraardsbergsesteenweg 267, BE-9090 Melle-Gontrode, Belgium (Twitter @ForNaLab)

*Corresponding author: Eline Lorer, Forest & Nature Lab, Ghent University, Geraardsbergsesteenweg 267, 9090 Melle-Gontrode, Belgium. Email: eline.lorer@ugent.be. Telephone: +32 (0)9 264 90 37**Orcid IDs (& social media accounts):**

ELINE LORER (Orcid ID: 0000-0003-3957-7969)

KRIS VERHEYEN (Orcid ID: 0000-0002-2067-9108)

HABEN BLONDEEL (Orcid ID: 0000-0001-9939-5994 – Twitter @BlondeelHaben)

KAREN DE PAUW (Orcid ID: 0000-0001-8369-2679 – Twitter @Karen_DePauw)

PIETER SANCZUK (Orcid ID: 0000-0003-1107-4905)

PIETER DE FRENNE (Orcid ID: 0000-0002-8613-0943 – Twitter @PieterDeFrenne)

DRIES LANDUYT (Orcid ID: 0000-0001-8107-5546)

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Results:	826	No of Supporting Information files:	19 (Fig. S1-S10, Table S1-S9)
Discussion:	2402		

Summary

- Species are altering their phenology to track warming temperatures. In forests, understorey plants experience tree canopy shading resulting in light and temperature conditions which strongly deviate from open habitats. Yet, little is known about understorey phenology responses to forest microclimates.
- We recorded flowering onset, peak, end, and duration of 10 temperate forest understorey plant species in two mesocosm experiments to understand how phenology is affected by sub-canopy warming and how this response is modulated by illumination, which is related to canopy change. Furthermore, we investigated whether phenological sensitivities can be explained by species’ characteristics, such as thermal niche.
- We found a mean advance of flowering onset of 7.1 days per 1°C warming, more than previously reported in studies not accounting for microclimatic buffering. Warm-adapted species exhibited greater advances. Temperature sensitivity did not differ between early- and later-flowering species. Experimental illumination did not significantly affect species’ phenological temperature sensitivities, but slightly delayed flowering phenology independent from warming.
- Our study suggests that integrating sub-canopy temperature and light availability will help us better understand future understorey phenology responses. Climate warming together with intensifying canopy disturbances will continue to drive phenological shifts and potentially disrupt understorey communities, therewith affecting forest biodiversity and functioning.

Key words: climate change, flowering phenology, forest understorey, light availability, mesocosm experiment, microclimate

Introduction

Climate change is increasingly threatening biodiversity, causing changes in species composition, species migrations and (local) extinctions (Pörtner *et al.*, 2021). To temporally track warming temperatures, species are altering their phenology (Fitter & Fitter, 2002; Root *et al.*, 2003; Cleland *et al.*, 2007; Miller-Rushing & Primack, 2008; Cohen *et al.*, 2018). Such phenological shifts are typically studied in relation to free-air temperatures (referred to as 'macroclimate') measured in standardized meteorological stations in open areas, and of which datasets are readily available in repositories such as WorldClim (Fick & Hijmans, 2017) and the Climate Research Unit Timeseries (CRU TS; Harris *et al.*, 2020). However, many organisms experience temperatures that are substantially different from those captured by weather stations (Potter *et al.*, 2013; De Frenne *et al.*, 2019). Forest understorey species, for instance, experience climate buffering from the tree canopy, attenuating climate warming below the canopy (De Frenne *et al.*, 2019; Zellweger *et al.*, 2019). Forest understorey phenology is thus driven by microclimate at the forest floor rather than by regional climate patterns. Indeed, phenological events can be influenced on small spatial scales by local microclimates, in landscapes with heterogeneous topography (Ward *et al.*, 2018), in forests with contrasting management (Willems *et al.*, 2021) and even in buds within one tree (Vitasse *et al.*, 2021; Peaucelle *et al.*, 2022). Across the few studies looking into the effects of climate warming on the phenology of the forest herbaceous layer, an advancement of leaf emergence and flowering onset is often reported, while the effects on end-of-season phenophases, such as end of flowering and leaf senescence, are more ambiguous or not investigated at all (Miller-Rushing & Primack, 2008; De Frenne *et al.*, 2011b; Ellwood *et al.*, 2013; Jacques *et al.*, 2015; Rice *et al.*, 2018; Heberling *et al.*, 2019b; Willems *et al.*, 2022; Miller *et al.*, 2022). Advanced forest herb phenology is found both in experimental and observational studies, although the latter typically rely on existing long-term climate data therewith not accounting for microclimatic buffering by the overstorey.

The tree canopy also affects light availability at the forest floor, where understorey plants below dense canopies can experience a deep shade after tree leaf flush (Neufeld & Young, 2014). Consequently, many herbaceous species in deciduous forests have adopted a shade-avoiding strategy, termed 'phenological escape' (Jacques *et al.*, 2015; Lee & Ibáñez, 2021; Lee *et al.*, 2022), advancing their emergence to take advantage of the ephemeral period of high light availability in early spring (Lapointe, 2001; Augspurger & Salk, 2017). During this period they obtain up to 95 % of their total cumulative annual radiation budget (Augspurger *et al.*, 2005; Heberling *et al.*, 2019a). Later emerging shade-tolerant forest species, on the other hand, maximize photosynthetic rates under low light availability (Bierzychudek, 1982). After canopy closure light availability varies with overstorey and shrub layer structure and density (Angelini *et al.*, 2015). Canopy changes resulting from anthropogenic (e.g. forest management interventions) or natural disturbances (e.g. insect outbreaks or windthrows) will thus also affect light conditions experienced by the understorey vegetation. This will alter the groundlayer microclimate as it is tightly connected to light conditions because the absorption and reflection of incoming solar radiation by the canopy is one of the main drivers of microclimatic buffering (De Frenne *et al.*, 2021). Recognizing the modulating effects of the canopy on herb layer responses is thus imperative, especially with climate change intensifying forest canopy disturbances (Seidl *et al.*, 2017; Senf & Seidl, 2021; Patacca *et al.*, 2022; Grünig *et al.*, 2022) and influencing overstorey phenology. Due to a stronger phenological response of the tree layer to climate warming, the high light availability period is expected to shorten, potentially leading to a phenological mismatch between deciduous canopy trees and understorey herbs (Heberling *et al.*, 2019b; Miller *et al.*, 2022). On the other hand, a recent study does not confirm a phenological mismatch for Asia and Europe (Lee *et al.*, 2022) and another study found that spring flowering herbs advance their phenology more than trees at higher latitudes in North America (Alecrim *et al.*, 2022). Any decrease of the spring light window would curtail the annual carbon gain of early-emerging species (Heberling *et al.*, 2019a). Even if these species are able to shift their growing season to the new period of high light availability, their carbon gain will be affected as photoperiod is shorter earlier in the year and the solar angle is lower.

It has been demonstrated that rising temperatures and changing light regimes have profound effects on understorey plant communities (De Frenne *et al.*, 2015; Blondeel *et al.*, 2020a,b; Chelli *et al.*, 2021; De Pauw *et al.*, 2021; Govaert *et al.*, 2021b,a), yet little is known about their phenological responses to both drivers and the interaction between the two. Given that the limited light availability in temperate forests has largely shaped the evolution of herb layer phenology (Lapointe, 2001; Augspurger & Salk, 2017), it is likely that illumination modulates phenological responses to rising temperatures. Rice *et al.* (2018) reported earlier leaf unfolding of forest herbs under a closed canopy compared to an open canopy, and a greater advance of leaf unfolding with warming under a closed canopy. However, since canopy opening increases both light availability and temperature at the forest floor, it is impossible to disentangle their separate effects based on observational data alone. As ongoing climate warming and forest disturbances will continue to drive phenological shifts, more research teasing apart understorey responses to both drivers is urgently needed, especially considering the importance of understory communities for forest biodiversity and functioning (Gilliam, 2007; Landuyt *et al.*, 2019). These insights will improve forecasts of future forest functioning and can guide climate-adaptive management of temperate forests towards more resilient systems.

While phenology responses to experimental warming are regularly studied in open ecosystems, in-situ understorey herb phenology experiments are very rare (see reviews by Wolkovich *et al.*, 2012; Stuble *et al.*, 2021). In the buffered microclimate beneath the canopy, experiments allow to study the impact of microclimate warming as they manipulate local temperatures. The few existing understorey phenology experiments have largely focused on leaf emergence of North American and Asian species, making future responses of flowering phenology in European temperate forests uncertain. Moreover, how illumination modulates herb layer phenology responses to microclimate warming is completely unknown. We address these research gaps by investigating temperate forest understorey flowering phenology within two large long-term mesocosm experiments applying warming and illumination treatments. Both experiments adopt a full-factorial design to disentangle responses to local light and temperature conditions. We monitored flowering, from onset until end, of ten herbaceous species to assess the impact of increased temperature and light availability on their flowering phenology. In our analysis, we addressed the following research questions:

1. How sensitive is understorey flowering phenology to warming?
2. Does light availability influence temperature sensitivity?
3. Are phenological temperature sensitivities related to species characteristics?

