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Late to bed, late to rise—Warmer autumn temperatures delay spring phenology by delaying dormancy

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Abstract

Spring phenology of temperate forest trees has advanced substantially over the last decades due to climate warming, but this advancement is slowing down despite continuous temperature rise. The decline in spring advancement is often attributed to winter warming, which could reduce chilling and thus delay dormancy release. However, mechanistic evidence of a phenological response to warmer winter temperatures is missing. We aimed to understand the contrasting effects of warming on plants leaf phenology and to disentangle temperature effects during different seasons. With a series of monthly experimental warming by ca. 2.4°C from late summer until spring, we quantified phenological responses of forest tree to warming for each month separately, using seedlings of four common European tree species. To reveal the underlying mechanism, we tracked the development of dormancy depth under ambient conditions as well as directly after each experimental warming. In addition, we quantified the temperature response of leaf senescence. As expected, warmer spring temperatures led to earlier leaf-out. The advancing effect of warming started already in January and increased towards the time of flushing, reaching 2.5 days/°C. Most interestingly, however, warming in October had the opposite effect and delayed spring phenology by 2.4 days/°C on average; despite six months between the warming and the flushing. The switch between the delaying and advancing effect occurred already in December. We conclude that not warmer winters but rather the shortening of winter, i.e., warming in autumn, is a major reason for the decline in spring phenology.

KEYWORDS
autumn, bud dormancy, climate warming, endodormancy, fall, leaf phenology, leaf senescence, rest break, temperate trees, winter ecology

1 | INTRODUCTION

Changes in phenology are one of the most evident responses of temperate forest trees to climate warming (IPCC, 2014; Menzel et al., 2006; Parmesan & Yohe, 2003; Piao et al., 2019). Depending on tree species and location, spring phenology has advanced by 2–7 days per degree of temperature increase in the temperate zone until now (Fu, Zhao, et al., 2015; Polgar et al., 2014; Zohner & Renner, 2014). An earlier start of the growing season potentially leads to higher net primary productivity and carbon sequestration

of the biosphere (Keenan et al., 2014; Kramer, 1995; Way, 2011; White et al., 1999).

However, this advancing trend is slowing down. With increasing climate warming, spring phenology is not following at the same rate, as shown in observational (Chen et al., 2019; Fu, Piao, et al., 2015; Fu, Zhao, et al., 2015; Vitasse et al., 2018) and experimental studies (Chung et al., 2013; Morin et al., 2010). While spring temperature is known to be the main driver of spring phenology for a very long time (Polgar & Primack, 2011), there are further parameters influencing the timing of leaf-out. In addition to photoperiodic constraints (Fu et al., 2019), increasing winter temperatures and consequently insufficient chilling are discussed as reasons for the decline in spring advancement. (Asse et al., 2018; Fu, Piao, et al., 2015; Fu, Zhao, et al., 2015; Laube et al., 2014; Polgar & Primack, 2011).

Temperate trees rely on safety mechanisms to prevent them from leafing out at the wrong time. When buds are formed during middle and late summer, they are initially only prevented from flushing by hormonal control of the active leaves (i.e., paradormancy) (Lang, 1994). At the time of leaf senescence and leaf fall, however, the buds need to be in a deep (endo-) dormant state, so that they will not open until spring, even if the weather should become temporarily warm again in autumn or winter. Thus, for dormancy release (also referred to as rest break), the buds need to be exposed to cool temperatures for a certain time (i.e., chilling) before becoming increasingly sensitive to warm (i.e., forcing) temperature and finally leaf-out (Polgar & Primack, 2011). The shift between the chilling and forcing period is seen as a gradual transition: With increasing accumulation of chilling, trees become more sensitive to forcing (Harrington et al., 2010). In other words, if they experienced less chilling due to winter warming, trees need more forcing temperatures to leaf-out (Fu, Piao, et al., 2015; Murray et al., 1989). Therefore, an increase in temperature may have contrasting effects on spring phenology, depending on the time at which it occurs.

Besides winter chilling, more recent studies have also reported on the impact of autumn temperature on spring phenology. A positive correlation between temperatures during autumn dormancy induction and spring leaf-out in the following year was found with warm autumn temperatures delaying spring phenology (Granhus et al., 2009; Heide, 2003; Søgaard et al., 2008; Westergaard & Eriksen, 1997). However, the causal link between autumn warming and subsequent spring phenology effects remains unclear. In addition, later autumn senescence was found to cause later spring leaf-out (Fu et al., 2014; Shen et al., 2020). While there is a growing body of research on spring phenology and the release of bud dormancy, the processes in autumn are comparatively less investigated. Not only are the environmental drivers of autumn leaf senescence not fully understood (Gallinat et al., 2015), also the timing of dormancy induction in tree buds and its environmental drivers are largely uncertain. The timing of dormancy induction, however, might be of particular interest, as it is very likely related to the time at which the accumulation of chilling temperatures starts. Therefore, we investigated the temperature sensitivity of the phenological cycle as a whole.

