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# Leaf-out in northern ecotypes of wide-ranging trees requires less spring warming, enhancing the risk of spring frost damage at cold range limits

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**Abstract**

**Aim:** Trees need to avoid frost damage to their young leaves by leafing out after the occurrence of the last frost, yet they also need to start photosynthesis early in the season to achieve sufficient growth. This trade-off leads to the hypothesis that 'safety margins' against spring frost should become shorter, the longer the winter duration, perhaps reaching an asymptotic limit where frost damage would occur in most years. Physiologically, shorter safety margins in high-latitude ecotypes might be achieved by lower degree-day requirements for leaf-out, compared to low-latitude ecotypes.

**Location:** Europe.

**Time period:** 1902–2009.

**Major taxa studied:** Temperate trees.

**Methods:** Using herbarium collections of *Acer platanoides*, *Carpinus betulus*, *Fagus sylvatica* and *Prunus spinosa* made over 108 years at 40° to 60° N latitude, we related historic leaf-out dates to winter and spring temperatures (chilling and degree-days), winter duration, and date of last frost occurrence in the relevant years and locations.

**Results:** In all species, frost safety margins decreased towards high-latitude regions with long winters, with each day increase in winter duration reducing frost safety margins by 0.48 days in *Fagus* and 0.32–0.21 days in *Prunus*, *Acer* and *Carpinus*. These latitudinal differences correlate with northern ecotypes' shorter degree-day requirements for leaf-out.

**Main conclusions:** The decline in spring frost safety margins in regions with long winters supports the new hypothesis that species may reach their geographic range limit where they 'bump up' against experiencing regular frost injury to their young leaves. Larger datasets are necessary to further corroborate our hypothesis and future efforts should thus be directed toward increasing the latitudinal range of existing phenological databases.

**KEYWORDS**

climate change, cold range limits, frost damage, herbarium collections, leaf-out times, long time series, phenology, spring warming

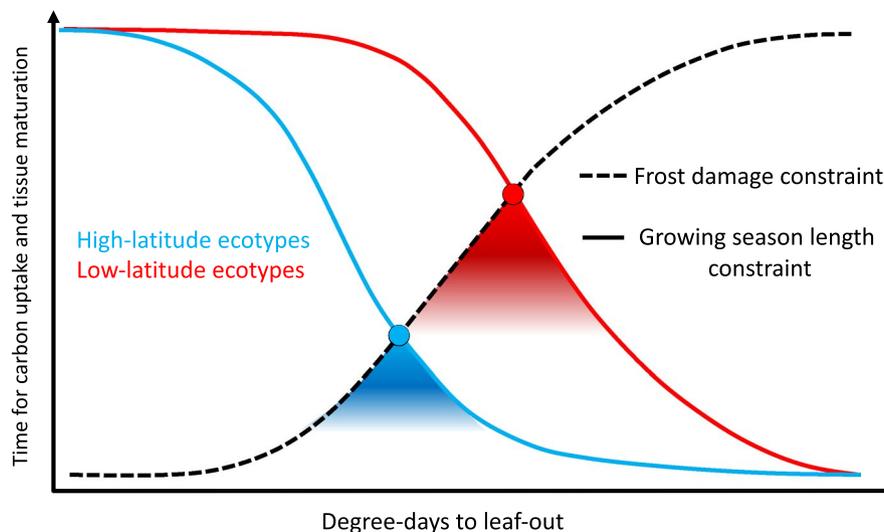
## 1 | INTRODUCTION

Widespread species experience different risks of being exposed to late spring frosts depending on latitude, elevation and climate (Falusi & Calamassi, 1996; Kreyling et al., 2014; Muffler et al., 2016; Osada et al., 2018; Vitasse, Schneider, Rixen, Christen, & Rebetez, 2018). Late spring frost—defined as frost occurring after the first leaf-out—is disproportionately important as a selective factor because trees are most vulnerable to frost during the initial stages of leaf emergence, with drastic effects on growth and reproduction (Kollas, Körner, & Randin, 2014; Lenz, Hoch, Vitasse, & Körner, 2013). Avoidance of late frost may thus control a species' persistence at a particular latitude (Körner et al., 2016). To underscore the crucial importance of young-leaf frost damage for population survival, Vitasse et al. (2018) referred to the period (number of days) between the average last spring frost and the local trees' leaf-out as a 'safety margin'. Based on leaf-out and frost occurrence data from Switzerland between 1975 and 2016, these workers showed that the frost safety margins in four deciduous tree species are larger in low-elevation than in high-elevation populations.