Materials and Methods

Experimental design

The study was carried out within two long-term understorey mesocosm experiments, installed in the long-term ecological research site (LTER) in the Aelmoeseneie forest in Belgium (50°58′30″N, 3°48′16″E, mean annual temperature = 10.6°C, mean annual precipitation = 786 mm, altitude = 20 m; DEIMS-SDR Database, 2022). The experimental site has a tree canopy dominated by *Fagus sylvatica*, *Quercus robur*, *Acer pseudoplatanus*, *Fraxinus excelsior* and *Larix decidua*. All details on the design of the experiments are available in Blondeel *et al.* (2020a, b; PASTFORWARD experiment established in 2016) and in De Pauw *et al.* (2022; FORMICA experiment established in 2019). The experimental set-ups are illustrated in Figs S1-S2. Both experiments apply warming and illumination treatments, in a full factorial design: light, warming, light + warming, and a control treatment. Additionally, the PASTFORWARD experiment used soils from different regions with contrasting past land-use histories, while the FORMICA experiment installed the plots in a forest edge-to-core transect and in locations with varying forest structure. These additional factors are not the focus of this study but are accounted for as random effects in our statistical models. Treatments are administered to small experimental plant communities planted in plastic trays (mesocosms) with different compositions of forest understorey herbaceous species. The plastic trays have drainage holes in the bottom and are completely buried into the forest soil such that the mesocosm soil surface was level with the forest soil surface, allowing heat and moisture exchange between the soil in the trays and the actual ground thereby minimizing unrealistic soil warming and drought due to experimental heating. In the PASTFORWARD experiment, each unique treatment is applied to 24 experimental units or plots consisting of four mesocosms, making a total of 384 mesocosms over all treatments. In this study, a subset of 40 plots (160 mesocosms), evenly distributed over the four treatments, was selected. The FORMICA experiment applies each treatment to four plots consisting of nine mesocosms, which amounts to 144 experimental plant communities.

Experimental warming was done with open-top chambers (OTCs; their construction and performance is explained in De Frenne *et al.*, 2010) in PASTFORWARD plots. The passive warming effect of open top chambers is typically most prominent in early spring, increasing air temperatures with 0.52°C in March and 0.59°C in April 2021 (Figs S3-S4). At that time the forest canopy is still open and solar radiation becomes more intense (De Frenne *et al.*, 2010, 2011b; Pelini *et al.*, 2011). FORMICA adopts a Free-Air Temperature Increase (FATI) system with two infrared (IR) heater arrays of 100 W (Elstein – Werk M Steinmetz GmbH & Co. KG, Northeim, Germany) at 100 cm above each plot, active during day and night. Non-heated plots had a dummy construction with empty heating lamp covers for standardization. Infrared heaters in the FORMICA experiment were turned on every year from February until October, consistently increasing air temperatures between 1.67°C and 2.59°C (Figs S3-S4; 1.89°C in March and 2.09°C in April). The difference in temperature increase between the two methods allows to investigate phenological responses of species present in both experiments to different degrees of microclimate warming and allows us to generalize our research findings, independent of the applied heating methodology.

The light addition treatment was administered only during daytime, from dawn till dusk, following the local photoperiod throughout the year, with one (PASTFORWARD) or two lamps (FORMICA) per plot. The performance and functioning of the lamps are explained in detail in De Frenne et al. (2015). Each lamp consists of two 18 W fluorescent tubes and does not significantly affect temperatures (De Frenne *et al.*, 2015; De Pauw *et al.*, 2021). Above the lamps, plastic shields were attached as rain protection. The control plots received ambient light and included a dummy construction with empty plastic lamp shields, to account for undesired side effects of the installation. Light addition added 23.98 ± 4.40 $\mu mol\ m^{-2}\ s^{-1}$ (PASTFORWARD experiment, see Blondeel *et al.*, 2020a) and 55.21 ± 38.33 $\mu mol\ m^{-2}\ s^{-1}$ (FORMICA experiment) PAR to the ambient light conditions in the control plots. Such increments in light availability mimic the illumination in a small forest gap, which can significantly increase carbon assimilation and growth rates in typical forest understorey plants (Rothstein & Zak, 2001).

The species pools in both experiments were compiled of species commonly found in temperate European forests, covering a gradient in colonization capacity (i.e. an index introduced by Verheyen *et al.* in 2003 that quantifies species' preferential occurrence in ancient vs. recent forests and which is linked to species' specialisation for forest habitat and life-history syndrome; CCI) (Verheyen *et al.*, 2003; De Frenne *et al.*, 2011a) and in FORMICA also species' temperature preference (for detailed information see '*Species characteristics*') was considered during species selection. We studied *Anemone nemorosa* L., *Carex sylvatica* Huds., *Ficaria verna* Huds., *Galium odoratum* (L.) Scop., *Hyacinthoides non-scripta* (L.) Chouard ex Rothm., *Polygonatum multiflorum* (L.) All and *Vinca minor* L. in PASTFORWARD and *Allium ursinum* L., *Anemone nemorosa* L., *Carex sylvatica* Huds. and *Geum urbanum* L. in FORMICA (Table S1).

Microclimate data

Soil (8 cm depth), surface (0 cm height) and air (15 cm height) temperatures were measured every 15 min from September 2020 onwards, using a TMS-4 datalogger (TOMST, Prague, Czech Republic; Wild *et al.*, 2019), which has two radiation shields to protect the surface and air temperature sensors from direct sunlight. In the PASTFORWARD experiment, loggers were placed in the centre of the four mesocosms for every plot; in the FORMICA experiment, they were placed in the central mesocosm of control and warming treatments (and thus not in light and light + warming treatments). We compiled the air temperature data (15 cm height) to calculate mean spring temperature (i.e. the average of daily true mean temperatures over the period Feb-May), as temperatures in this period are most relevant for forest understorey phenology and it allows for comparison with previous studies (Ellwood *et al.*, 2013; Heberling *et al.*, 2019b; Willems *et al.*, 2021, 2022; Miller *et al.*, 2022). Moreover, Stuble *et al.* (2021) showed that warming during spring had a larger effect on phenological advancement than warming during other seasons. Previously, Cook *et al.* (2012) demonstrated that many species in our species pool do not significantly respond to winter temperatures. Following Conner & Foster (2008), true mean temperature was calculated as the sum of all temperature measurements within a day, divided by the number of measurements within a day as opposed to the meteorological mean where daily minimum and maximum temperature are summed and divided by two. We tested the predictive performance of other metrics (soil temperature; minimum, maximum or meteorological mean temperature) from the same period, but none came out as a consistently better performing predictor (Table S2-S7). Using open-top chambers increased mean spring air temperature with 0.38 ± 0.05°C, while infrared heaters invoked a warming of 1.84 ± 0.24°C.

Phenology monitoring

From February to October 2021, we monitored the flowering phenology of ten herbaceous species in the experimental forest understorey communities (160 mesocosms for PASTFORWARD and 144 mesocosms for FORMICA, Table S1). For every species, except *Carex sylvatica* and *Galium odoratum*, we counted the total number of open individual flowers per mesocosm, two to three times a week (mean (±SD) number of days between counts = 2.89 ± 0.97). For *C. sylvatica* and *G. odoratum* we counted the number of racemes or inflorescences, resp., with at least one fully open flower. For clarity, we hereafter use ‘flower’ for all species. A flower was considered open from the moment stamen and/or pistil were visible until it shed all petals. For each species per mesocosm we derived four phenological variables. Onset of flowering (or first flowering date, FFD) was determined as the first day where a species presented a fully open flower, and end of flowering (or last flowering date, LFD) as the date when no open flowers could be found anymore. The day of the year with the highest abundance of open flowers, raceme or inflorescences was defined as the peak flowering (FP) date; if there were multiple dates with equal flower abundance, we used their median date. For *Geum urbanum*, taking into account its bimodal flowering pattern (Sercu *et al.*, 2021), we identified a first peak between mid-May and end of July, and a second one between beginning of August and end of October. Flowering season length (FSL) was calculated as the number of days between the onset and the end of flowering.

To explore interannual variation in phenological sensitivity we repeated our monitoring in 2022 for a subset of species (*Allium ursinum*, *Anemone nemorosa* and *Hyacinthoides non-scripta*).