In order to project future growing season lengths and, consequently, terrestrial carbon sequestration, a causal understanding of seasonal differences in temperature sensitivity of leaf phenology is urgently needed. Most of our knowledge to date comes from extensive observations (Piao et al., 2019). However, experiments are needed to disentangle the environmental factors from each other and to provide a mechanistic understanding of plants' phenological response to increasing temperature (Hänninen et al., 2019), allowing for predictions of phenological shifts beyond the range of current conditions.

In this study, we investigated the phenological response of temperate trees to warming by disentangling temperature effects during different seasons from each other. We answer the question, during which period of the year elevated temperatures have an advancing or a delaying effect on leaf phenology. In a series of monthly warming manipulations at a realistic level of ca. 2.4°C from late summer until leaf-out in spring, we quantified the effects on leaf senescence, dormancy, and spring phenology in seedlings of two early and two late flushing common European forest tree species. To reveal the underlying mechanism, we tracked the progression of bud dormancy by repeatedly quantifying dormancy depth and tested how its induction and release are modulated by temperature. We hereby contribute to a deeper mechanistic understanding of the complex effects of climate warming on plant leaf phenology.

2 | METHODS

2.1 | Site

We conducted our study at the University of Greifswald campus (54.0919 N, 13.3647 E) in northeast Germany. The climate is temperate with maritime influence with a mean annual temperature of 8.8°C and mean annual precipitation of 565.0 mm. January is the coldest month with a mean temperature of 0.7°C and July is the warmest month with a mean temperature of 16.7°C (meteorological data provided by DWD [German Meteorological Service] from 1981 to 2010). For monthly mean temperatures during the experiment, see Table 1.

2.2 | Plant material

As study species we chose four common European tree species: *Fagus sylvatica* (European beech), *Quercus robur* (pedunculate oak), *Betula pendula* (silver birch), and *Alnus glutinosa* (black alder). *Fagus* and *Quercus* are late flushing species, *Alnus* and *Betula* flush early. We obtained 2-year-old seedlings with seed sources from northern Germany from a local nursery in June 2018, planted them in 2 l pots each, and placed them in a common garden under ambient conditions. The species were evenly distributed among each other in blocks of four plants of each species. Each block was randomly assigned to a part of the experiment before the start. The pots were

	Treatment period		Mean temperature [°C] (standard deviation)				
Month	**Start**	**End**	**1981–2010[a]**	**Ambient**	**Control**	**Warming**	**Δ_{W-C} [°C]**
Sept	30-Aug	27-Sep	13.8	17.3 (4.8)	18.1 (3.7)	20.6 (3.6)	2.5
Oct	27-Sep	25-Oct	9.4	12.6 (4.0)	13.9 (3.7)	15.8 (3.5)	1.9
Nov	1-Nov	29-Nov	4.7	7.1 (3.4)	7.2 (3.9)	9.4 (3.9)	2.2
Dec	30-Nov	28-Dec	1.5	5.4 (2.5)	5.4 (2.7)	7.6 (2.5)	2.2
Jan	3-Jan	31-Jan	0.7	2.5 (2.7)	3.5 (3.1)	6.1 (3.2)	2.6
Feb	31-Jan	28-Feb	1.0	5.8 (3.0)	6.1 (3.5)	8.5 (3.6)	2.4
Mar	28-Feb	28-Mar	3.7	7.3 (2.8)	8.4 (3.0)	11.1 (2.9)	2.6
Apr	28-Mar	25-Apr	7.6	11.3 (5.0)	11.4 (4.8)	13.9 (4.7)	2.5

[a]Long-term mean temperatures for Greifswald according to data provided by DWD acquired from https://opendata.dwd.de/climate_environment/CDC/observations_germany/climate/monthly/kl/historical/.

TABLE 2 Chilling and forcing units accumulated during each experimental period in warming and control treatment, respectively, as well as under ambient conditions

	Chilling units				Forcing units GDD			
Month	**Control**	**Warming**	**D_{W-C} [°C]**	**Ambient**	**Control**	**Warming**	**D_{W-C} [°C]**	**Ambient**
Sept	0	0	0	2	(366)	(439)	(72)	(313)
Oct	0	0	0	11	(251)	(307)	(55)	(188)
Nov	19	11	8	26	(83)	(129)	(46)	(51)
Dec	26	25	1	26	(34)	(72)	(39)	(21)
Jan	28	26	2	24	12	51	39	3
Feb	28	15	13	28	49	100	52	22
Mar	20	13	7	27	95	168	73	41
Apr	10	5	5	18	173	243	70	106

Note: Values for forcing units before January 1 are given in brackets because temperature before January 1 is not assumed to have a forcing effect. Note that for the early flushing *Betula* and *Alnus*, the experiment was only conducted until February.

placed into sand to stabilize them and to prevent the roots from frost damage in winter. They were watered as needed. In total, we worked with 1324 seedlings, 294 each of the early flushing *Betula* and *Alnus*, and 356 each of the late flushing *Fagus* and *Quercus*.