But do we expect safety margins against spring frost to become narrower (and hence riskier) or instead broader (longer and safer) at higher latitudes? And how would different safety margins be achieved? A conceptual scheme (Figure 1) helps to clarify the main constraints and trade-offs in high- and low-latitude ecotypes. It appears that because of trees' need to start growth early in the

season to achieve sufficient tissue maturation and their need to minimize the risk of frost damage by delaying the onset of leaf-out, high-latitude ecotypes should have narrower (riskier) frost safety margins than trees from low latitudes. The physiological way in which high-latitude ecotypes could achieve narrower frost safety margins could be by requiring less spring warming (lower degree-day requirements) to leaf-out than low-latitude ecotypes. Selection at high latitudes for lower degree-day requirements should be strong because of the short growing season and limited time for carbon uptake and tissue maturation (Hänninen, 2016; Körner et al., 2016; Linsser, 1868; Figure 1).

So far, evidence for the conceptually expected latitudinal clines in degree-day requirements for leaf-out is limited and has never been related to the average late frost risk. In *Acer saccharum*, *Fagus crenata* and *Populus balsamifera*, plants originating from southern populations leafed out later than individuals from more northern populations when grown together in a common garden (Kriebel, 1957; Olson et al., 2013; Osada et al., 2018). The opposite was found in *Juglans nigra* and *Ulmus minor*, in which plants of more southern origin started growth earlier in the year compared to more northern plants (Bey, 1979; Ghelardini, Falusi, & Santini, 2006). Equivocal results were also obtained in a common garden study on elevational ecotypes, with no significant phenological differences between high and low-elevation individuals found for *Abies alba*, *Acer pseudoplatanus* and *Ilex aquifolium*, later leaf-out in high-elevation individuals in *Fraxinus excelsior* and *Quercus petraea*, and earlier leaf-out



**FIGURE 1** Conceptual scheme depicting why trees from high latitudes should have lower warming (degree-day) requirements for leaf-out and narrower safety margins against spring frost than trees from low latitudes. There is a trade-off between maximizing the time for tissue maturation by starting growth early in the season (solid lines) and minimizing the risk of frost damage by delaying it (dashed line). In trees that have low degree-day requirements and hence leaf out early, frost damage should be the limiting factor for carbon uptake and tissue maturation; in trees that have high degree-day requirements and hence leaf out late, growing season length should be the limiting factor. Because trees from high latitudes experience comparably short and cold summer periods, growing season length exerts a higher limitation on the time for tissue maturation than it does for trees from low latitudes (compare blue and red solid lines). As a result, the maximum time for tissue maturation in trees from high latitudes (blue circle) is realized at lower degree days to leaf-out compared to trees from low latitudes (red circle). The blue and red filled areas represent the degree-day ranges that represent the best compromise between the two limiting factors [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

in high-elevation individuals in *Fagus sylvatica* (Vitasse, Delzon, Bresson, Michalet, & Kremer, 2009; Vitasse, Delzon, Dufrene, et al., 2009; Vitasse, Josée Porte, Kremer, Michalet, & Delzon, 2009).