Species characteristics

To gain a better understanding of the interspecific variation in phenological responses to climate warming, we related phenological sensitivity to three species characteristics: temperature preference and colonizing capacity, both used as selection criteria for the compilation of the experiments’ species pools, and intrinsic phenology. Previous research found that early-flowering species are more sensitive to warming than late-flowering species (Fitter & Fitter, 2002; Sherry *et al.*, 2007; Miller-Rushing & Primack, 2008; Cook *et al.*, 2012; CaraDonna *et al.*, 2014; König *et al.*, 2018). We therefore incorporated the ‘intrinsic phenology’ as the mean phenology (i.e. mean FFD, FP, LFD or FSL) of plants in the control treatment, to investigate whether this is also true within our group of typically spring-flowering understorey species. Secondly, we looked at the influence of the colonizing capacity index (CCI; Verheyen *et al*., *2003*), which quantifies a species colonizing capacity based on occurrences in ancient vs recent forests and is tightly linked to several life-history traits, such as life cycle type and plant height. Third, since species’ thermal niches can also determine responses to warming, we included a measure for thermal preference, the thermal niche optimum based on the mean annual temperature across the species’ distribution range. For this purpose, we used the ClimPlant database (Vangansbeke *et al.*, 2021a,b) which includes thermal preferences for almost 1200 European forest plants. We adopted the microclimate-adjusted thermal niche optima in which the temperature experienced by forest plants is corrected for microclimate buffering. This is determined following the methods of Vangansbeke *et al.* (2021b), but with a correction for forest microclimate buffering using the ForestTemp layers of gridded mean monthly temperature offsets (Haesen *et al.* 2021a) and macroclimate temperature extracted from the ERA5-Land reanalysis dataset (Muñoz-Sabater *et al.*, 2021). In this way the thermal niche of species is inferred as the mean annual microclimatic temperature across a species' distribution range.

Statistical analysis

The statistical analysis was subdivided into three parts, consistent with our three research questions. For each question, only species that were flowering in at least three mesocosms per treatment were included in the statistical analysis. This unfortunately led to the complete removal of the data on *Oxalis acetosella* and exclusion of data on *Anemone nemorosa* and *Carex sylvatica* in FORMICA plots and *Polygonatum multiflorum* and *Vinca minor* in PASTFORWARD plots for question 2 (Table S1). Throughout the analysis, data from the two experiments were analysed independently. All data analyses were performed in R v.4.2.2 (R Core Team, 2022).

Mixed-effects models

We addressed the first two questions using linear mixed-effects models with mean spring air temperature and light (for question 2) as fixed effects (implemented in R with the package *lme4)* (Bates *et al.*, 2015). To decide on the structure of the random component, we considered the different experimental designs, resulting in two distinct random effect structures. The PASTFORWARD experiment used soils from eight regions, planted mesocosms with 12 possible understorey community compositions and combined four mesocosms into one plot, resulting in the following set of crossed random effects (expressed in *R* syntax).

$$\boldsymbol{(1|region) + (1|community) \ + (1|plot)}$$

The FORMICA experiment installed plots, which consisted of nine mesocosms, in groups of four (one per treatment) in a forest edge-to-interior transect (two levels: edge and interior) within locations with varying canopy structure (two levels: simple and complex structure), resulting in the random component below reflecting the spatial nesting of plots. The plot variable is explicitly nested into transect:structure, coded as *structure-transect-treatment* (e.g. 'complex-interior-L' for the light treatment plot in the interior location of the complex canopy structure).

$$\boldsymbol{(1|transect\colon structure) \ + (1|plot)}$$

Sensitivity of flowering phenology to climate warming

To infer sensitivity of flowering phenology to mean spring air temperature, we used models with phenology variables (FFD, FP, LFD or FSL) as responses, mean spring air temperature as the only fixed predictor and the random effect structures as explained above. Such models were made for each species separately, computing species-specific sensitivities, and for all species together with ‘species’ as an additional random factor, to estimate the overall sensitivity in our experiments. In these overall models for FP, only the first peak of *Geum urbanum* was included. The slope of these models represents the sensitivity to mean spring air temperature of the examined phenophases (or flowering duration) for the considered species and is expressed in number of days per 1 °C mean spring air temperature increase. For *Allium ursinum*, *Anemone nemorosa* and *Hyacinthoides non-scripta*, we constructed the same models for the 2022 data to calculate their species-specific sensitivities in 2022.

After estimating phenological temperature sensitivity, we examined whether the advanced phenology could be explained by enhanced thermal accumulation, by comparing thermal accumulation between control and warmed plants with *t*-tests. It is accepted that temperature accumulations are a reliable method to reference phenological development in plants because the heat required to advance life cycles typically remains constant (de Réaumur, 1735). To calculate thermal accumulation, temperature cues for a specific phenophase are summarized as cumulative heat sums above a threshold level (Cannell & Smith, 1983; Rathcke & Lacey, 1985). Using the air temperature data from the TMS-4 loggers, with a high temporal resolution of 15 minutes, we calculated thermal accumulation as the cumulative temperature above 5°C from February 1 until the day of the phenological event. For instance, thermal accumulation until FFD was calculated as:

$$TA_{FFD} = \sum_{t=01/02/2021\ 00:00}^{FFD} (T_t - T_{base}),$$

where, TA_{FFD} is the accumulated number of thermal units above the base temperature (T_{base}) of 5°C, between February 1 and FFD, and T_t is the air temperature measured every 15 minutes.

Influence of light availability on phenological temperature sensitivity

To study the influence of illumination on phenological temperature sensitivity, we added the binary ‘light’ variable (0 or 1) and its interaction with mean spring air temperature to the models, resulting in the model structure below.

$$\boldsymbol{Phenology\ variable \sim 1 + T_{spring} + Light + T_{spring}\ x\ Light + random\ component}$$

Here, the temperature variable was scaled and centred using a z-transformation (mean = 0, SD = 1), to simplify parameter coefficient comparisons and model interpretation.

Relationship between phenological temperature sensitivity and species characteristics

Finally, we investigated relationships between the species characteristics and phenological temperature sensitivities using Bayesian linear models (implemented with the package *brms* with a Gaussian distribution family) (Bürkner, 2017, 2018, 2021), with intrinsic phenology, CCI and thermal niche optimum as predictors and estimated temperature sensitivities as response variables. The *brms* package allows to take into account the standard errors of the response term, by specifying them as an addition to the response term ('|se (standard error response)'). The Bayesian models thus considered the standard errors on the sensitivities, which are slopes estimated by the models in question 1, as weights when calculating the regression slope estimates. For intrinsic phenology, the standard error of the mean was also considered, specified as 'measurement error' in *brms*. For all Bayesian models we used four chains, consisting of 2000 iterations after a warm-up of 2000 iterations. We used default uninformed priors: for slopes uniform flat (-∞ ∞) and for intercepts student-t with 3 degrees of freedom, mean (location) of -6.1, -4.7, -5, 0.5 and scale of 3.1, 5.5, 8.1, 2.8 for respectively, FFD, FP, LFD and FSL models. Convergence and mixing of chains were visually inspected. To further inspect these relationships, we performed the same modelling with the species-specific sensitivities of *Allium ursinum*, *Anemone nemorosa* and *Hyacinthoides non-scripta* in 2022.

$$\boldsymbol{Temperature\ sensitivity|SE \sim 1 + species\ characteristic\ (|SE)}$$

Results

Sensitivity of flowering phenology to climate warming

We found an overall advance of FFD and FP with increasing mean spring air temperature (Figs 1 & 2). Even though this shift was only significant in some species: *Allium ursinum*, *Carex sylvatica* (only in FATI), *Hyacinthoides non-scripta* and *Polygonatum multiflorum*, the pattern is clear throughout the studied species pool and is also reflected in the significant overall advance in both experiments (Fig. 2; OTC: FFD 8.94 ± 3.45 days °C^{-1}, FP 7.32 ± 2.67 days °C^{-1}; FATI: FFD 5.22 ± 1.40 days °C^{-1}, FP 5.03 ± 1.31 days °C^{-1}). Interspecific variability in the observed responses was quite large, ranging from an insignificant advanced FFD of 4.03 ± 8.47 days °C^{-1} in *Ficaria verna* to a significant advance of 14.91 ± 3.77 days °C^{-1} in *Hyacinthoides non-scripta*. Intraspecific variation also differed between species, with a high variation in e.g. *Ficaria verna* compared to the more consistent response of *Allium ursinum*. For the species present in both experiments, we observed a similar shift in *Anemone nemorosa* but *Carex sylvatica*'s advance is smaller when warmed with IR heaters. Furthermore, LFD advances slightly but is generally less sensitive to climate warming (OTC: 6.74 ± 3.16 days °C^{-1}; FATI: 3.30 ± 2.51 days °C^{-1}). Together with a strongly advancing FFD this leads to a prolonged flowering season in some species (only significant for *Hyacinthoides non-scripta*: 10.93 ± 4.97 days). Other species' FSL is unchanged due to a uniformly shifting FFD and LFD. Only *Ficaria verna*'s flowering duration is shortened as this species experienced a significantly large advance of LFD (20.79 ± 7.52 days °C^{-1}) while FFD was not affected. To explore interannual variation in phenological sensitivity we repeated monitoring for three species in 2022. *Hyacinthoides non-scripta* and *Allium ursinum* also advanced flowering phenology in 2022, but not as much as in 2021, and *Anemone nemorosa* showed no significant response in both years (Table S8). In 2022, where mean spring temperature inside the forest was c. 2 °C warmer than 2021, flowering occurred earlier for all species even in control plots (Table S9).