2.3 | Dormancy development under ambient conditions

To track the pattern of dormancy induction and development, we assessed bud dormancy depth from August 2018 onward until spring flushing. Bud dormancy depth is defined as the time or growing degree days (GDD) required for a bud to flush under standardized optimal growing conditions (Halbritter et al., 2020). In late summer, the buds undergo a transition from shallow paradormancy to deep (endo-) dormancy, which is then gradually released over winter. High dormancy depth indicates that a plant is far away from leafing out, while low dormancy depth values indicate that the plant will soon leaf out with only a low input of additional warmth.

We started the dormancy depth assessment already in August, because we aimed to include the period of (endo-) dormancy

induction, recognizable by increasing dormancy depth. Every week, we transferred three plants of each species from the common garden into a warm greenhouse with optimal growing conditions (21.5°C ± 2.3°C SD and 16 h light). If there were still leaves on the plants, we removed them to eliminate any inhibiting influence of leaves on the buds (Halbritter et al., 2020). Dormancy depth was quantified as the amount of GDD required by the seedling from its transfer into this warm greenhouse onward until unfolding of its first new leaf. GDDs were calculated as:

$$GDD = \begin{cases} \sum_{t_0}^{t_1} (T_{mean} - T_{base}), & T_{mean} \geq T_{base} \\ 0, & T_{mean} < T_{base} \end{cases} \quad (1)$$

where t_0 is the starting day at which the seedling was transferred to the warm, t_1 is the day at which leaf unfolding was observed, T_{mean} is the daily mean temperature, and T_{base} is a constant set to 5°C, representing a minimum temperature threshold required for stimulating budburst (Fu et al., 2016; Polgar & Primack, 2011). To minimize potential small-scale environmental differences in the greenhouse, we reshuffled the position of the single pots three times a week.

2.4 | Temperature manipulation

We applied 4-week warming manipulations from September onward until February for the early flushing species and until March for the late flushing species. Two compartments of a greenhouse were used with natural light and fluctuating temperatures according to outside conditions. The control compartment with open windows and no heating had temperatures slightly above outside (0.6°C) and the warming compartment's temperature was maintained on average 2.4°C above the control (Table 1).

Each month, we transferred the preselected plants (32 per species) into the greenhouse and divided them equally between the two treatment compartments (16 plants per species and treatment), hereby evenly distributing them according to their outer appearance like leaf coloration stage and plant size. They remained in the corresponding greenhouse compartment for 4 weeks. After the treatment, half of the plants (eight per species and treatment) were directly placed back in the common garden for the observation of autumn and spring phenology, while the other half was used to destructively assess the dormancy depth directly after the treatment by the same method as described above for the dormancy development under ambient conditions (Figure S1).

The resulting chilling and forcing units accumulated during each monthly warming period for each treatment are given in Table 2. Chilling units were calculated as the number of days with daily mean temperatures between −2 and 10°C, according to recent findings of Baumgarten et al. (2021). Forcing units were calculated as GDD according to equation (1), where t_0 is the starting day and t_1 is the end of the respective manipulation period.

2.5 | Assessment of phenology

We observed autumn phenology at weekly intervals before, during, and after the September and October warming manipulation on those seedlings that were not used for dormancy depth assessments (8 seedlings per species and per treatment). For quantifying chlorophyll degradation, we used an SPAD 502 Plus Chlorophyll Meter. In order to avoid selection bias, we always choose the greenest leaves.

For evaluating the timing of senescence and chlorophyll degradation, we calculated the day at which the chlorophyll content reached 50% of its maximum value for each individual plant: The maximum value was calculated as the maximum of the means of three consecutive measurements before the start of chlorophyll degradation and was set to 100%. For each plant, a sigmoid curve was then fitted on the relative chlorophyll content values over time, from which the date of the inflection point, that is, the day with 50% mean chlorophyll content, was used for further analysis.

For spring phenology, we observed the plants three times per week and recorded the date at which the first leaf was unfolded, which was defined by the petiole being visible (Meier, 2001).

2.6 | Statistical analysis

The effect of warming on chlorophyll degradation, dormancy depth, and leaf-out dates was tested with linear mixed-effects model ANOVAs with the warming treatment, the month of the treatment, and the species as explanatory variables (R-package "lmerTest," (Kuznetsova et al., 2017)). Since data of dormancy depth and leaf-out were assessed only until February for early flushing Betula and Alnus and until March and April for late flushing Fagus and Quercus, two separate models were applied—one for all species until February and one for the late flushing species for the remaining months, respectively. Heteroscedasticity and normal distribution of the residuals were tested for each model by visual diagnostics, that is, inspecting the residuals versus fitted plots and the qq-plots of the residuals (Faraway, 2005). If necessary (i.e., for dormancy depth of all species until February), data were rank transformed. A Tukey's HSD post hoc test (R-package "emmeans," (Lenth, 2020)) was used to test for significance of differences between warming and control treatment for each month.

