1   Shifts in the temperature-sensitive periods for spring phenology in European beech and

2   pedunculate oak clones across latitudes and over recent decades

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4   **Running title**: Chilling and forcing phases in oak and beech

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ABSTRACT

16   Spring phenology of temperate trees has advanced worldwide in response to global warming.

17   However, increasing temperatures may not necessarily lead to further phenological advance,

18   especially in the warmer latitudes because of insufficient chilling and/or shorter daylength.

19   Determining the start of the forcing phase, i.e. when buds are able to respond to warmer

20   temperatures in spring, is therefore crucial to predict how phenology will change in the future.

21   In this study, we used 4,056 leaf-out date observations during the period 1969-2017 for clones

22   of European beech (*Fagus sylvatica* L*.)* and pedunculate oak (*Quercus robur* L.) planted in 63

23   sites covering a large latitudinal gradient (from Portugal ~41°N to Norway ~63°N) at the

24   International Phenological Gardens in order to (i) evaluate how the sensitivity periods to forcing

25   and chilling have changed with climate warming, and (ii) test whether consistent patterns occur

26   along biogeographical gradients, i.e. from colder to warmer environments.

27   Partial Least Squares regressions suggest that the length of the forcing period has been extended

28   over the recent decades with climate warming in the colder latitudes but has been shortened in

29   the warmer latitudes for both species, with a more pronounced shift for beech. We attribute the

30   lengthening of the forcing period in the colder latitudes to earlier opportunities with

31   temperatures that can promote bud development. In contrast, at warmer or oceanic climates, the

32   beginning of the forcing period has been delayed, possibly due to insufficient chilling.

33   However, in spite of a later beginning of the forcing period, spring phenology has continued to

34   advance at these areas due to a faster satisfaction of heat requirements induced by climate

35   warming. Overall, our results support that ongoing climate warming will have different effects

36   on the spring phenology of forest trees across latitudes due to the interactions between chilling

37   and forcing requirements and photoperiod.

38

39   Keywords: chilling, dormancy, forcing, leaf-out, phenology, plasticity, temperate tree

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INTRODUCTION

As a result of climate warming, earlier spring bud break and onset of growth has been observed in temperate forests worldwide during the last 50 years (Menzel & Fabian, 1999, Fu *et al.*, 2014). However, it is uncertain whether further warming will continue to elicit earlier leaf-out. In fact, several studies suggest that the apparent phenological sensitivity of temperate trees to warmer spring temperature (i.e. the advance of leaf-out dates per degree of warming during the period of time that correlates best) has already declined since the 1980s in Europe, slowing down the advancement of spring onset in response to warming (Fu *et al.*, 2015, Chen *et al.*, 2019). The reasons of such decline in the apparent sensitivity to spring warming could be related to: (i) chilling requirement necessary to break dormancy which may nowadays be either partially satisfied or achieved later (Laube *et al.*, 2014, Fu *et al.*, 2015) and (ii) earlier spring phenology, which advances bud development to shorter daylength periods. Shorter daylength during budbreak may directly slow down bud development rate (Vitasse & Basler, 2013, Fu *et al.*, 2019c), or indirectly because daytime temperatures are more efficient than night-time temperatures for bud development in spring (Piao *et al.*, 2015, Fu *et al.*, 2016, Rossi & Isabel, 2017). Consistently, phenological responses to warmer climate were also observed to be less pronounced towards the warmer parts of species distribution, leading to more uniform timing for the vegetation onset between northern and southern latitudes in Europe (Ma *et al.*, 2018, Liu *et al.*, 2019) or between low- and high-elevation sites in the European Alps (Vitasse *et al.*, 2018).

Chilling requirement and photoperiod limitation are thought to represent tree safeguards preventing from a too early bud development that would expose leaves to potentially damaging spring frosts (Vitasse *et al.*, 2014). However, chilling and photoperiod requirements are still poorly understood for numerous species. This is likely because the two environmental cues interact with each other as well as with the response to forcing temperature (also named heat requirements), complicating their quantification even in climate chamber experiments (Caffarra & Donnelly, 2011, Flynn & Wolkovich, 2018). Besides, the range of efficient chilling temperatures to break winter dormancy is not well known but typically assumed to range between 0 and 10°C (Polgar & Primack, 2011), though this may strongly vary depending on species. Finally, it is also unclear how the period when buds become sensitive to warmer temperature, hereafter referred to as the forcing period, might change under warmer climates. Because spring phenology has occurred progressively earlier with climate warming in Europe, an unchanged or even delayed start of this period due to later accomplishment of chilling requirement would indicate a shortening of the forcing period with nevertheless a faster heat

74 accumulation (Fu *et al.*, 2019a). To what extent warmer climate may compensate for the
75 progressive lack of chilling is key to predict how phenology and the vitality of temperate trees
76 will change in the future.

77 Latitudinal and elevational gradients are very valuable to assess the response of bud phenology
78 to contrasting light and temperature conditions. However genetic adaptations occur along these
79 gradients (Vitasse *et al.*, 2013, Osada *et al.*, 2018), which may hamper accurate evaluation of
80 heat, chilling and photoperiod requirements for predicting future phenological changes of tree
81 populations. For this reason, warming experiments in controlled conditions were generally
82 preferred to quantify these physiological characteristics. However warming experiments were
83 found to underestimate tree phenological responses to warming compared to *in situ*
84 observations (Wolkovich *et al.*, 2012), possibly due to experimental direct and indirect artefacts
85 (Ettinger *et al.*, 2019). In addition, these experiments cannot be conducted on mature adult trees
86 and use either cuttings which can only be used for one winter-spring season or juvenile trees
87 that are known to exhibit different phenology than adult trees (Vitasse, 2013, Osada & Hiura,
88 2019). Here, we used phenological observations from the International Phenological Gardens
89 (IPGs, Chmielewski *et al.*, 2013) which gathers locations where genetically identical trees
90 (clones) have been planted since 1957 over a large latitudinal gradient (from Portugal ~41°N to
91 Norway ~63°N). By limiting the bias caused by possible genetic variation, these data allow us
92 to robustly quantify the periods when buds respond to either chilling temperature (for dormancy
93 release) or forcing temperature (for bud development) under different climatic conditions.