Here, we test the new hypothesis that in wide-ranging tree species, high-latitude ecotypes should have lower degree-day requirements to leaf-out and hence narrower frost safety margins than do low-latitude ecotypes (Figure 1). To do this, we used spring leaf-out data obtained from herbarium specimens collected over 108 years at 40° to 60° N latitude to quantify the relationships between leaf-out, late frost occurrence, degree-days, chilling-days and winter duration across a large latitudinal range and in four species. The approach of obtaining phenological data from collections has been used since the mid-1980s and has been tested against phenological observations made in the field (e.g., Borchert, 1996; Davis, Willis, Connolly, Kelly, & Ellison, 2015). Based on these tests, species-specific phenological behaviour obtained from sufficiently large numbers of herbarium specimens is similar to behaviour observed in field studies (Davis et al., 2015; Jones & Daehler, 2018; Robbirt, Davy, Hutchings, & Roberts, 2011). By georeferencing each tree and comparing its leaf-out time in a particular year and place with the relevant winter and spring temperatures we were able to calculate frost 'safety margins' and test how they change with winter duration (latitude). In essence, we quantified by how much frost safety margins decrease with latitude until reaching a limit where a species would experience spring frost damage almost every year. We end by discussing the limitations of our findings as well as avenues for future research to corroborate our hypothesis using in situ phenological observations.

## 2 | MATERIALS AND METHODS

Leaf-out dates in *Acer platanoides*, *Carpinus betulus*, *Fagus sylvatica* and *Prunus spinosa* were inferred from herbarium specimens in seven herbaria (Aarhus University herbarium, AAU; Berlin herbarium, B; Copenhagen herbarium, C; Florence herbarium, FLO; Munich herbarium, M; Herbarium Senckenbergianum Frankfurt, F; Stockholm herbarium, S). While all specimens of these species were photographed, only specimens in the initial leaf-out stage were used for further analysis, which was defined as (a) not all leaves entirely unfolded and (b) leaves not yet full sized (Everill, Primack, Ellwood, & Melaas, 2014; Zohner & Renner, 2014). For specimens that met these criteria, we recorded species name, collection date and collection location. Only low-elevation sites (<800 m a.s.l.) were included to remove climate variation due to elevational gradients. This resulted in a total of 392 leaf-out dates (84 *Fagus*, 136 *Prunus*, 82 *Carpinus* and 90 *Acer*) covering the years 1902 to 2009 (data available in Supporting Information Table S1).

Information on temperature parameters was derived from a gridded climate dataset of daily minimum and maximum temperatures at 0.5° spatial resolution (approximately 50 km; Beer et al., 2014). The optimal pre-season for each species was defined as the period (with 15-day steps) before the mean leaf unfolding date for which the correlation coefficient between leaf unfolding and air temperature was

highest (pre-season length = 60 days for *A. platanoides* and 75 days for the remaining three species). Spring temperature was defined as the mean temperature for the optimal pre-season.

For each species, we calculated the amount of warming (degree-days, DD) required to leaf-out in a particular place and year. DD until leaf-out were calculated from 1 January until the date of leaf unfolding using 5 °C as the base temperature. Temperature ( $T_{\text{hour}}$ ) at any time of the day ( $\text{time}_{\text{day}}$ ) was simulated with a sine curve based on daily maximum ( $T_{\text{max}}$ ) and minimum temperatures ( $T_{\text{min}}$ ) using the following equation:

$$T_{\text{hour}} = \frac{(T_{\text{max}} - T_{\text{min}})}{2} \times \sin\left(\frac{\pi}{12} \times \text{time}_{\text{day}} - \frac{\pi}{2}\right) + \frac{(T_{\text{max}} + T_{\text{min}})}{2} \quad (1)$$

From each hourly temperature value, we subtracted the value 5 (base temperature), then set all values below the base temperature to 0 (because negative development is biologically not possible), and finally calculated the mean of all 24 values for each day, weighting day-time values (= time when sun is above the horizon) three times more than night-time values. This weighting was done because the effect of day-time temperature on leaf unfolding is c. 3 times higher than that of night-time temperature (Fu et al., 2016; Piao et al., 2015).