The effect size of warming on autumn and spring phenology was calculated as the difference in timing of phenological events divided by the difference in temperature between warming and control treatment. All statistical analyses were done in R version 4.0.2 (R Core Team, 2020). For graphical visualizations, the R packages ggplot2 (Wickham, 2016) was used.

3 | RESULTS

3.1 | Effect of warming at different periods on spring leaf phenology

We found contrasting effects of warming, depending on the time at which it was applied, while no difference between the species' responses to warming was observed (Table 3). From January onward, the seedlings responded with earlier spring leaf-out (Figure 1 and Figure S2). This advancing temperature effect increased toward the time of flushing, reaching 2.5 days/°C in the month before leaf-out on average across all four species. However, while warming in winter did not postpone spring phenology at any time, we found a surprisingly strong delaying effect of warming in October on spring leaf-out (Figure 1). Averaged over all species, leaf unfolding in spring was delayed by 2.4 days for every 1°C temperature increase in October. Figure S2 provides leaf unfolding dates of all trees and allows for comparison between warming and control of each manipulation period.

3.2 | Dormancy development under ambient conditions

Bud (endo-)dormancy induction started in September under ambient conditions, indicated by the increase in dormancy depth (Figure 2). Dormancy depth increased then rapidly and reached its peak in the middle of October on average at 43 days to leaf unfolding under

	All species until February		*Fagus* and *Quercus* in March and April	
	F-value	p-value	F-value	p-value
Warming	0.6	.438	40.5	**<.0001**
Month	15	**<.0001**	15.5	**.0002**
Species	1057	**<.0001**	53.9	**<.0001**
Warming: month	7.1	**<.0001**	1.3	.256
Warming: species	2.1	.103	0.6	.427
Month: species	1	.458	17.7	**.0001**
Warming: month: species	1.2	.299	0.5	.468

Note: Bold indicates statistical significant value.
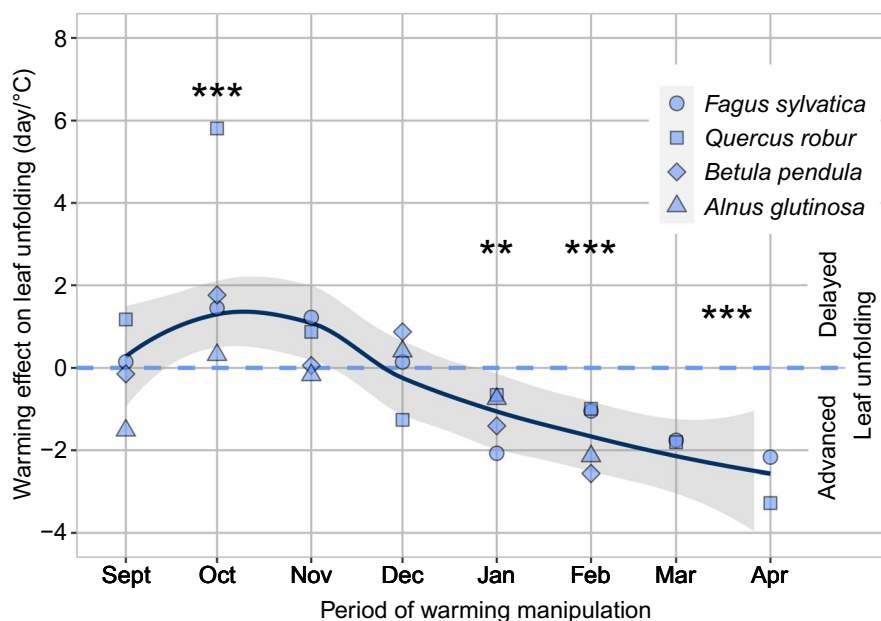

FIGURE 1 Effect of warming on spring leaf unfolding in days per °C warming at different periods during autumn, winter, and spring. Each warming manipulation lasted 4 weeks. Positive values indicate a delaying effect of warming on spring leaf unfolding. Asterisks denote significant differences in leaf unfolding days between warming and control with *$p < .05$, **$p < .01$, ***$p < .001$ (Tukey's HSD). The line is a LOESS curve integrating all species, for illustration of the overall trend. Note that no significant interaction between species and warming occurred in the first model until February (Table 3). The gray-shaded area represents the 95% confidence interval of the loess curve

forcing conditions for *Fagus*, *Quercus* and *Betula*, and at 62 days for *Alnus*. Afterward, the early flushing species *Betula* and *Alnus* showed a steep decrease of dormancy depth from mid-October to mid-November, while in the late flushing species, dormancy decrease was more gradual and irregular. From the beginning of January onward, dormancy depth generally declined continuously and evenly until final leaf-out in all species.

3.3 | Dormancy depth under warming

Warming had significant effects on dormancy development at the beginning and at the end of the dormant period (Figure 3 and Table 4). At the time of dormancy establishment in September and October,

warmer conditions resulted in lower dormancy depth compared to the control by 110 GDDs (Tukey's HSD $p < .001$) and 104 GDDs (Tukey's HSD $p = .036$), respectively, averaged over all species. In the month before leaf-out (March for *Fagus* and *Quercus*, February for *Betula* and *Alnus*), dormancy depth was again lower after warming by 43 GDDs (Tukey's HSD $p < .001$), averaged over all species. No significant difference between the species regarding their response to warming was observed (Table 4).