94 Here we studied spring phenology of two dominant and economically important tree species in
95 central Europe, European beech (*Fagus sylvatica* L.) and pedunculate oak (*Quercus robur* L.).
96 These two species are known to respond differently to temperature increase. Typically, the leaf-out
97 timing of European beech is less variable from year to year or along elevational and latitudinal
98 gradients than sessile or pedunculate oak (Vitasse *et al.*, 2009a). Beech phenology is expected to
99 advance to a much lower extent in response to warming than other species because shorter
100 photoperiod has been shown to reduce its sensitivity to warming (Basler & Körner, 2012, Basler &
101 Körner, 2014, Fu *et al.*, 2019b). Besides, its chilling requirement for a full dormancy release (i.e.
102 leading to a minimal amount of forcing required to bud burst) seems to be very high compared to
103 other co-existing species (Murray *et al.*, 1989, Laube *et al.*, 2014, Vitra *et al.*, 2017). In a long-term
104 perspective, the species-specific sensitivity to climate warming may lead to major changes in the
105 competitive balance between co-existing species and therefore may lead to changes in species
106 distribution and composition (Vitasse *et al.*, 2011).

Partial least squares (PLS) regression has been previously used to correlate variation in daily temperature to budburst or flowering dates (Luedeling & Gassner, 2012, Luedeling *et al.*, 2013b, Guo *et al.*, 2015) and to identify specific response periods to chilling or warm temperatures, especially for fruit trees (Luedeling *et al.*, 2013a, Guo *et al.*, 2014, Martínez-Lüscher *et al.*, 2016). Here we extended this approach to study how winter dormancy affects tree clones of two major European forest trees planted across latitudes from 41°N to 63°N. Specifically, we addressed the following questions:

(1) Can we evaluate differences in the response to chilling or warm temperatures during dormancy in beech and oak trees?

(2) Is the period when buds are sensitive to warm temperatures shortening under warmer climates (i.e. towards warmer latitudes) and ongoing climate warming (i.e. over recent decades)?
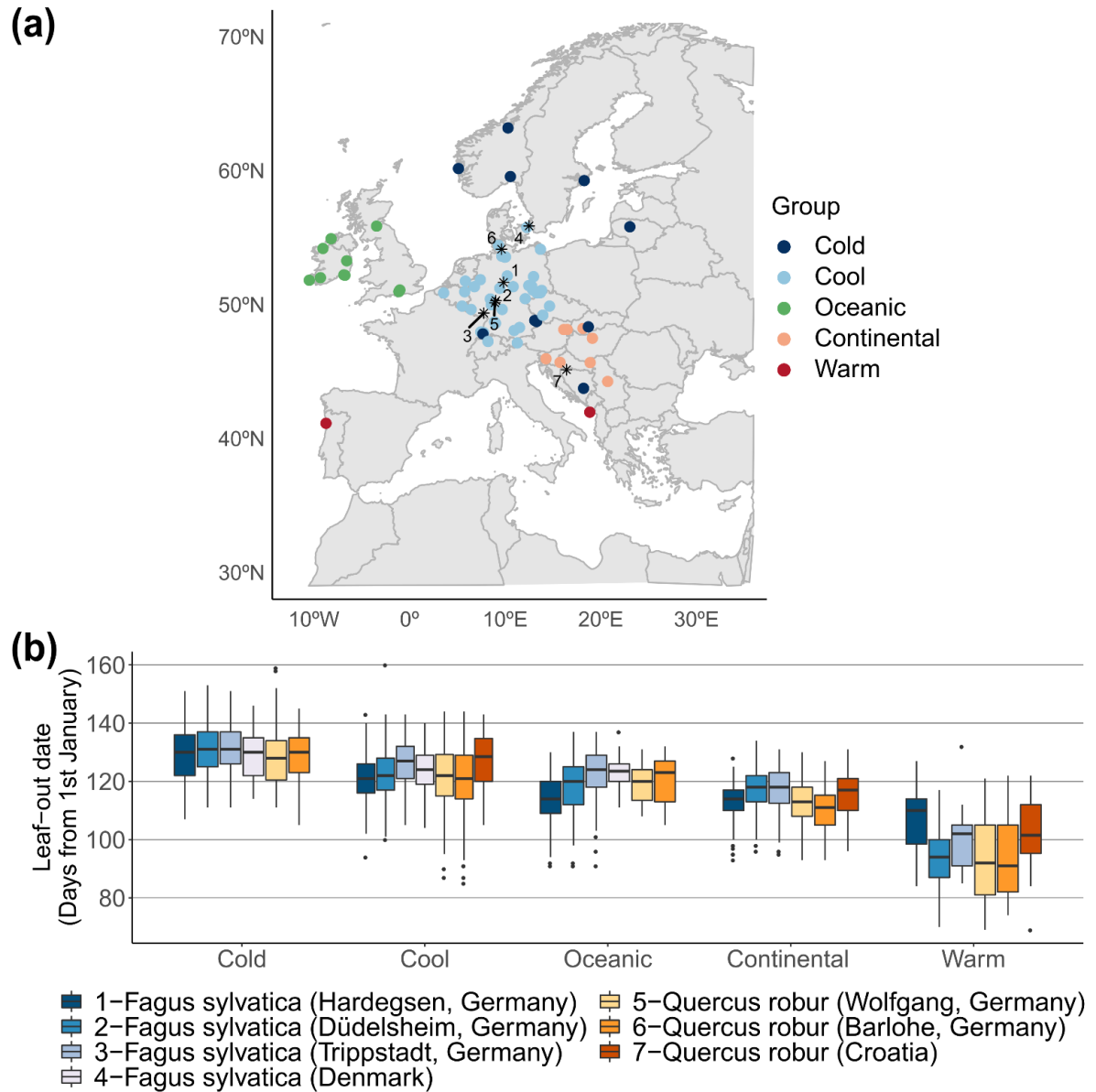
Figure 1. Climatic and phenological characterization of the study sites from the International Phenology Gardens. IPG study sites were classified into five groups using a hierarchical cluster analysis (with Ward linkage) on the euclidean distance matrix calculated on the profiles of average daily temperatures (period 1969-2017). Climatic characteristics for each group are based on the average daily temperature profiles and the degree of continentality. (a) Location of the study sites (circles) and origin of the studied clones (numbers): clones 1, 2, 3 and 4 are European beech clones sampled in Germany and Denmark while clones 5, 6 and 7 are pedunculate oak clones sampled in Germany and Croatia (see further details about the origin of the clones in Table S1); (b) leaf-out dates for the *Fagus sylvatica* and *Quercus robur* clones.