Fig. 1 illustrates how the complete flowering patterns are affected by warming and light separately. For instance, although *Geum urbanum* shows no real phenological shift in response to experimental treatments, the flower abundance increases in a warmer or brighter environment with much higher flowering peaks. Another striking observation is that some species exhibit a forward uniform shift, such as *Allium ursinum*, while others' pattern shape is changed with warming. *Polygonatum multiflorum*'s flowering pattern is compressed while that of *Hyacinthoides non-scripta* is spread. In most species the flowering distribution is unchanged under illumination, except in *Allium ursinum* and *Galium odoratum*, where flower density decreased, and *Polygonatum multiflorum*, where density increased. When warmed plants shifted their phenology, they generally required similar thermal sums as control plants to reach each phenophase (Fig. 3). Plants under IR heating seemed to require greater cumulative heat before reaching each phenophase, however this pattern mostly disappeared when only including daytime thermal units (Fig. S5).

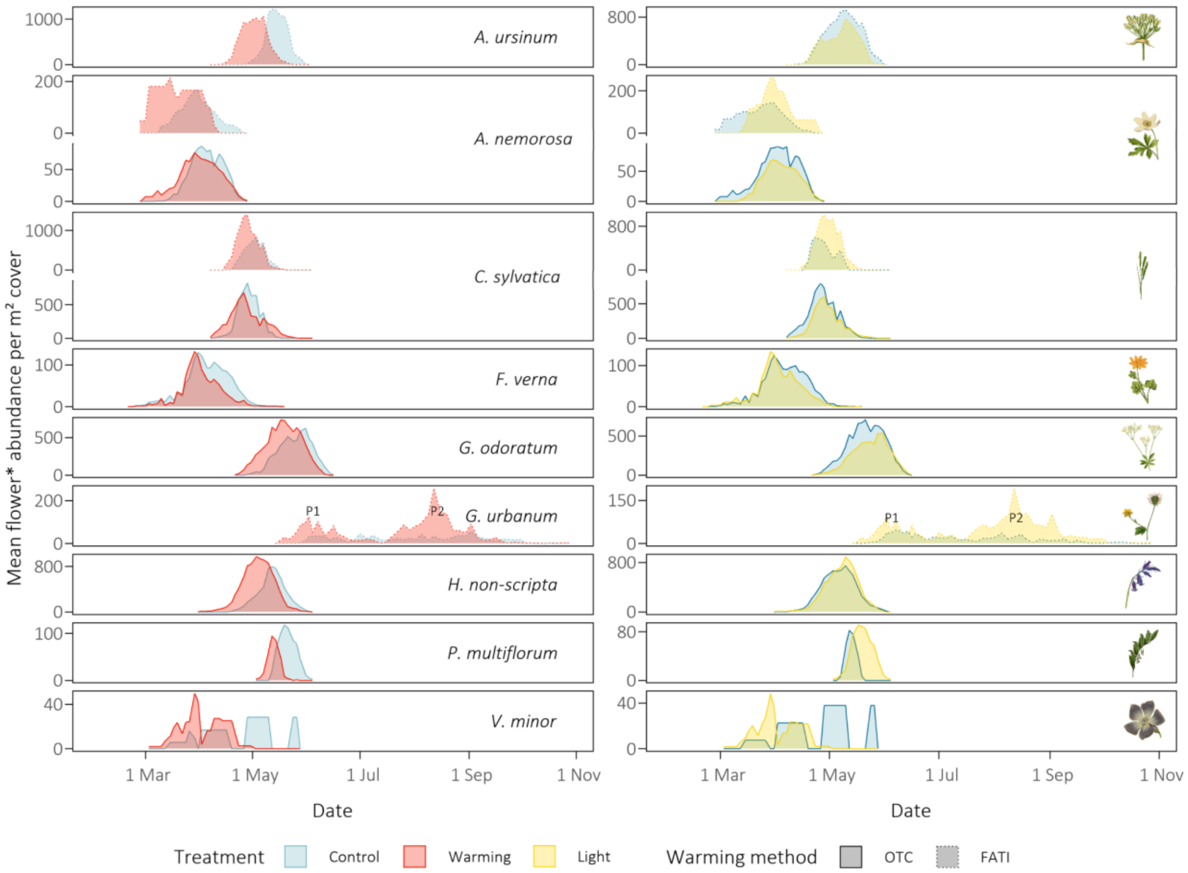

Fig. 1. Observed flowering patterns of the nine studied forest understorey herb species in control, warmed (left) and illuminated (right) plots, in both experiments (OTC = open-top chamber, FATI = Free-Air Temperature Increase). Mean number of flowers (*or raceme for *Carex* and inflorescences for *Galium*) per 1 m^2 of species cover, over time. For *Geum urbanum*, two distinct flowering peaks (P1, spring, and P2, summer) are discernible. Botanical drawings were obtained from scans available in the Biodiversity Heritage Library (https://www.biodiversitylibrary.org/), and are all free of copyright.

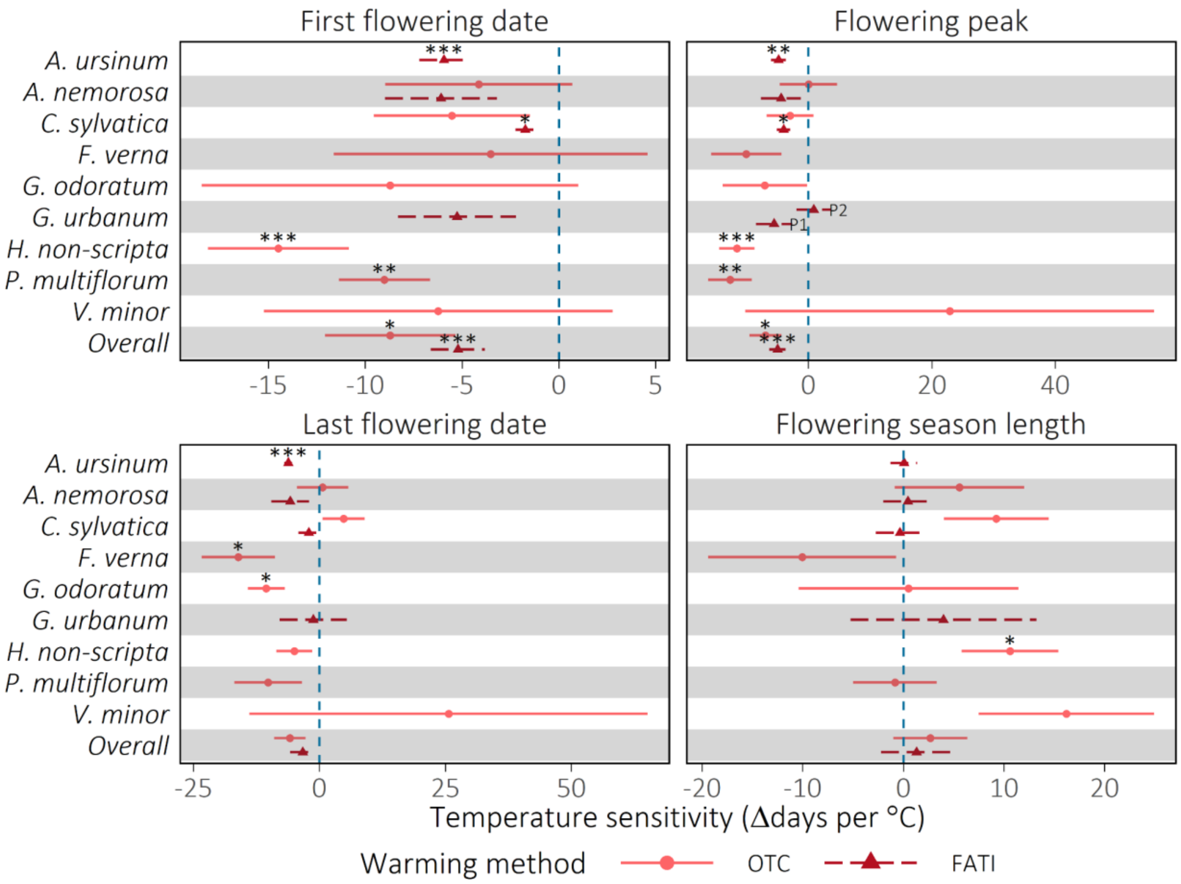

Fig. 2. Mean (± standard error) spring temperature sensitivity for flowering onset, peak, end and duration estimated from linear mixed models, marked with significance levels: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***). OTC = open-top chamber, FATI = Free-Air Temperature Increase. Negative (positive) estimates indicate an advancing phenology, or shortened flowering season, (delaying, or prolonged) in response to warming. Overall estimates were calculated by grouping data from all species and adding species as an extra random factor. For *Geum urbanum*, the two flowering peaks are indicated with P1 (spring) and P2 (summer).