To characterize the winter temperature regimes experienced by the four species, for each year and location, we calculated the number of winter days and accumulated winter chilling. Winter days (WD) were calculated as the sum of days below 5 °C from 1 October until leaf-out (e.g., Fu et al., 2015):

$$\text{Winter Day} = 1 \text{ if } T \leq 5 \quad (2)$$

Chilling days (CD) were calculated as the sum of daily chilling from 1 October until leaf-out, with temperatures between 0 and 5 °C being considered to be effective for chilling accumulation (e.g., Caffarra, Donnelly, Chuine, & Jones, 2011; Coville, 1920):

$$\text{Chill}_{\text{hour}} = 1 \text{ if } 0 \leq T \leq 5 \quad (3)$$

where chilling ( $\text{Chill}_{\text{hour}}$ ) at any given time of the day depends on the temperature  $T$ . We then calculated daily chilling proportions: For example, a .75 chilling day is a day in which 75% of the time, temperatures are within the chilling range.

To characterize safety margins, we calculated the difference (in days) between the observed leaf-out date and the date of the last leaf-killing frost for each leaf-out observation (herbarium specimen). Positive values indicate that leaf-out occurred during the safe period, whereas negative values indicate potential freezing damage. Because the sensitivity of leaves to spring frost [measured as the lethal temperature at which 50% of observed leaves die ( $\text{LT}_{50}$ )] is species-specific, we used different temperature thresholds to calculate occurrence dates of the last frost (< -3 °C for *F. sylvatica* and < -5 °C for the remaining three species; Lenz, Hoch, Körner, & Vitasse, 2016; Lenz et al., 2013). We used freezing temperatures 2 °C above species' freezing thresholds measured in the laboratory (*A. platanoides*

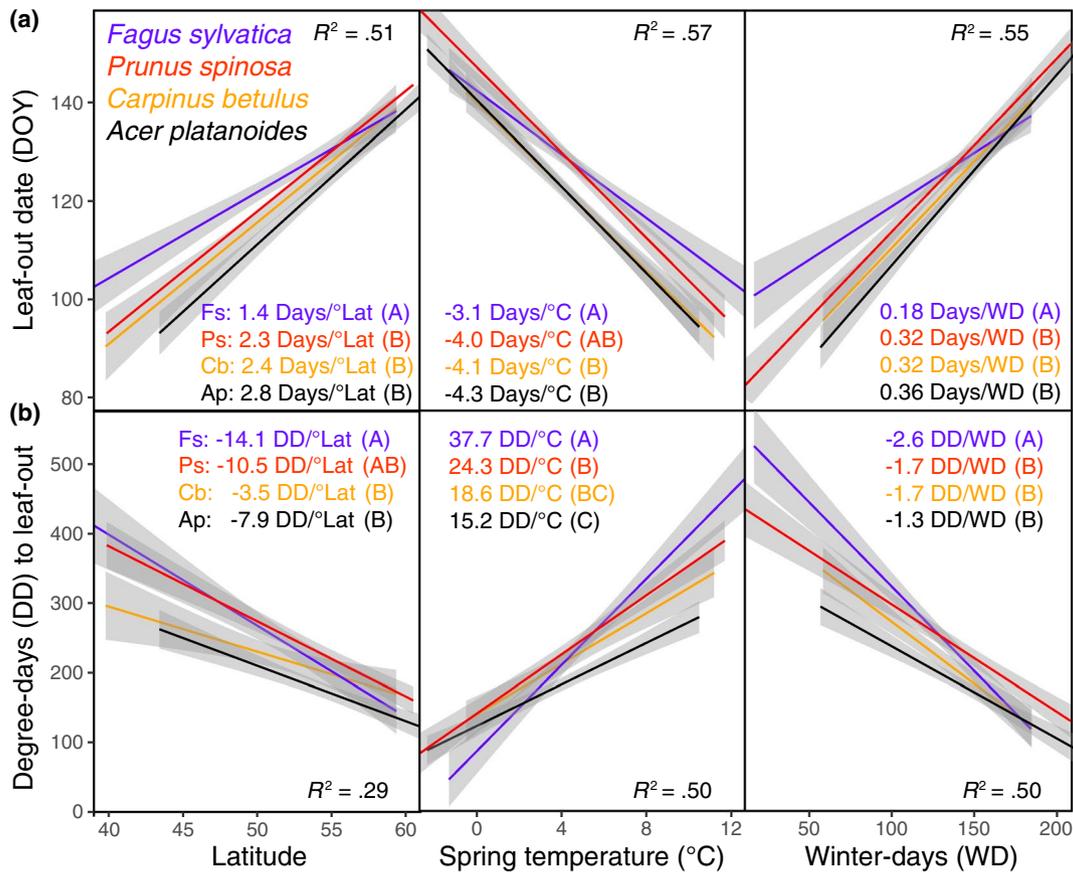
-7 °C, *C. betulus* -7 °C, *F. sylvatica* -5 °C, *P. spinosa* -7 °C) because during clear nights, radiative cooling may lead to temperatures in plant tissues 2 to 5 °C lower than those measured between 1.25 and 2 m height in Stevenson screens (e.g., Cannell, 1985). After extracting all climate information (DD, WD, CD, spring temperatures and last frost dates) for each leaf-out observation, we aggregated data from different years within each 1° pixel, because we were interested in spatial, not temporal, variation within sites, resulting in a sample size of  $n = 44$  for *F. sylvatica*, 57 for *P. spinosa*, 43 for *C. betulus* and 50 for *A. platanoides*.