119

120 **MATERIAL AND METHODS**

121 *Climatic and phenological characterization of the observation sites*

Leaf-out data

123   We analysed a total of 4,300 observations of leaf-out dates (BBCH 11; Meier *et al.*, 2009) for

124   European beech (*Fagus sylvatica* L.) and pedunculate oak (*Quercus robur* L.) clones. Leaf-out

125   dates were recorded during the period 1969 to 2017 at the International Phenological Gardens

126   (IPGs) stations, covering a wide range of latitudes (41°N-63°N) and longitudes (10°W-24°E)

127   across Europe (Fig. 1a, Fig S1, Chmielewski *et al.*, 2013).

128   Data were recorded from identical clones: clones 1, 2, 3 and 4 are European beech clones that

129   originate from Germany and Denmark while clones 5, 6 and 7 are pedunculate oak clones that

130   originated from Germany and Croatia (Fig. 1a, Table S1). Quality controls of phenological data

131   were conducted for detecting possible outliers due to change in the observers or mistakes, and

132   we discarded 194 observations (4.5% of the records) which deviated more than 2.5 times the

133   median absolute deviation from the median (moderately conservative threshold) within a station

134   across the study period (Leys *et al.*, 2013). For robustness, we restricted our analysis to sites

135   where at least five years of observations were available, resulting in 4,056 observations from

136   63 sites (Fig. S1).

137   *Temperature records*

138   Daily minimum, maximum and mean air temperature data were obtained for each site's latitude

139   and longitude using the European observation (E-OBS) gridded temperature dataset with 0.25°

140   resolution (v.17; Haylock *et al.*, 2008). Every E-OBS points reflect average temperature and

141   elevation of the corresponding cell (Kyselý & Plavcová, 2010). However, variation in elevation

142   between the grid points (providing average elevation covered by the pixel) and the study sites

143   may introduce substantial errors in mountainous regions. To correct the average temperature of

144   the pixel by the actual elevation of our study sites, we selected the closest gridded dataset point

145   from our study site and we calculated the theoretically expected temperature by applying a

146   conventional temperature lapse rate of 0.65°C $(100m)^{-1}$. This lapse rate is commonly used in

147   climatology studies and roughly corresponds to the mean mid-latitude tropospheric lapse rate

148   (Scherrer & Appenzeller, 2014).

149   *Hierarchical cluster analysis*

150   In order to better understand the tree phenological response to different climates, sites were

151   classified into five groups using a hierarchical cluster analysis (with Ward linkage) on the

152   euclidean distance matrix calculated on the profiles of average daily temperatures (period 1969-

153 2017; Fig. S2a). For each site, climate continentality coefficients *KC* were also calculated using
154 Conrad's equation (Conrad, 1946):

155 $$KC = \frac{1.7A}{\sin(\varphi + 10°)} - 14$$

156 where A is the annual range of temperature, i.e. the difference between the highest and lowest
157 mean monthly temperatures, and φ the geographical latitude. High coefficients indicate
158 continental climates whereas low coefficients are associated with oceanic climates. Average
159 profiles for each group reveal differences in seasonal temperature dynamics over the years (Fig.
160 S2b-d), reflecting different degrees of continentality (Fig. S2d). The "Cold" group corresponds
161 to Scandinavian sites in Norway and Sweden and a few sites in Germany, Lithuania, Slovakia
162 and Bosnia and Herzegovina, some of them located at high altitude (see Fig. S1). These sites
163 are characterized by cold continental climatic conditions. Most of the German sites are grouped
164 in the "Cool" climatic group with rather continental features (Fig. S2d). Conrad's continentality
165 coefficient led to the distinction of the "Oceanic" sites (KC = 6), characterized by warmer fall
166 and winter but mild spring and summer temperatures and the mild "continental" sites (KC =
167 29) characterized by warm temperatures in summer and cold temperatures in winter, with the
168 largest amplitude between the two seasons. Finally, two "Warm" sites in Romania and Portugal
169 were characterized by the warmest temperatures throughout the year (Fig. 1a, Fig. S2).
170 However, following analyses are run on datasets with long-term series and sufficient data to
171 fully capture the variability of response, which excludes the "Warm" sites where no data were
172 available after 1997 (Fig. S3).

173 ***Statistical analyses***

174 *Comparison of data for two periods*

175 To investigate how leaf-out and temperature data changed during the period 1969–2017, we
176 separated the data between two periods of equal length: 1969-1993 (fall 1969 to spring 1993)
177 and 1993-2017 (fall 1993 to spring 2017). Two-tailed Wilcoxon tests were used to compare
178 leaf-out dates and the forcing and chilling phases characteristics between the two periods.

179 *Multisite PLS regression analysis*

180 To explore the influence of daily temperatures on spring phenology, temperature and leaf-out
181 data were analysed using partial least squares (PLS) regressions similarly to previous studies
182 (Luedeling & Gassner, 2012, Luedeling *et al.*, 2013b), using the chillR package (R package

183   v.0.70.6, Luedeling, 2013). Because of the high day-to-day variability in temperatures, daily
184   mean temperatures do not allow meaningful interpretation of PLS results (Luedeling &
185   Gassner, 2012). Therefore, we constructed a running mean of daily temperatures, which
186   smoothes the temperature curve and facilitates the interpretation of the PLS regression results.
187   We tested a range of window length for the running mean and we found that results obtained
188   for windows between 5 and 15 days were similar (Fig. S4c). As proposed by Luedeling and
189   Gassner (2012), we used an 11-day running mean of daily temperatures.

190   Dependent variables, *i.e.* leaf-out dates, were regressed using a PLS regression against
191   independent variables, *i.e.* smoothed daily temperatures, as described above, spanning from
192   September 1st to the average leaf-out date, in each study site group. PLS regression coefficients
193   give information on the strength and the cold/warm effect of temperatures on phenology, i.e.
194   high absolute values for the coefficients indicate that departures from expected seasonal
195   temperatures have a high effect on leaf-out dates. Negative and positive coefficients indicate
196   whether there is negative or positive correlation between temperatures and leaf-out timing. In
197   addition, variable importance in the projection (VIP) values characterize for each day whether
198   temperatures during that day are important for explaining variations in the leaf-out dates. More
199   precisely, unless otherwise specified, only the periods characterized by a VIP value greater than
200   0.8, are considered to have a significant effect (Luedeling & Gassner, 2012), and higher VIP
201   values are associated with more significant effects of temperatures.