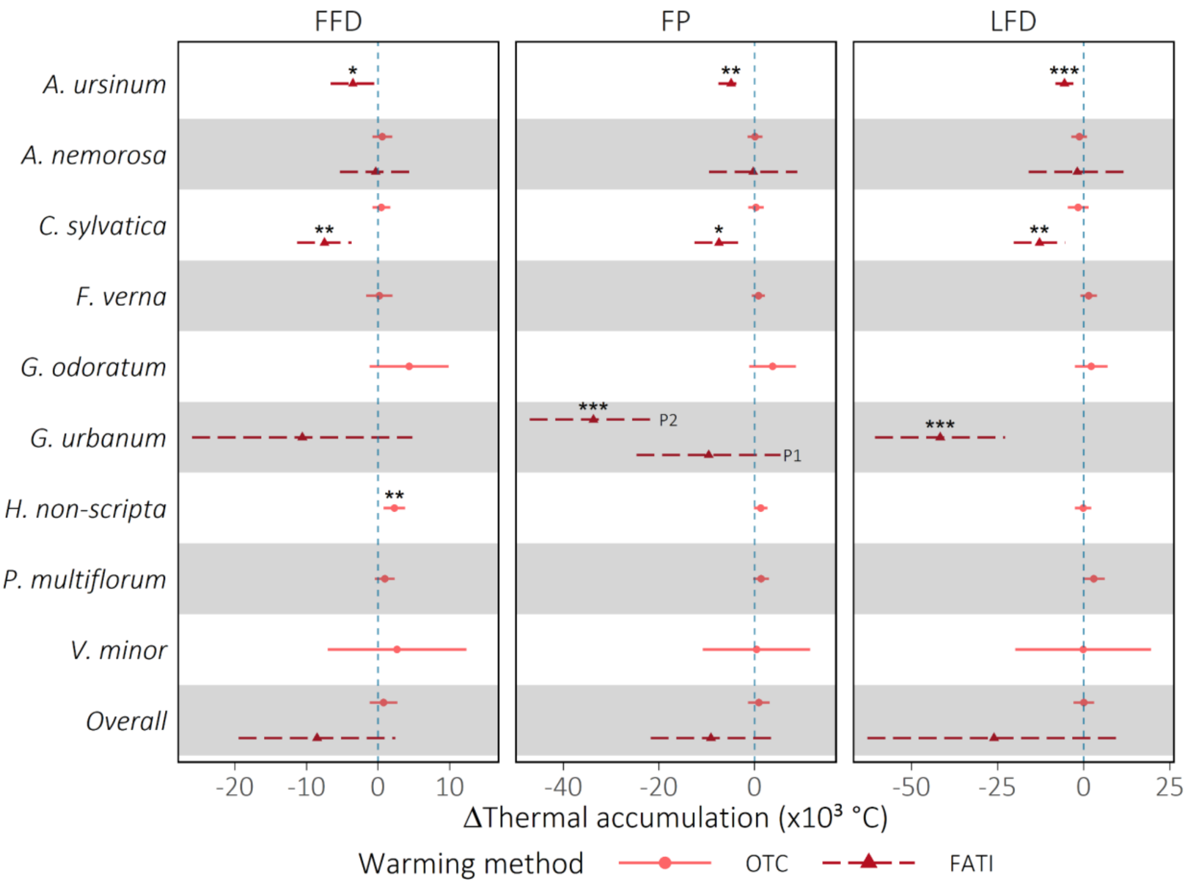

Fig. 3. Difference in species-specific thermal accumulation until flowering onset (FFD), peak (FP) and end (LFD) between warmed (OTC = open-top chamber, FATI = Free-Air Temperature Increase) and control plants. Values correspond to the mean difference estimated with t-tests and error bars represent 95% confidence interval. Differences significantly deviating from zero are marked with significance levels: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***). Negative (positive) values indicate that plants in warmed plots accumulated more (less) heat before reaching the phenophase. Overall estimates were inferred by grouping data from all species together. For *Geum urbanum*, the two flowering peaks are indicated with P1 (spring) and P2 (summer).

Influence of light availability on phenological temperature sensitivity

In general, we observed no effect of illumination on phenological temperature sensitivity (Fig. 4). Only in *Galium odoratum* we observed an interaction between illumination and mean spring air temperature (insignificant for FFD, significant for FP). For this species, the advancing effect of warming only appears under conditions of higher light availability. The effect of light addition alone is very small and mainly insignificant. However, we do observe a pattern of an overall slightly delayed phenology in response to illumination. For most species, the sum of the warming-induced advance and the small illumination-induced delay amounts to a smaller observed flowering advance in plots with combined warming and illumination than in warming-only plots (observed shifts in Fig. S6). In contrast, *Allium ursinum* FP and LFD was significantly advanced in response to light addition, which resulted in a greater advance in plots with combined warming and illumination compared to plots with warming only (Fig. S6).

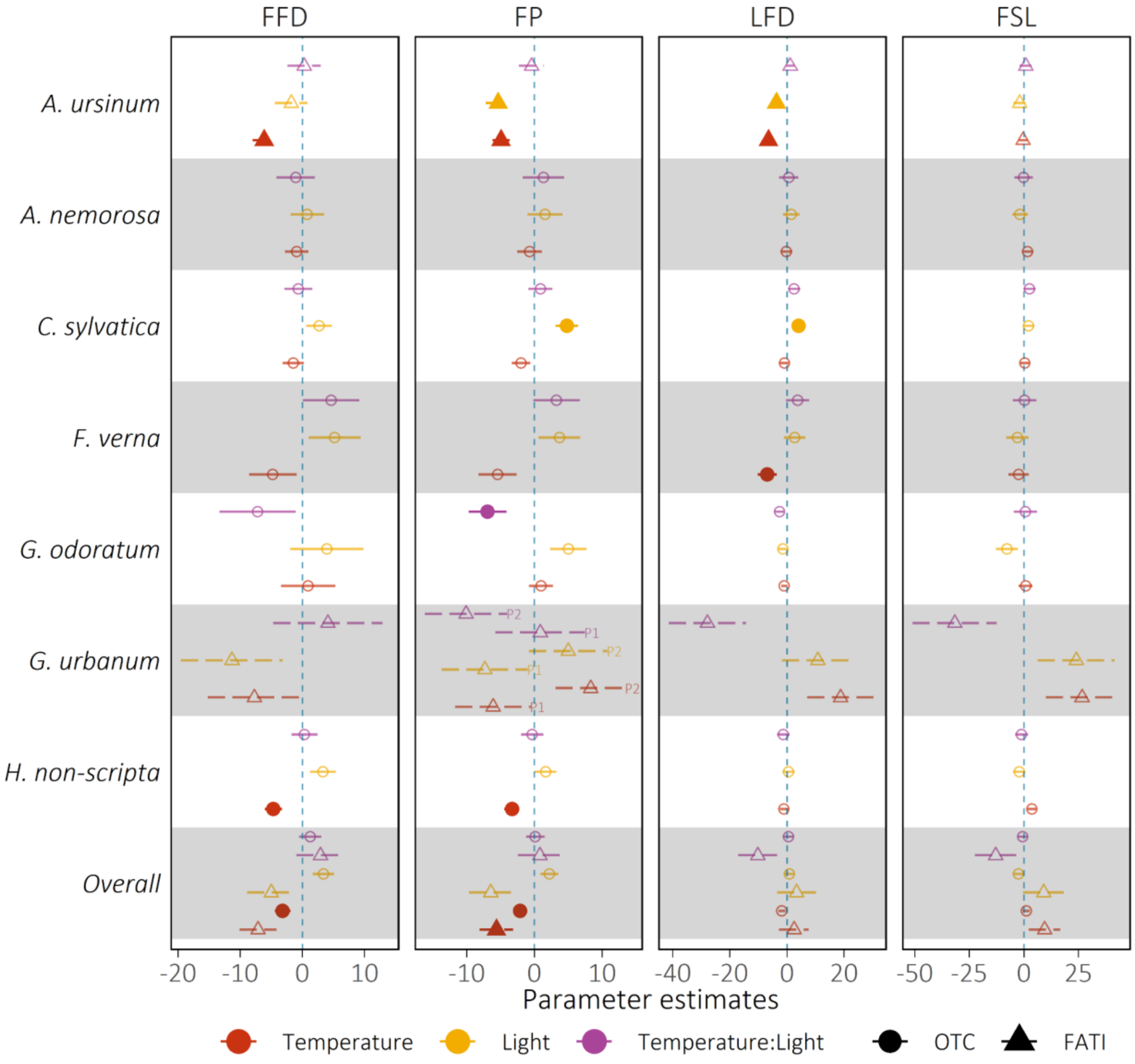

Fig. 4. The response of species-specific (and overall) flowering phenology to mean spring air temperature, illumination and their interaction. OTC = open-top chamber, FATI = Free-Air Temperature Increase. Parameter estimates (± standard error) from linear mixed-effect models for flowering onset (FFD), peak (FP), end (LFD) and duration (FSL) are shown. Nonsignificant coefficient estimates ($p > 0.05$) are made transparent. The temperature variable was z-transformed to facilitate comparisons of the parameter estimates. Negative (positive) estimates indicate an advancing phenology, or shortened flowering season, (delaying, or prolonged) in response to the parameter.