3.4 | Autumn senescence and leaf fall

While warming in September had no effect on autumn phenology, October warming by 1.9°C delayed autumn senescence and leaf
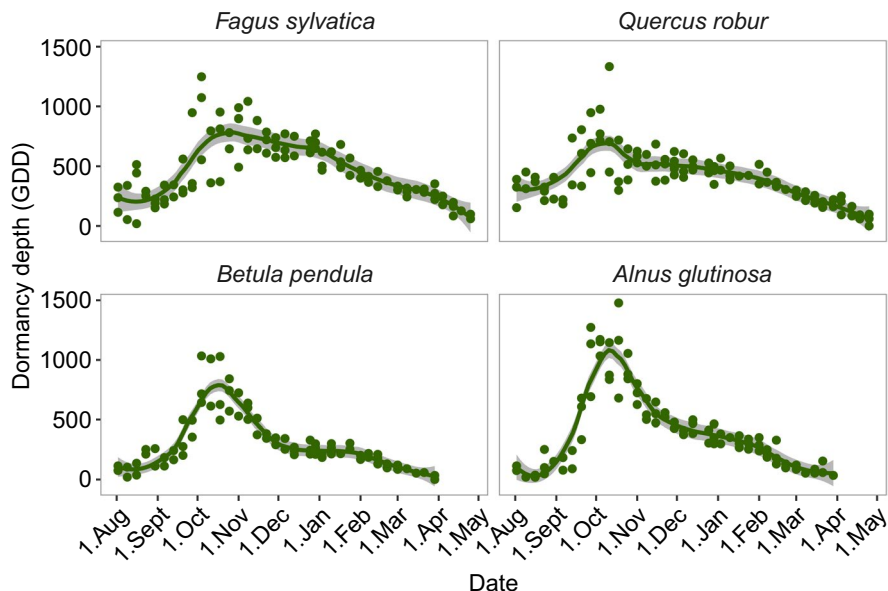
FIGURE 2 Dormancy development from August until leaf-out in the following year. Dormancy depth was quantified as growing degree days (GDD) needed for leaf unfolding under favorable condition (21.5°C and 16 h light)
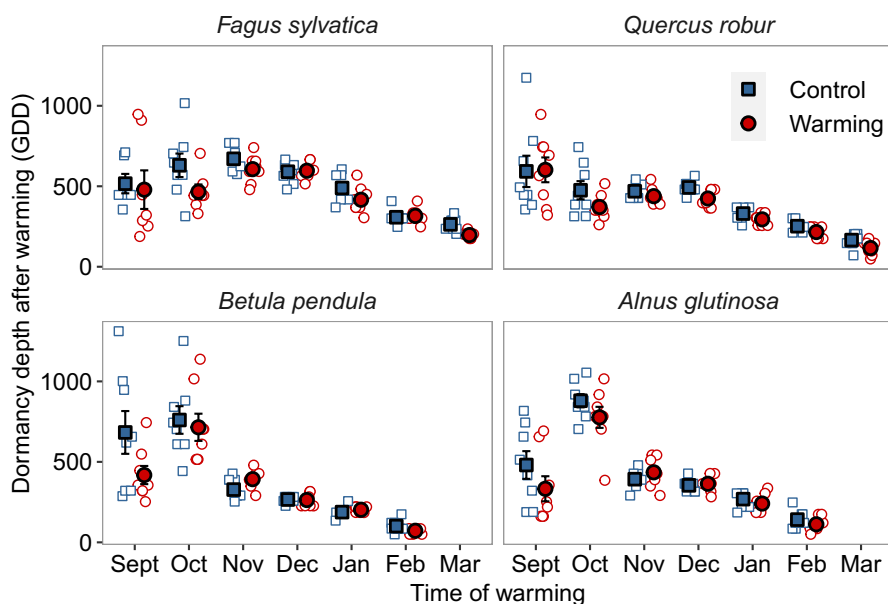

FIGURE 3 Dormancy depth as influenced by 4 weeks of moderate warming (red, right) compared to a control (blue, left) during the time of dormancy establishment (September and October) and dormancy release (November until leaf out). Dormancy depth was quantified directly after each treatment as growing degree days (GDD) needed for leaf unfolding under favorable conditions. Small open circles and squares represent single plants, big filled circles and squares represent the mean of each group, "whiskers" represent standard error bars

fall substantially (Table 5, Figure 4, Table 6). The day when SPAD values reached 50% was on average 11.7 days later after October warming compared to the control (Tukey's HSD *p*-value <.001, Figure 4), a warming effect of 6.2 days/°C. The first day with all leaves fallen or brown delayed by 11.5 days. No significant difference between the species regarding their response to warming was observed.