202   *Definition of chilling and forcing phases*

203   In order to explore the chilling and forcing phases controlling spring phenology in different
204   climates, we identified the beginning and end of each phase using the positive and negative
205   coefficients of the PLS regressions, with sufficient importance characterized by the values of
206   the VIP. Automatic detection was applied to the PLS coefficients results in order to identify
207   periods of at least five consecutive days with VIP ≥ 0.8 and continuously negative or positive
208   coefficients. We tested different VIP thresholds (between 0.8 and 1.2) as well as different
209   thresholds of minimum consecutive days (between 1 and 10) for the detection of the forcing
210   phases and we found that these thresholds had only little effect on the overall results for the
211   forcing phase (Fig. S4). This approach allowed to highlight emerging patterns in the PLS
212   outputs and exclude short periods that may not be biologically important. In other words, we
213   defined statistically significant chilling and forcing clustered periods from the 365 coefficients
214   (see Fig. 2a for illustration). In our context, PLS regression results highlight periods when small

deviations from average conditions may affect the outcome. Consequently, PLS regression allows to detect the beginning and end of phases rather than the continuing period. Therefore, we defined the chilling and forcing phases as the phase delimited between the first and last significant chilling and forcing periods automatically detected, respectively (see Fig. 2b for illustration). In addition, based on the hypothesis that forcing periods cannot begin before a period of chilling, we constrained the automatic detection so that no forcing period could be detected before December 1st. For all groups and species, VIP values were high for the selected periods (Fig. S5), suggesting that the periods selected as the chilling and forcing phases are statistically robust irrespective of the climatic groups.

Calculation of the heat accumulation

Hourly mean temperatures were estimated using a sine curve for daytime temperature and a logarithmic decay function for night-time cooling, based on daily minimal and maximal temperatures and photoperiod (stack_hourly_temp from the chillR package v.0.70.17, Luedeling, 2013). Heat accumulation was calculated using Growing Degree hours (GDH), as implemented in the chillR package, that uses an asymmetric cosine curve with a base temperature of 4°C, an optimum temperature of 25°C and a critical temperature of 36°C (Anderson *et al.*, 1985, Luedeling *et al.*, 2009). For validation purposes, we also calculated heat accumulation using two additional models. The linear GDH was used with a base temperature of 5°C:

$$\left(\sum GDH\right)_n = \sum_{i=1}^{n} max(0, T_i - T_b)$$

where *n* is the hour when the sum of GDH is calculated, T_i is the hourly mean air temperature for a given hour *i* comprised between Day 1 hour 1 and *n*. T_b is the base temperature above which temperatures are considered for the heat accumulation. The Growing Degree Days (GDD) model was applied with the same base temperature of 5°C:

$$\left(\sum GDD\right)_n = \sum_{i=1}^{n} max(0, T_i - T_b)$$

where *n* is the day of the year when the sum of GDD is calculated, T_i is the daily mean air temperature for a given day *i* comprised between Day 1 and *n*. T_b is the base temperature above which temperatures are considered for the heat accumulation.

All data analyses were performed using the R programming language (R Core Team, 2017).

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RESULTS

The progress of winter dormancy varies across bioclimatic regions

The clustering analysis highlighted five main climatic groups (Fig. 1, Fig. S2) and revealed different leaf-out dates among these different climatic groups for both European beech (*Fagus sylvatica* L.) and pedunculate oak (*Quercus robur* L.) clones (Fig. 1b). The leaf-out dates occurred the earliest for the sites from the 'warm' group followed by the mild 'continental', 'oceanic', 'cool', and 'cold' groups, matching well with the average temperature of each group from mid-winter to late spring (Fig. 1b, Fig. S2b-d).

The PLS regressions showed that the timing and the length of the chilling and forcing phases vary among the four climatic groups and between the two species (Fig. 2). The chilling periods occurred earlier in the cold and cool climatic groups, while they begin later in the oceanic and mild continental climatic groups for oak. An overlap between the chilling and forcing phases was noticeable for the two species and all groups, but was more pronounced for beech. Interestingly, chilling periods started later and ended earlier in winter for oak and were consequently shorter compared to the ones of beech, especially towards warmer climates ('oceanic' and mild 'continental'). Overall, the forcing phases appear to start later and be shorter towards the warmer winter climates for both species, except for the cold sites characterized by late and short forcing periods.

Although results for the oak and beech clones confirmed the overall patterns found for the whole species data (Fig. 3 and Fig. S6), slight differences could be observed among clones. For example, the beginning of the forcing phase was detected later for the beech clone 3 compared to the other clones in all climatic groups except the oceanic group (Fig. 3 and Fig. S6). Similarly, the beginning of the forcing phase was earlier for the oak clone 6 compared to the other clones except for the mild continental group (Fig. 3 and Fig. S6).