Overall estimates were inferred by grouping data from all species together. For *Geum urbanum*, the two peaks are indicated with P1 (spring) and P2 (summer).

Relationship between phenological temperature sensitivity and species characteristics

We observed several significant relationships between phenological temperature sensitivity of FFD and FP, and species characteristics, whereas no significant relationships were found for LFD or FSL. The relationships between sensitivity of FFD and FP and microclimate-adjusted thermal niche optimum were negative in 2021 (Fig. 5) and in 2022 (Fig. S7). Warmer-adapted species exhibited greater advances of FFD and FP, than species with a colder thermal niche optimum. We also found a slightly positive relationship between FFD-sensitivity and CCI, with species with a higher colonization capacity (lower or negative CCI) having a somewhat greater sensitivity to mean spring air temperature than slower colonizing species (Fig. S8), but the slope is almost flat (slope = 0.057) and the relationship is weak (R^2 = 0.187). Moreover, in the three species monitored in 2022 there is no relationship at all (Fig. S9). There were no significant relationships between the intrinsic phenology and temperature sensitivity in both years (Fig. 6 and Fig. S10).

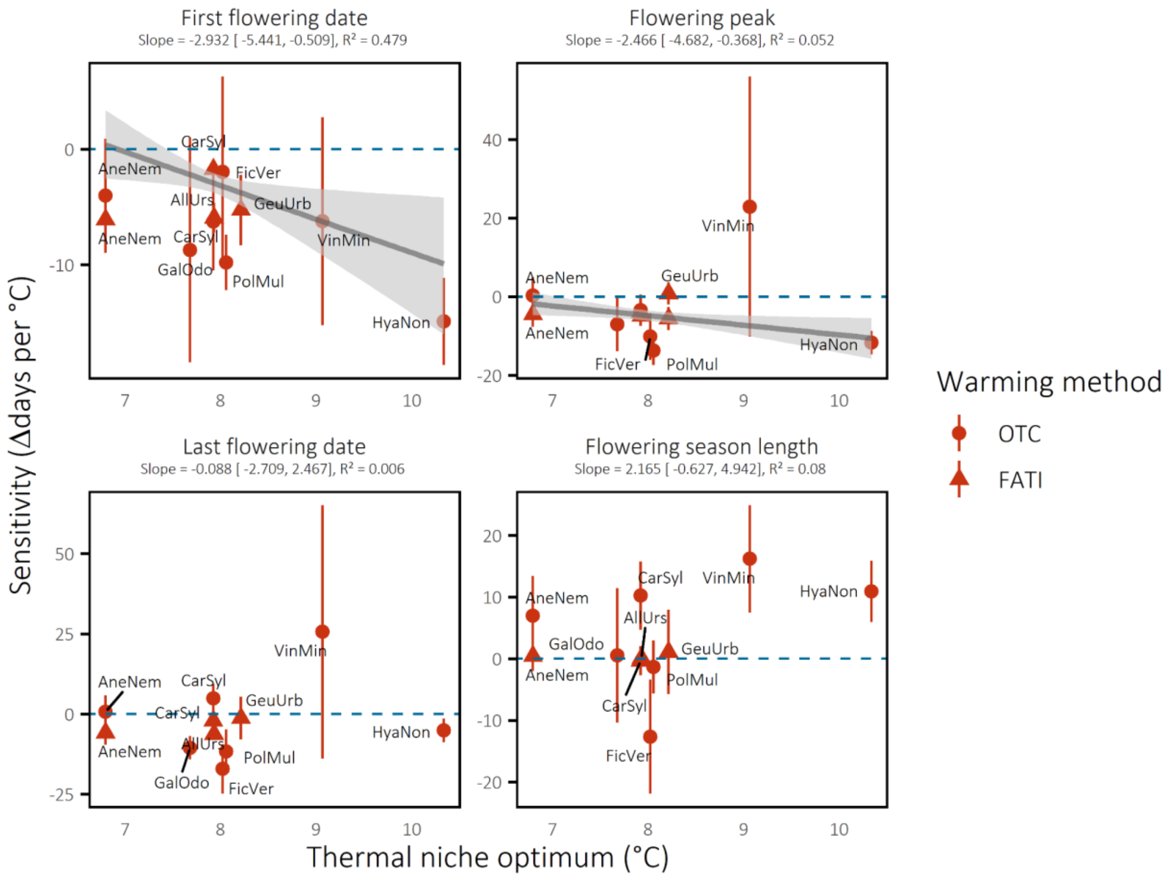

Fig. 5. Linear regressions between the species' spring temperature sensitivity (mean ± standard error) of each phenology variable and the species-specific microclimate-adjusted thermal niche optimum.

OTC = open-top chamber, FATI = Free-Air Temperature Increase. The standard errors on the temperature sensitivity estimates (specified as an addition to the response term) were considered by the linear model. Regression lines represent significant (95% credible interval not overlapping zero) slopes. Shading delineates 95% credible intervals.

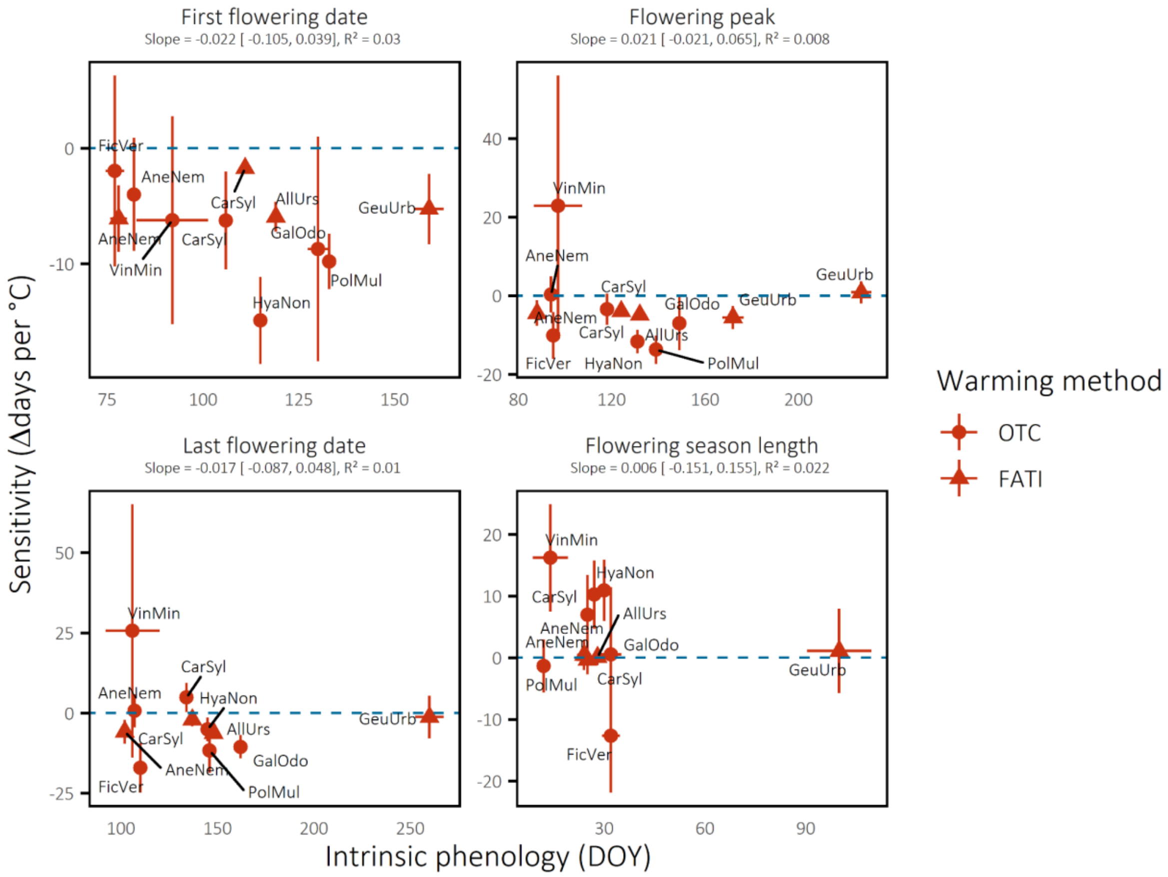

Fig. 6. Linear regressions between the species' spring temperature sensitivity (mean ± standard error) of each phenology variable and the species-specific intrinsic phenology (mean ± standard error). OTC = open-top chamber, FATI = Free-Air Temperature Increase. Intrinsic phenology is calculated as the mean day of the year (DOY) of flowering onset, peak, end and duration in control plots. The standard errors on the temperature sensitivity estimates (specified as an addition to the response term) and standard errors on the intrinsic phenology means (specified as measurement error) were considered by the linear model. No significant (95% credible interval overlapping zero) slopes were found.