4 | DISCUSSION

4.1 | Autumn warming delayed spring phenology

Warm temperatures in October delayed spring phenology in the following year (Figure 1). The effect of October warming (2.4 days/°C delay in leaf unfolding) was almost as strong in magnitude

	All species until February		*Fagus* and *Quercus* in March	
	F-value	p-value	F-value	p-value
Warming	9.3	**.003**	17.3	**<.001**
Month	135.9	**<.001**	—	—
Species	59.4	**<.001**	41.1	**<.001**
Warming: month	2.6	**.025**	—	—
Warming: species	0.8	.480	0.4	.550
Month: species	14.2	**<.001**	—	—
Warming: month: species	1.1	.341	—	—

Note: Bold indicates statistical significant value.

TABLE 5 Effect of warming, month (September or October), and species on senescence date (50% reduction in chlorophyll content) with their interactions

	F value	p-value
Warming	12.6441	**<.001**
Month	1.6501	.202
Species	24.8956	**<.001**
Warming: month	24.5599	**<.001**
Warming: species	0.5893	.623
Month: species	4.1147	**.008**
Warming: month: species	1.3263	.269

Note: Bold indicates statistical significant value.

effect (i.e., leaf-out in spring). A similar delay of spring phenology by autumn warming has been shown before in an exceptionally long phenological time series, the Marsham record from Norfolk, United Kingdom, where Roberts et al. (2015) found a positive correlation between spring leaf-out dates and temperatures in previous autumn, for example, a delay in spring phenology after warmer autumn temperatures. Likewise, Heide (2003) observed a delaying effect of autumn temperatures on spring leaf-out at 2.6 days/°C by comparing September mean temperatures and leaf-out dates of *Betula pendula* and *B. pubescens* saplings during six consecutive years.

One potential explanation for the delay in spring phenology after autumn warming would be reduced chilling. However, warming in October did not affect the amount of chilling in comparison
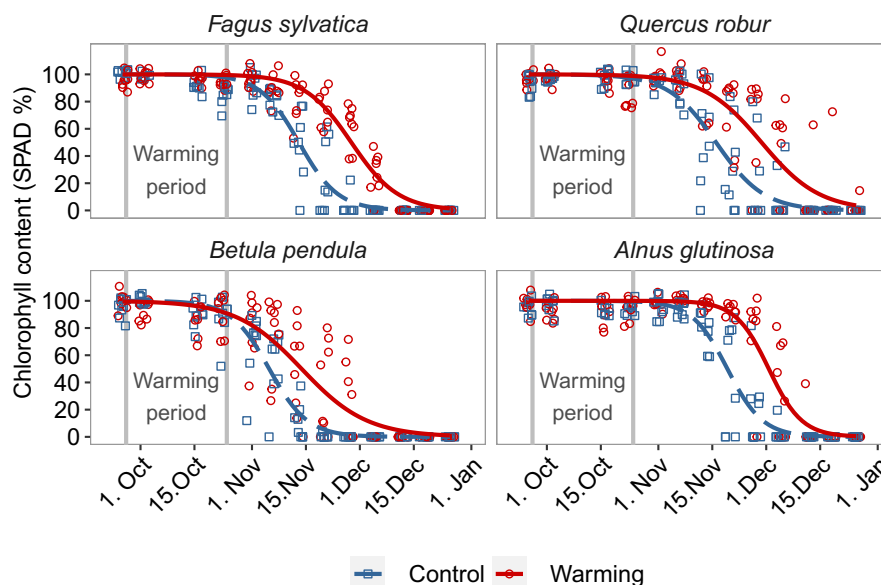

FIGURE 4 Decline of chlorophyll content (measured as SPAD values, in relation to maximum SPAD) after warming manipulation in October in comparison to the control treatment. Mean temperatures: warming 15.8°C (red dots and line), control 13.9°C (blue dots and line)

as warming right before leaf-out in spring, albeit in the opposite direction. This is surprisingly high, given the long time span of up to 6 months between the cause (i.e., warming in October) and the

to the control, as neither under warming nor under control conditions any chilling units accumulated (Table 2). Also, when using different models (Hänninen, 1990; Wang et al., 2020), there was

	Day of 95% chlorophyll content			Day of 50% chlorophyll content			Day of 5% chlorophyll content		
	Control	Warming	Diff	Control	Warming	Diff	Control	Warming	Diff
Fagus	01. Nov	10. Nov	8.9	14. Nov	28. Nov	**13.8**	27. Nov	15. Dec	**18.7**
Quercus	06. Nov	18. Nov	**12.2**	18. Nov	30. Nov	**12.7**	29. Nov	12. Dec	**12.6**
Betula	24. Oct	28. Oct	4.0	05. Nov	14. Nov	**9.3**	17. Nov	01. Dec	**14.5**
Alnus	12. Nov	25. Nov	**12.9**	20. Nov	01. Dec	**11.0**	28. Nov	07. Dec	8.7
Mean			9.5			11.7			13.6