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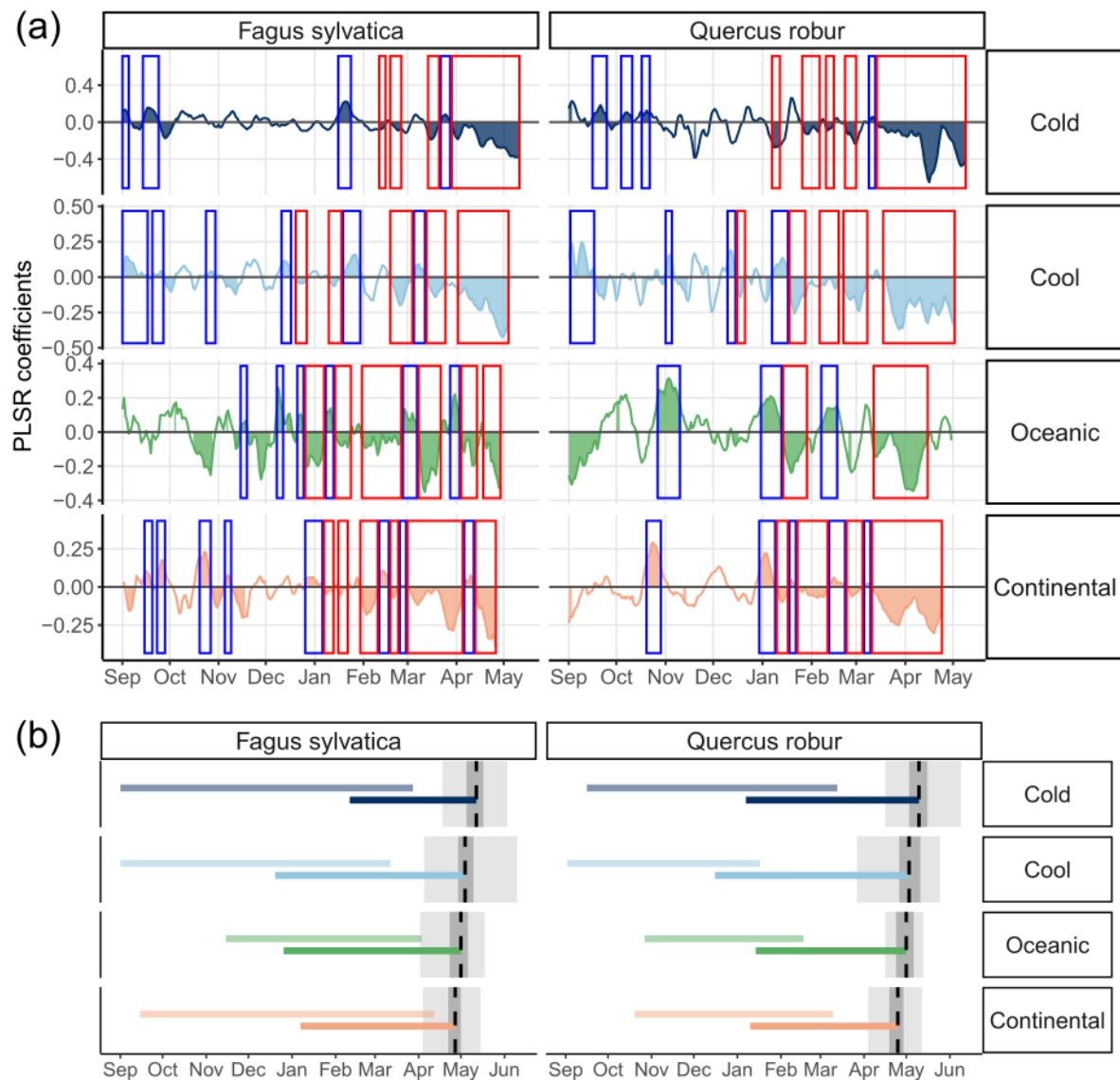
Figure 2. Chilling and forcing phases identified with PLS regressions for European beech (*Fagus sylvatica* L.) and pedunculate oak (*Quercus robur* L.).
(a) Coefficients for the PLS regressions run on data from the five groups. Shaded zones correspond to the period with a VIP > 0.8. Positive coefficients (blue rectangles) indicate that warm temperatures during the given period delay leaf-out, or that cold temperatures hasten leaf-out (chilling), whereas negative coefficients (red rectangles) reveal that warmer temperatures lead to earlier leaf-out dates (forcing). (b) Chilling (upper light line) and forcing (lower dark line) phases identified from the PLS regression analysis. Grey areas correspond to leaf unfolding dates (dash line: median, dark grey: 25 - 75 % quantiles, light grey: range of leaf unfolding dates).

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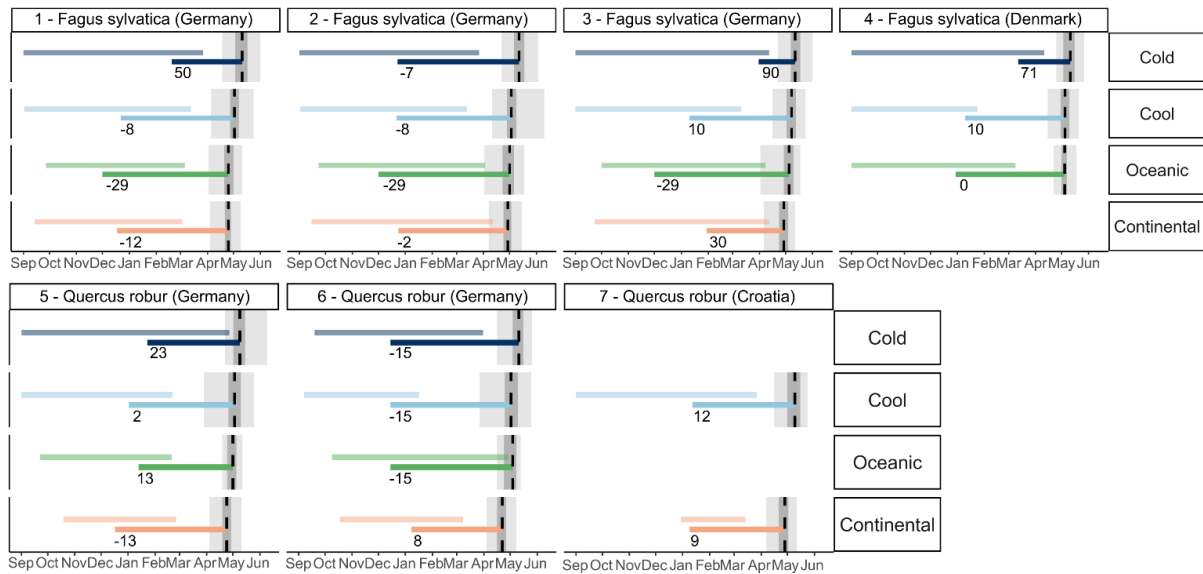
**Figure 3. Chilling and forcing phases for the seven clones.**
Chilling phases (upper light lines) and forcing phases (lower dark lines) identified from the PLS regressions for the four *Fagus sylvatica* and the three *Quercus robur* clones. Information between brackets indicate the origin (Country) of the different clones planted in the sites, see Table S1 for more details. Grey areas correspond to leaf unfolding dates (dash line: median, dark grey: 25 -75 % quantiles, light grey: range of leaf unfolding dates). Numbers correspond to the beginning of the forcing phase, expressed in days to 1st January.

Forcing periods shorten under warming conditions

Since the start and the length of the forcing periods were shown to be different among the different climatic regions, we investigated whether these periods have also shifted due to the rising spring temperatures observed in all climatic group sites during the period 1969–2017 (Fig. 4). Although the increase in temperature between January and June was similar among the groups between the period 1969-1993 and 1993-2017 (from 1.0°C to 1.2°C, Fig. S7a), spring phenology has advanced more in the colder sites (7-8 days advance for beech and 4-8 days advance for oak, Fig. S7b) than in the warmer groups (4 and 1-3 days advance for beech and oak respectively in the oceanic and mild continental groups, Fig. S7b).