Discussion

Sensitivity of flowering phenology to climate warming

Our study shows that climate warming advances understorey plant flowering phenology, supporting many previous findings of advancing phenology in temperate forests (Miller-Rushing & Primack, 2008;

Ellwood *et al.*, 2013; Marchin *et al.*, 2015; Jacques *et al.*, 2015; Rice *et al.*, 2018; Heberling *et al.*, 2019b; Willems *et al.*, 2022) and other environments (Fitter & Fitter, 2002; Wolkovich *et al.*, 2012; Stuble *et al.*, 2021). We found an overall advance of flowering onset with 5.2 days °C^{-1} under FATI and 8.9 days °C^{-1} in OTCs (note the distinct species pools in the two warming experiments in Table S1). Although the latter is in part driven by the extremely high sensitivity of *Hyacinthoides non-scripta* and sensitivities were smaller in the subsequent warmer year, our experiments suggest stronger understorey flowering responses than previously reported. Experimental warming of understorey herbs has also been found to induce very large advances of leaf emergence with up to 9 days °C^{-1} (Rollinson & Kaye, 2012; Jacques *et al.*, 2015). Past studies based on observations or herbaria, conducted in temperate zones estimated advances of understorey flowering between 2.2 days °C^{-1} and 4.9 days °C^{-1} (Miller-Rushing & Primack, 2008; Heberling *et al.*, 2019b; Alecrim *et al.*, 2022; Willems *et al.*, 2022; Miller *et al.*, 2022; Lee *et al.*, 2022). It is clear that observational and experimental phenology studies can produce results that differ in magnitude. Wolkovich *et al.* (2012) found that warming experiments generally underpredict phenology advances compared to long-term observations. Such discrepancies can exist because of different temperature quantification methods between studies based on interannual temperature variation(Clark *et al.*, 2014). Furthermore, experimental set-ups can create environmental artefacts which also influence phenology (Sherry *et al.*, 2007; Marchin *et al.*, 2015), but effects of OTCs on wind speed and precipitation patterns are generally limited in forests due to the buffering role of the canopy and shrub layer (De Frenne *et al.*, 2010). Observational studies, on the other hand, rely on long-term climate datasets that do not account for microclimatic variation, thereby relating phenological shifts to increasing macroclimate temperatures, which deviate substantially from the buffered forest floor temperatures (De Lombaerde *et al.*, 2022), even in spring before tree leaf flush (Haesen *et al.*, 2021; but see also Fig. S4 for offset between air temperature in our experimental forest and outside). Canopy buffering has probably attenuated understorey responses, resulting in smaller phenological shifts than would be expected from increased above-canopy temperatures. Using above-canopy ΔT to calculate phenological sensitivity will, hence, purely mathematically, lead to smaller sensitivities than reported in our study focusing on the actual microclimate ΔT experienced by the plants. The weaker response of understorey herbs found in overstorey-understorey mismatch research (Heberling *et al.*, 2019b; Miller *et al.*, 2022; Lee *et al.*, 2022 based on macroclimate temperature series), is probably not due to a lower phenological sensitivity of these species compared to trees, but rather because forest interiors are warming at a slower rate than above-canopy temperatures (De Frenne *et al.*, 2019; De Lombaerde *et al.*, 2022). Although it is impossible to formally test whether canopy buffering has attenuated phenology responses of understorey species with our data, we encourage future observational research to further investigate below-canopy species' phenology with forest microclimate sensors or forest sub-canopy temperature maps (Haesen *et al*., 2021).

In two species, *Anemone nemorosa* and *Carex sylvatica*, we were able to observe the warming response in OTCs (mean spring air temperature increase of 0.38 °C) and under infrared heaters (mean spring air temperature increase of 1.84 °C). The fact that we report a smaller sensitivity of *Carex sylvatica* with FATI, as opposed to a similar (but non-significant) days-per-degree shift in both experiments for *Anemone nemorosa*, could indicate that *Carex sylvatica*'s response to temperature changes is non-linear.. Such non-linear responses can occur because plant phenology is also influenced by genetic controls and/or other environmental cues, such as winter temperature, photoperiod, irradiance and soil moisture and interactions with spring temperature might exist (Marchin *et al.*, 2015; Flynn & Wolkovich, 2018; Piao *et al.*, 2019). Alternatively, thermal accumulation until flowering may be non-linear in itself (Wolkovich *et al.*, 2021; Walde *et al.*, 2022) or phenological shifts can reach a plateau with increased warming as species approach the limits of their phenological plasticity (Iler *et al.*, 2013; Fu *et al.*, 2015; Fox & Jönsson, 2019). This non-linearity can explain the increased thermal accumulation until flowering of *Carex sylvatica* (and *Allium ursinum* and *Geum urbanum*) under FATI. However, there are other factors that may play a role, such as night-time temperatures. The infrared heaters are active around-the-clock inducing greater temperature differences, and thus further accelerated thermal accumulation, at night. This is in line with climate projections (IPCC, 2021), but night-time warming is not as effective as daytime temperature increases in driving phenology (Fu *et al.*, 2016; Rossi & Isabel, 2017). Indeed, when only including daytime thermal units this pattern largely disappeared (Fig. S5). Finally, decreased soil moisture under infrared heaters (De Pauw *et al.*, 2021) can also affect plant phenology (Rathcke & Lacey, 1985; Jacques *et al.*, 2015; König *et al.*, 2018) and may have obscured responses to warming. In 2022, where mean spring temperature in the forest was c. 2°C warmer than in 2021, *Hyacinthoides non-scripta* and *Allium ursinum* flowered nine and six days earlier, respectively, but exhibited smaller advances in response to experimental warming. This can be explained by a non-linear concave relationship between flowering phenology and spring temperature, resulting in species being more sensitive (to experimental warming) in colder years (Fu et al., 2015; Mulder et al., 2017). We emphasize, however, that because we did not include other environmental conditions, such as winter temperature or photoperiod, in our analysis, we do not know to which factors the observed non-linearity can be attributed. Presumably, the respective influence of genetic controls, other environmental cues or plasticity limits are species-dependent. Moreover, in plants with storage organs such as spring geophytes, temperatures of previous years may also affect phenology in the current year resulting in a time lag between warming and phenological responses (Mulder *et al.*, 2017).

Consistent with several previous studies (Fitter & Fitter, 2002; Wolkovich *et al.*, 2012; Cook *et al.*, 2012; Willems *et al.*, 2021), we observed substantial interspecific variation in phenological responses to temperature. Differences between species can be driven by species-specific flowering time, and its inherent sensitivity to rising temperatures, dependency on other environmental cues and autumn/winter chilling requirements (i.e. vernalization), or even differences in the representativeness of the chosen temperature integration period (Keenan *et al.*, 2019). *Hyacinthoides non-scripta* exhibits a very early leaf emergence compared to the other species in our species pool (Blackman & Rutter, 1954; Vandelook & Van Assche, 2008). Accordingly, its extreme flowering shifts in OTCs might be due to an extended potential for thermal accumulation and concurrent carbon gain with leaves exposed to light, in a warmer environment, leading to a greater advance of flowering onset (Sola & Ehrlén, 2007). Especially since *Hyacinthoides non-scripta* has no vernalization requirements (Thompson & Cox, 1978) and can withstand frost temperatures (Blackman & Rutter, 1954). The compressed flowering pattern of *Polygonatum multiflorum* under increased temperatures is potentially driven by slug herbivory, which seemed to be higher in warmed communities (potentially an artefact of OTCs).

Influence of light availability on phenological temperature sensitivity

The role of light in driving understorey plant trait responses and community dynamics has been well-demonstrated (De Frenne *et al.*, 2015; Blondeel *et al.*, 2020a,b; De Pauw *et al.*, 2021; Govaert *et al.*, 2021b,a), but its impact on phenology shifts of temperate forest herb species is not entirely clear. Rice *et al.* (2018) and Sercu *et al.* (2021) suggest advances of, leaf emergence and flowering onset under low light conditions while Galloway & Burgess (2012) and Willems *et al.* (2021) find opposite results.