Note: The values are averages of eight tree seedlings, respectively. Bold numbers indicate significance ($p < .05$).
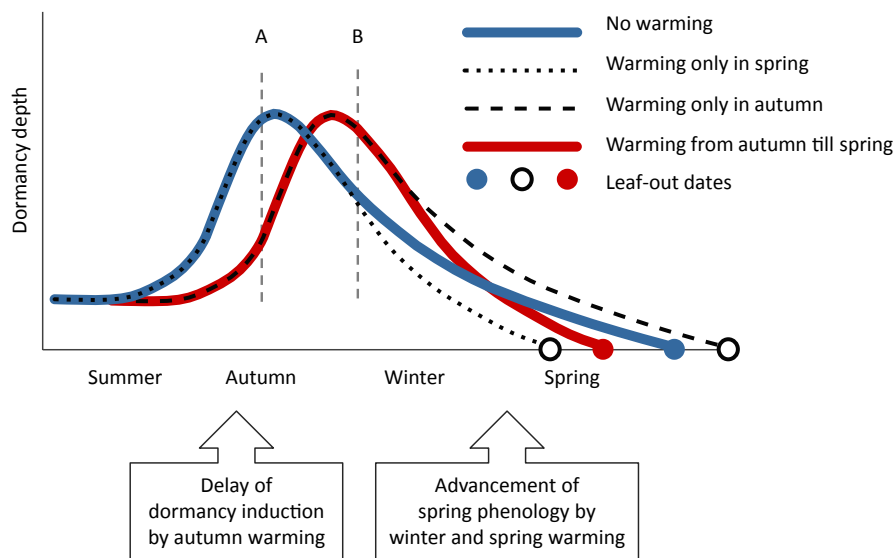

FIGURE 5 Schematic illustration of the effect of warming on bud dormancy during its induction and its release. Autumn warming delays dormancy induction (resulting in lower dormancy depth values before (e.g., at time A), and higher dormancy depth values after (e.g., at time B) peak of dormancy and hereby reduced spring advancement of leaf phenology. The x-axis represents time and crosses the y-axes at 0 so that at the point where the dormancy depth curve crosses the x-axis, represents the time of a dormancy depth value of 0, that is, the time of leaf out

no reduction in chilling, because the temperatures were still above the commonly accepted temperature threshold for chilling of 10°C. In fact, the plants of the September and October treatment experienced the coolest temperature over the whole dormant season, compared to the other plants, because they remained outside under ambient conditions during all the other manipulation periods (Table 2). Therefore, a lack of chilling cannot explain the later leaf-out after October warming.

Furthermore, the term "chilling" refers to the gradual decrease of dormancy depth under cool temperatures. At the beginning of the October warming period (27 September to 25 October), however, dormancy was still increasing and had not yet reached its peak (Figure 2). Therefore, we propose that it was the establishment of dormancy, not its release, that was affected by warming in October. Dormancy establishment has rarely been studied to date, as neither the process itself nor its beginning or end is visible to our eyes.

4.2 | Delayed dormancy establishment due to warmer autumn temperatures

Warm temperatures during the establishment of bud dormancy in September and October caused a lower dormancy depth (Figure 3). This could be interpreted in two different ways: (1) as an induction of weaker dormancy or (2) as a delay in dormancy induction. If the first interpretation was correct, this weaker dormancy would result in faster dormancy release and in earlier leaf-out, which is not supported by our results. Therefore, we follow the second interpretation and conclude that autumn warming caused a delay in dormancy induction. This inference provides a mechanistic link between autumn warming and the delay of spring phenology: A later dormancy establishment delays the whole dormant phase, with a later peak and later release of dormancy. The buds become sensitive to warm temperatures later and, consequently, leaf-out later (Figure 5).

In contrast to our results, some earlier studies found deeper dormancy depth after warming during dormancy induction, but also associated with later leaf-out (Granhus et al., 2009; Heide, 2003; Malyshev, 2020; Søgaard et al., 2008; Westergaard & Eriksen, 1997). This has been interpreted as a reinforcement of dormancy induction under warm temperatures (Hänninen & Tanino, 2011; Olsen et al., 2014). However, in all these studies, dormancy depth assessments were conducted either several weeks after the beginning of dormancy induction or the time of dormancy induction was unknown. In both cases, dormancy depth assessment very likely have taken place after the peak of dormancy depth, which is also supported by the continuously descending dormancy depth over time in the studies of Granhus et al. (2009) and Heide (2003). This suggests an alternative interpretation: What has been understood as an enhancement of dormancy under warmer temperatures was in fact a delay in dormancy induction, with a later peak and therefore later decrease of dormancy depth, resulting in higher dormancy depth values at the time of its assessment (Figure 5, time point B).

In our experiment, October was the most sensitive month for dormancy induction, but in general it can be assumed that the crucial period is determined by the timing of autumnal temperature decline. Which temperatures trigger dormancy induction and how they interplay with other environmental factors such as photoperiod clearly needs more research. In addition, although the dormancy delaying effect was apparent in all tested species, future studies on other species will examine the generality of our findings. In particular, the species and ecotypes are likely to be adapted in this regard to the climate and the typical duration of the non-growing at their place of origin.