Our results revealed different patterns between the two study species in the forcing phase dynamics between the recent period 1993–2017 compared to 1969–1993 (Fig. 4, Fig. S8 and Fig. S9). For beech, the forcing periods start earlier and get longer during the 1993-2017 period compared to 1969-1993 in the cold and cool groups, whereas the beginning of the forcing phase remains rather constant for oak and get therefore shortened for this species due to the advance of the leaf-out date. On the other hand, the forcing periods start later and are shorter during the recent 1993-2017 period in the oceanic and mild continental sites which are characterized by a warmer late winter/early spring, especially for beech. Overall, these trends were confirmed

when using different VIP thresholds, window lengths for the temperature running mean or different threshold for the number of consecutive high-VIP days to detect forcing and chilling phases, demonstrating the statistical robustness of the pattern described (Fig. S4).
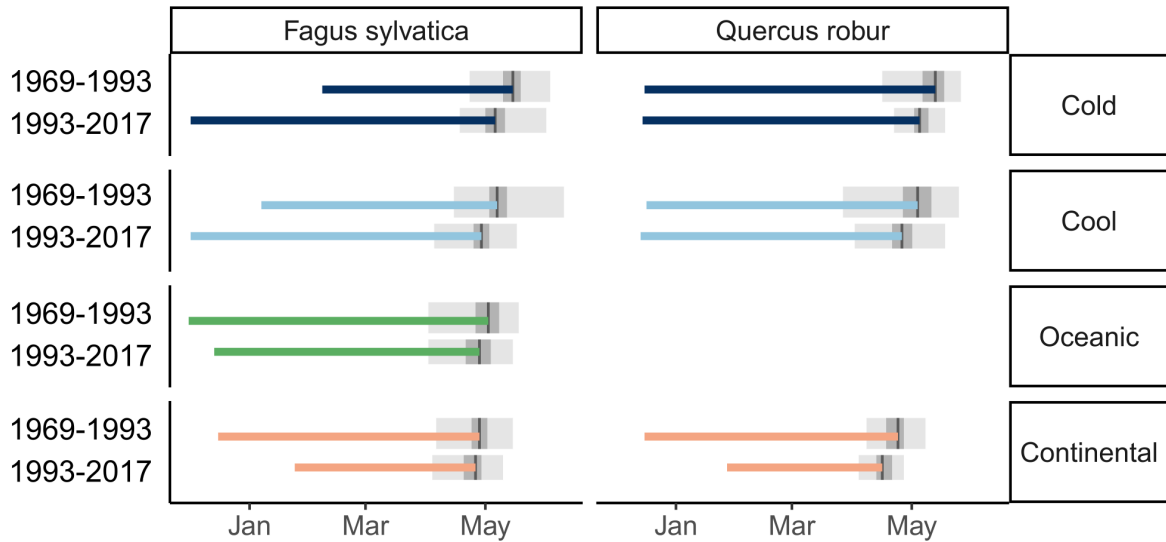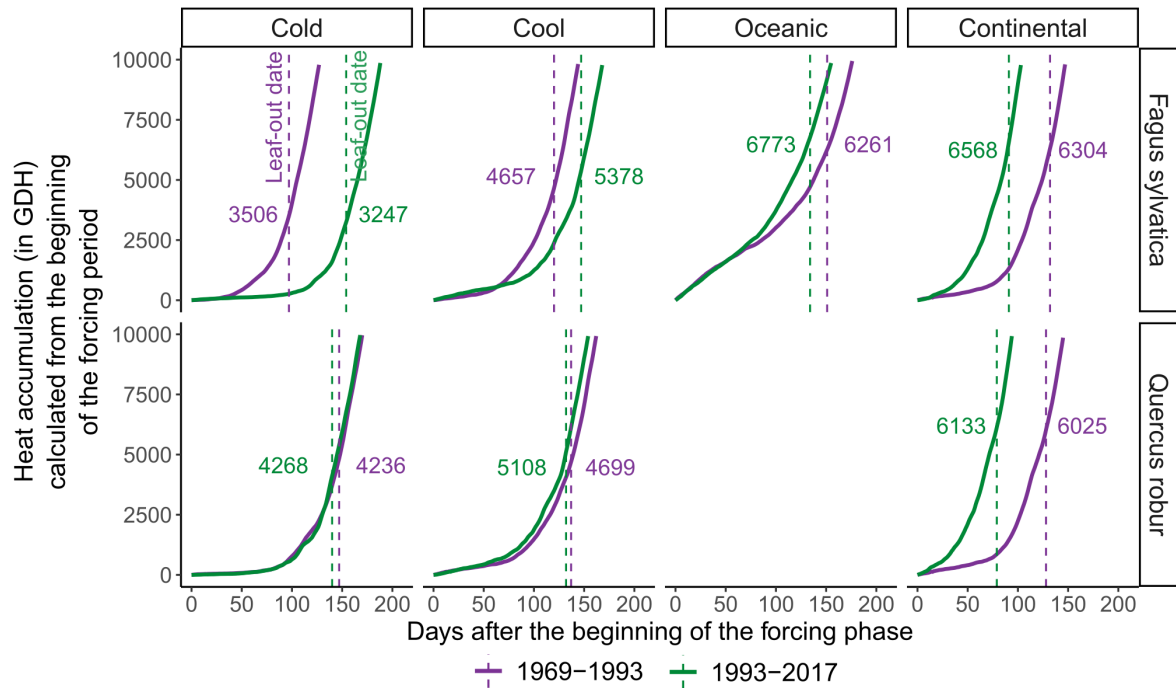

Figure 4. Start, end and length of the forcing phases between 1969-1993 and 1993-2017 periods for beech (*Fagus sylvatica*) and oak (*Quercus robur*)
The forcing periods were estimated using PLS regression for leaf-out dates recorded for the 1969-1993 (upper line) and 1993-2017 (lower line) periods. Grey areas correspond to leaf-out dates (dash line: median, dark grey: 25 -75 % quantiles, light grey: range of leaf-out dates)

Forcing requirements to leaf-out across bioclimatic regions and under warmer climate

To further explore the underlying temperature effects that might influence the changes in the forcing periods observed across bioclimatic groups and after 1993, we investigated how heat accumulation changed between the groups and over time (Fig. 5). Overall, higher heat accumulation was reached at the time of flushing for both species under warmer climatic groups exceeding 6,200 GDH and 6,000 GDH for beech and oak respectively in the oceanic and mild continental groups (Fig. 5). In contrast, for both species less than 4,300 GDH was accumulated at the time of flushing in the cold climatic group. Interestingly, a slight increase of forcing requirement was observed between the periods 1969-1993 and 1993-2017 for beech (~ +400 GDH, i.e. +8%) in the two warmer bioclimatic groups whereas it remained quite stable for oak (+1.6%). A larger increase of accumulated heat was observed for the two species in the sites from the cool group between the two study periods (+15% for beech and +9% for oak). In contrast, a slight decrease of accumulated heat was found between the two study periods for

beech in the sites from the cold group (-7%) and no substantial changes for oak (+0.8%). Similar results were found when testing linear GDH or GDD models as commonly used (Fig. S10).