To test for effects of latitude and climate on phenology, leaf-out dates or DD to leaf-out were regressed on the respective latitude, spring temperature, WD and CD (Figure 2 and Supporting Information Figure S1). To test whether slopes differ among species, we inserted an interaction term between the respective predictor variable (latitude, spring temperature, WD or CD) and species. Finally, we tested for an effect of latitude, spring temperature, WD and CD on species' safety margins against late frosts. The numbers

of observations for each species were not fully balanced across time and space. To control for a possible temporal component in our data, we ran multivariate linear regression models including year as an additional effect term to calculate the slopes,  $p$  values, and partial  $R^2$  values for the effect of latitude on species' leaf-out dates, degree-days to leaf-out, and safety margins against late frosts.

### 3 | RESULTS

With each 1° increase in latitude, *Fagus* showed a delay in leaf unfolding of 1.4 days, *Prunus* and *Carpinus* of 2.3 or 2.4 days and *Acer* of 2.7 days; each 1° increase in spring temperature advanced leaf-out by 3.1 days in *Fagus* and by 4.0 to 4.3 days in *Prunus*, *Carpinus* and *Acer*, and each extra WD delayed leaf-out by 0.18 days in *Fagus* and by 0.32–0.36 days in *Prunus*, *Carpinus* and *Acer* (Figure 2a). Conversely, a 1° increase in latitude caused a decrease in DD required to leaf-out of 14.1 in *Fagus* and of 3.5–10.5 in *Carpinus*, *Acer* and *Prunus*; a