4.3 | Delayed leaf senescence

Like bud dormancy establishment, autumn leaf senescence and leaf fall were delayed by warm temperatures in autumn. This is in line with previous studies which report a delay in leaf senescence due to warm temperatures in late summer and autumn (Delpierre et al., 2017; Fracheboud et al., 2009; Gunderson et al., 2012; Liu et al., 2016; Zani et al., 2020; Zohner & Renner, 2019). Fu et al. (2018) found in their experimental study a delaying temperature effect on leaf senescence by 6–8 days/°C in Fagus, which is well comparable to our results (Table S3).

Leaf senescence is not only important with respect to an elongation of the growing season, but it is functionally related to bud dormancy: As long as the leaves are active, their hormone release prevents the buds from opening (paradormancy, Howe et al., 2015). However, from the time of leaf senescence onward, the buds depend on another reliable mechanism to avoid leaf-out at the wrong time, even if relatively warm temperatures still might occur. Therefore, bud dormancy induction and leaf senescence are very likely to be synchronized with each other, either triggered by related environmental drivers or internally coordinated. The temporal correspondence of autumn senescence and dormancy induction on the one hand and the impact of the timing of dormancy induction on spring

phenology on the other hand provide now a causal explanation for the correlation between autumn and spring phenology (Fu et al., 2014; Shen et al., 2020): Later leaf senescence indicates later dormancy induction, which causes later leaf-out. If the temporal correspondence of leaf senescence and dormancy induction is maintained under atypical environmental conditions, such as drought, remains to be subject to further investigations.

4.4 | No delayed spring phenology after warming in winter

During November and December, warming had no significant effect on spring leaf-out despite reduced accumulation of chilling units (Table 2). Empirical knowledge on the effective chilling temperature ranges is still limited (Chuine et al., 2016). Baumgarten et al. (2021) recently reported a wide range of effective chilling temperatures from −2 to +10°C, temperatures that were given under both of our treatments. Another nonexclusive explanation would be that chilling and forcing temperatures can both reduce the dormancy depth (Malyshev, 2020), since both processes, chilling and forcing, operate simultaneously in the bud (Harrington & Gould, 2015). In the control compartment, the plants could have experienced more chilling, whereas in warming compartment, they experienced more forcing, both of which drive dormancy release and eventually resulting in similar spring budburst dates. In any case, chilling temperature in November and December does not seem to be a limiting factor, even though the study site has mild winters and the specific study year was 3.4 warmer than the long-term mean (1981–2010, average over September–April, Table 1).

During meteorological winter, that is, January–March, warming caused an earlier leaf-out, both in early and in late flushing species. The advancing effect started already in January and increased continuously toward the time of flushing (Figure 1), reaching 2.5 days/°C in the month before leaf-out (averaged over all species). Interestingly, Roberts et al. (2015) report the shift between delaying and advancing effect of warm temperatures also around New Year. By that time, the buds had experienced enough chilling to become increasingly sensitive to warm forcing temperatures, in other words, they gradually entered the state of ecodormancy. Since we could not find any delaying effect of warming on from November onward, we conclude that the actual chilling temperatures is of less importance for dormancy release than the chilling time, that is, the duration of the cold period (Baumgarten et al., 2021). If this is true for other species and regions than investigate in Roberts et al. (2015), Baumgarten et al. (2021) and our study remain subject to further investigations.

Chilling units are usually calculated from a fixed day onward, very often from September 1. In this way, chilling might actually capture the process of dormancy establishment as well, as a high amount of accumulated chilling at a given time in spring is likely to be related to an early onset of cold temperatures in autumn in the year before. By investigating the whole cold period separated

in monthly intervals, we found an advancing effect of cold temperatures only at its beginning. This suggest that the timing of the start of the cold season mainly determines the chilling effect on spring phenology.

5 | CONCLUSION

Our staggered monthly warming experiments indicate that the observed decline in phenological sensitivity of trees to spring warming can be explained by a delay of dormancy induction due to warmer autumn temperatures. Elevated temperatures during winter (i.e., January–March) per se do not delay spring phenology, but rather have an advancing effect. However, climate warming is accompanied by a reduction in the number of days cold enough for chilling. A shorter period of winter rest due to later dormancy induction in response to warm autumns decreases the effectiveness of forcing temperatures in spring and herby delays spring phenology. These insights will help to improve future process-based modeling of leaf phenology and growing season length. Our findings also call for greater attention to the phenological processes in the autumn, in particular to the mechanisms driving dormancy induction and their sensitivity to temperature.

AUTHORS CONTRIBUTION
AVM and IB conceived the study; IB together with CM and NL conducted the experiment and collected the data; IB performed the statistical analysis with contributions from JK; all authors discussed the results; IB wrote the manuscript with support from JK and AM.

DATA AVAILABILITY STATEMENT
The data will be made publicly available via dryad.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.