Figure 5. Length of the forcing phases depends on chill and heat accumulation in beech (*Fagus sylvatica*) and oak (*Quercus robur*).
Average heat accumulated (calculated as the sum of growing degree hours - GDH), starting from the beginning of the forcing phases estimated by PLS regression for *Fagus sylvatica* (upper panel) and *Quercus robur* (lower panel) during the 1969-1993 and the 1993-2017 periods. Lines represent the average GDH sum for all sites and years; dashed lines are the estimated end of the forcing phase, calculated as the average leaf-out date. Numbers correspond to the accumulated heat at the average leaf-out dates.

DISCUSSION

We used PLS regressions to identify the beginning and length of the forcing phases of beech and oak clones across bioclimatic regions and across time. Our results show for the first time on identical genetic materials that the forcing phases are overall shorter towards warmer climate and have shortened under the recent period in the warmer climatic groups. In contrast, longer forcing periods were detected at the coldest sites over the last decades. In addition, we show that beech clones have a stronger dependence to chilling than oak, resulting in more important changes in heat requirement under warmer climatic conditions. This study further demonstrates that ongoing climate warming may have different impact on the phenology of different co-existing trees depending on the climatic regions, leading to changes in the structure and functioning of forest ecosystems.

319

Differences between oak and beech dormancy

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321   Our study suggests that shorter forcing periods under warmer climates are partly due to a later

322   satisfaction of chill requirements. In contrast in the coldest sites, climate warming may have

323   led to longer periods with temperatures being in the range of chilling efficiency, advancing the

324   satisfaction of chill requirements and subsequently the beginning of the forcing periods

325   (Chmielewski *et al.*, 2012). Higher chilling may have also reduced the amount of heat required

326   for flushing as demonstrated in controlled experiments (Murray *et al.*, 1989), and as found here

327   for beech. However, when we compared earlier and later periods in cold and cool climates, such

328   patterns were not observed for oak, displaying conserved timing for the beginning of the forcing

329   period. This result suggests that oak is not constrained by high chilling requirement, which is

330   consistent with experiments (Dantec *et al.*, 2014). Hence, oak shows a high phenological

331   sensitivity to spring temperature (-6.5 d $°C^{-1}$ compared to -1.9 d $°C^{-1}$ across an elevational

332   gradient in the French Pyrenees where chilling and/or photoperiod might be more limiting for

333   beech, (Vitasse *et al.*, 2009b). This high plasticity to spring temperature for oak trees is

334   consistent with the literature (Kramer, 1995, Chen *et al.*, 2019) and with our findings that

335   suggest only low chilling requirements for this species in comparison to beech. In addition,

336   beech is known to be strongly sensitive to photoperiod (e.g. Basler & Körner, 2012, Zohner &

337   Renner, 2015, Fu *et al.*, 2019b). Thus, spring phenology of European beech becomes

338   increasingly regulated by both chilling and photoperiod towards the southern part of its

339   distribution.

340   One of the remaining questions is how chilling precisely drives the beginning of the forcing

341   periods in oak and beech. Our results suggest that chilling has decreased in all groups except in

342   the coldest group where it may have increased because a warmer climate would give longer

343   period of temperatures that are efficient as chilling, i.e. that allows to reduce dormancy depth.

344   However, the range of temperature that is efficient to reduce dormancy depth is still largely

345   unknown for temperate trees. Previous studies have attempted to evaluate chilling in temperate

346   forest trees, but the results show that an accurate estimation of the range of chilling efficiency

347   is particularly difficult (e.g. Murray *et al.*, 1989, Laube *et al.*, 2014, Gauzere *et al.*, 2017, Flynn

348   & Wolkovich, 2018). For example it is still unclear whether freezing temperatures contribute

349   to reduce dormancy depth of temperate trees and can either be include or not in the range of

350   chilling efficiency depending on the phenological models (Hänninen, 2016). Further

351 experimental evaluation of dormancy release, e.g. in controlled climatic conditions, are now
352 essential to accurately assess this temperature range and improve our predictions for future tree
353 phenology.

354 Interestingly, our results slightly diverge from the recent analysis led by Fu et al. (2019a). Using
355 the time period with the best statistical correlation between mean temperature and leaf-out
356 dates, they found that forcing periods did shorten with climate warming, as found here, but the
357 beginning of the forcing period remained unchanged, consistently with our results for oak in
358 the cold and cool sites but not for beech. However, the long-term datasets used in Fu et al.
359 (2019a) were recorded from sites in central Europe, belonging to both Cool and mild
360 Continental sites from this study. Here we found opposite patterns for these two groups, i.e. an
361 advance in the beginning of the forcing period for the cool sites and a delay of the forcing
362 periods in the mild continental sites, which could explain the unchanged timing observed when
363 all sites are combined. In contrast, analyses conducted in climatically contrasting sites showed,
364 similarly to our results, that chilling was the main driver of the variation on the blooming dates
365 of Apricot trees in the warmer sites whereas forcing played the major role in the cooler sites
366 (Guo *et al.*, 2015). This stresses the importance of distinguishing different climatic groups when
367 running phenology analyses over large spatial scales.