Apart from one species, *Galium odoratum*, we found no effect of illumination on phenological temperature sensitivity (i.e. the interaction between temperature and illumination). This species, in which flowering onset and peak are irresponsive to warming alone, might reach reproductive maturity (in terms of age or height) earlier under combined warming and light treatments, leading to earlier flowering. The effect of light alone was only significant in two out of seven species, but throughout our species pool we observed slightly delayed phenologies in response to illumination. The additive effects of both treatments consequently resulted in smaller observed flowering advances in plots with combined warming and illumination compared to warming-only plots (see observed shifts in Fig. S6). This is in line with the observations of Rice *et al.* (2018), noting a greater advance of leaf unfolding for several species under a closed canopy. We hypothesize that especially for spring ephemerals illumination might loosen constraints of light scarcity driving their phenological escape, and thus allow for a delayed phenology. Alternatively, enhanced illumination may allow plants to grow bigger before reproducing (Blondeel *et al.*, 2020b and De Pauw *et al.*, 2021 report increased plant height under experimental light addition) or to increase investment in clonal reproduction at the expense of sexual reproduction, which both could lead to slightly delayed flowering. Such response is reflected in the later but higher flowering peak of *Polygonatum multiflorum*, which grew taller and carried more flowers under brighter conditions. Given that illumination also affects peak flowering density and reproductive output can be reduced due to earlier shading (Ida & Kudo, 2008), further research into the effects of warming and illumination on reproductive output and its relation to phenological shifts is necessary. The illumination treatment only adds a relatively small amount of light under an open canopy (Blondeel *et al.*, 2020b), which can explain why phenological responses to light addition were so small. Even if illumination could induce greater shifts, the drastically advancing effect of warming will likely overrule any delay caused by increased light availability leading to earlier flowering under canopy gaps, definitely for species like *Allium ursinum* which also advanced phenology in response to light addition.

Relationship between phenological temperature sensitivity and species characteristics

Several previous studies have shown that early-flowering species are more sensitive to climate warming than late-flowering species (Fitter & Fitter, 2002; Sherry *et al.*, 2007; Miller-Rushing & Primack, 2008; Cook *et al.*, 2012; CaraDonna *et al.*, 2014; König *et al.*, 2018) and that species emerging during or after canopy closure exhibit limited phenology changes (Ishioka *et al.*, 2013). Such differences may be attributed to a higher rate of temperature rise during spring, which has been the case in Europe over the last decades (Twardosz *et al.*, 2021). In forests, summer species may be less sensitive to macroclimate warming due to a greater decoupling of forest microclimate from above-canopy temperatures during their growing season (De Frenne *et al.*, 2019; Zellweger *et al.*, 2019). Within our communities, which are composed of early and late spring-flowering species with exception of *Geum urbanum*, we did not detect a relationship between intrinsic flowering time and temperature sensitivity. When exposed to microclimate warming later-flowering species, which experience a higher degree of temperature buffering by the canopy, may exhibit larger phenology shifts than those previously found by observational studies using macroclimate data. Rice *et al.* (2018) and Marchin *et al.* (2015) even reported a stronger response to microclimate warming by late-spring and summer bloomers relative to (early-)spring bloomers. Fast-colonizing species tend to be more adaptable to changes in their environment, often exhibiting a greater capacity for plastic responses (Blondeel *et al.*, 2020b; De Pauw *et al.*, 2021). We noticed a slightly positive relationship between the 2021 temperature sensitivity of flowering onset and CCI, but with a virtually flat slope and no relationship in 2022 we conclude that there are other more important attributes that define species' phenological responses to warming, or that opposite relationships might exist between phenological sensitivity and the different life history traits that are captured within the CCI. Finally, we found that warmer-adapted species advanced flowering onset and peak more than species with a colder thermal niche optimum. Although this relationship might be driven by the very responsive species *Hyacinthoides non-scripta* and there are only three species to draw the relationship in 2022, similar patterns have been noted before, with plants in northern regions having lower temperature sensitivities (Dai *et al.*, 2014; Zhang *et al.*, 2015; Shen *et al.*, 2015; Park *et al.*, 2018). Plants in northern regions may rely more on photoperiod to avoid frost damage in their variable climates, while in warmer regions where the climate is more stable there is greater payoff of tracking spring temperatures because the risk of late-spring frost is smaller (Zhang *et al.*, 2015; Renner & Zohner, 2018; Park *et al.*, 2018). There is, however, not yet a consensus on the association between latitude and phenology; Zohner *et al.* (2016), for instance, concluded that climate-driven shifts in leaf unfolding of woody plants would be constrained by photoperiod only at lower latitudes.

Implications and outlook

Our study confirms the now recognized trend that temperate forest understorey phenology advances substantially under warmer climate conditions. The observed phenological shifts and their large degree of interspecific variation will likely have profound consequences for plant fitness and may disrupt understorey communities, therewith changing forest biodiversity and associated functioning. Although early emergence of understorey herbs may increase their carbon gain during the spring light window (Jacques *et al.*, 2015; Alecrim *et al.*, 2022), it possibly also increases frost damage (Augspurger & Salk, 2017) and herbivory (Meineke *et al.*, 2021) and earlier flowering may lead to lower reproductive output (Scheepens & Stöcklin, 2013) and mismatches with pollinators (Kudo & Ida, 2013; Kharouba *et al.*, 2018). Moreover, competitive interactions between coexisting species can be altered. The potential mismatch between tree phenology and herb layer phenology (Heberling *et al.*, 2019b; Miller *et al.*, 2022; Lee *et al.*, 2022) may lower understorey carbon budgets (Heberling *et al.*, 2019a). And within the understorey layer, we may expect increased competition for early-season resources as growing seasons start to overlap (Rice *et al.*, 2018) due to contrasting phenological sensitivities of herbaceous species but also tree seedlings.

Finally, our study suggests that to further our understanding of understorey herb phenology responses to future climate change, an increased representation of forest microclimates (in terms of temperature and light availability) will be necessary. Such investigations will prove to be important as climate change will aggravate forest canopy disturbances (Seidl *et al.*, 2017; Grünig *et al.*, 2022) and understorey herbs will potentially exhibit larger phenology shifts in canopy gaps, where temperatures (and light availability) are drastically increased.

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Author Contribution

PDF, DL, EL and KV conceived the ideas and designed methodology for this study. HB, PDF, KDP, PS and KV designed and installed the long-term experiments; HB, KDP, DL, EL and PS collected data and coordinated the maintenance of the experiments. EL led the data analysis and the writing of the manuscript in close collaboration with PDF, DL and KV. All authors contributed significantly to the drafts and gave final approval for publication.

Data Availability

The phenology and spring temperature data for 2021 and 2022 are publicly available through figshare: https://figshare.com/s/384dd777095bba3d9e42.

Competing interests

None declared.

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Supporting information

Fig. S1 Illustration of PASTFORWARD experimental set-up.

Fig. S2 Illustration of FORMICA experimental set-up.

Fig. S3 Effect size of warming treatment for both warming methods.

Fig. S4 Daily true mean air temperatures from September 2020 until October 2021: difference between control, OTC and FATI plots and between micro- and macroclimate.

Fig. S5 Difference in daytime thermal accumulation until flowering onset, peak and end between warmed and control plants.

Fig. S6 Observed response of flowering phenology to warming, illumination and their combination.

Fig. S7 Linear regressions between species' 2022 spring temperature sensitivity of each phenology variable and the species-specific microclimate-adjusted thermal niche optimum.

Fig. S8 Linear regressions between species' 2021 spring temperature sensitivity of each phenology variable and the species-specific colonizing capacity index.

Fig. S9 Linear regressions between species' 2022 spring temperature sensitivity of each phenology variable and the species-specific colonizing capacity index.

Fig. S10 Linear regressions between species' 2022 spring temperature sensitivity of each phenology variable and the species-specific intrinsic phenology.

Table S1 Number of replicates for each studied species and treatment combination.

Table S2 Marginal R^2-values for univariate linear mixed models of flowering onset/peak against the different temperature variables.

Table S3 Marginal R^2-values for univariate linear mixed models of flowering end/duration against the different temperature variables.

Table S4 Regression coefficients derived from univariate linear mixed models of flowering onset/peak against the different temperature variables.

Table S5 Regression coefficients derived from univariate linear mixed models of flowering end/duration against the different temperature variables.

Table S6 P-values for regression coefficients derived from univariate linear mixed models of flowering onset/peak against the different temperature variables.

Table S7 P-values for regression coefficients derived from univariate linear mixed models of flowering end/duration against the different temperature variables.

Table S8. Spring temperature sensitivity of flowering phenology for three species in 2022.

Table S9. Mean ± SD date of flowering onset (FFD), peak (FP) and end (LFD) in control (C) and experimentally warmed (T) plots in 2021 and in 2022.