368

369 *Future changes of spring phenology of beech and oak and ecological consequences*

370 Currently, the leaf-out dates of beech and oak are still advancing in response to warmer
371 temperature even for beech in spite of the delaying start of its forcing phase in the oceanic and
372 mild continental regions, which is likely associated with increasing chilling and photoperiod
373 limitation. Thus, to date, warmer spring temperatures have compensated for a shorter period of
374 forcing through faster heat accumulation, resulting in advanced leaf-out dates as found in Fu et
375 al. (2019a). The faster heat accumulation results from the non-linear effect of spring
376 temperature on budbreak with much higher efficiency of warmer temperatures for bud
377 development (Harrington & Gould, 2015, Bigler & Vitasse, 2019). However, our results
378 suggest that this advance could level off with further warming, i.e. when the beginning of the
379 forcing period would occur too late to be compensated by the increasing temperatures during
380 the forcing season as already observed during extremely warm springs in the French Alps (Asse
381 *et al.*, 2018). Beyond these warmer temperatures, leaf-out dates could therefore occur later for
382 species with high chilling or photoperiod requirement such as beech (Asse *et al.*, 2018) or

383   Apricot (Guo *et al.*, 2015) and defaults in the bud breaks may appear (necrosis, buds not

384   bursting, abnormal growth after budburst) due to insufficient chilling, as evidenced for fruit

385   trees (Erez, 2000, Campoy *et al.*, 2019) and temperate forest trees (Harrington & Gould, 2015).

386   Both effects would negatively affect the vitality of these species, thereby reducing their

387   competitiveness with the other co-existing species.

388   Our results suggest that the phenology of oak is better adapted to track climate warming than

389   beech, especially in the warmer regions. On the one hand, oak has lower chilling requirement

390   which allows this species to greatly advance the beginning of its growing season when early

391   spring temperature permits. Oak could therefore have earlier access to resources (water and

392   nutrients) compared to species exhibiting lower phenological plasticity to temperature. This

393   phenological advantage could be a significant asset for facing spring/summer droughts that are

394   expected to increase in frequency and magnitude. On the other hand, our results support that

395   further warming could be detrimental for beech, especially in the southern part of its distribution

396   range because its chilling requirement may not be fully satisfied. In this area, this species may

397   increasingly be maladapted by flushing too late compared to other species or by showing erratic

398   budburst which would decrease its ability to compete for resources and its tolerance to summer

399   drought. However in the northern part of its distribution range, its phenological plasticity should

400   be sufficient to track ongoing climate warming, as recently shown in the United Kingdom

401   (Tansey *et al.*, 2017).

402

Limitation of the study

404   The PLS regressions used in this study allowed to statistically identify the periods when chilling

405   and forcing play critical roles in regulating the leaf-out dates of the two study species. Although

406   PLS regression is widely used in chemistry and physics, it has only been recently applied in

407   phenology and the suitability of this technique was successfully assessed for relating

408   temperature variables to tree phenology (Luedeling & Gassner, 2012). In this regard, using PLS

409   regressions to define chilling and forcing periods is very different from the traditional

410   approaches that estimate chilling and heat requirements through functions of sensitivity to cold

411   and warm temperatures (e.g. Legave *et al.*, 2013, Dantec *et al.*, 2014, Pope *et al.*, 2014), or

412   using statistical correlation between mean temperatures and the study phenophase during a

413   given time window (Ruml *et al.*, 2011, Fu *et al.*, 2019a). In addition, this time window may

414   change from year to year complicating the estimation of the phenological temperature

sensitivity (Keenan *et al.*, 2019). As previously reported, PLS analyses have the advantage to highlight quantitative efficiency of temperatures during the different dormancy phases and may overcome some issues encountered with the more traditional approaches (Luedeling & Gassner, 2012). Indeed, the main strength of the analysis is that it highlights the predictor variables, here the daily mean temperatures, that are characterized by high VIP scores and high absolute values for the model coefficients. In other words, it allows to identify the periods when changes in temperature have the strongest effect on the timing of leaf-out. Therefore, the method is powerful to identify the beginning and end of phases when uncommon temperature patterns will significantly affect the phenology, including rare events such as early chill or forcing temperatures.

However, because temperature and phenology variability is required for PLS analysis, long-term datasets are necessary. Here, benefiting from clones sharing the same genetic materials, we even went a step further by compiling data from numerous sites characterized by similar climatic characteristics, which allowed us to robustly explore the different responses associated with a wide range of conditions without being affected by possible genetic adaptations. However, the number of clones tested was insufficient and the clones mostly originate from Germany. Further investigations are necessary to confirm that the same patterns would be found for all populations of the species. Nevertheless, even though genetic variation among populations of beech and oak can be found across Europe (Kremer *et al.*, 2010, Mátyás *et al.*, 2010, Kramer *et al.*, 2017), the phenological plasticity to temperature is higher and often conserved at species scale (Vitasse *et al.*, 2010, Vitasse *et al.*, 2013, Kramer *et al.*, 2017, Tansey *et al.*, 2017).

Environmental conditions, including interaction between photoperiod and temperature, controlling the beginning of the chilling phase are not well understood (Maurya *et al.*, 2018) but this complexity might explain why temperature patterns at the beginning of dormancy could not solely explain variations in the spring phenology. We are therefore more confident in the PLS determination of the forcing period than the chilling period, as the forcing period is mainly driven by warm temperatures. Indeed, we could identify patterns of interest for the length and beginning of the forcing periods across climatic groups and time which were conserved between clones, therefore suggesting robust trends. Furthermore, the changes estimated in the last decades for the forcing requirements may be a response to increasing temperatures or may also arise from model inaccuracies for the heat response. The temperature response included in the GDH model is mainly extrapolated from growth regulation during the non-dormant season and

448 is largely related to photosynthesis. This is a limitation widely shared in recent phenological
449 approaches, strictly based on observational records from natural conditions. Further
450 comprehensive understanding of physiological and molecular processes involved in the
451 response to temperature during dormancy progression is cruelly lacking for the development of
452 more accurate processed-based phenological modelling (Hanninen *et al.*, 2019).

453

CONCLUSION

454

455 Our results reveal that beech and oak exhibit different phenological strategies to leaf-out and
456 show different phenological changes under warmer climate either induced geographically
457 towards southern latitudes or temporally due to climate warming. Oak shows higher
458 phenological plasticity than beech, likely due to lower chilling requirement and lower -or no-
459 photoperiodic sensitivity for bud development. Thus, the higher phenological plasticity of oak
460 could provide an adaptive advantage over beech under global warming as it allows the species
461 to track the shift of the optimal leaf-out time for resource competition. Although this study
462 focuses only on two species, we expect a large array of phenological plasticity depending on
463 each species-specific chilling and photoperiod requirement, eventually leading to changes in
464 the structure and functioning of forest ecosystems. Furthermore, our results support that further
465 global warming may lead to insufficient chilling for some temperate trees such as European
466 beech, especially towards their warmer distribution areas, potentially reducing further their
467 vitality.

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