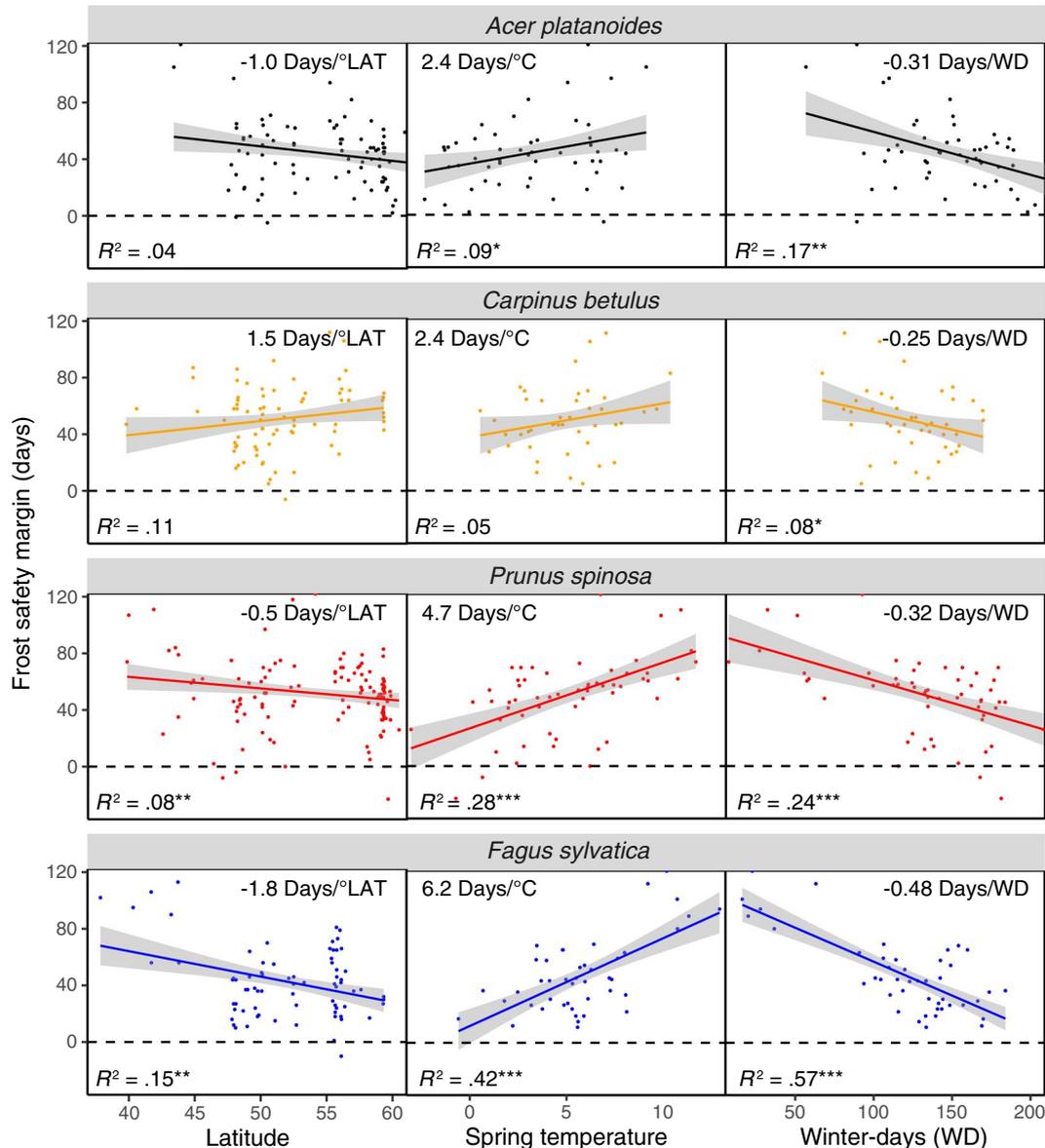
**FIGURE 2** Species-specific effects of latitude, spring temperature and winter duration (number of winter-days) on leaf-out dates (day-of-year, DOY) and spring warming requirements (degree-days). Plots show linear regression lines and 95% confidence limits.  $n = 84$  *Fagus sylvatica*, 136 *Prunus spinosa*, 82 *Carpinus betulus* and 90 *Acer platanoides*. Because we were interested in spatial, not temporal patterns, data for the spring temperature and winter-days analyses (middle and right panels) were averaged at the 1-degree pixel scale ( $n = 44$  *F. sylvatica*, 57 *P. spinosa*, 43 *C. betulus* and 50 *A. platanoides*). The effects of spring temperature and winter days are indicated by partial  $R^2$  values inferred from models that include species as additional fixed effects as well as an interaction term between species and spring temperature/winter days. The partial  $R^2$  values and slopes for the effect of latitude (left panels) are based on multivariate linear regression models including latitude, species and year (to control for a possible temporal component in our data) as fixed effects as well as an interaction term between latitude and species. Capital letters denote which slopes differ significantly ( $p < .05$ ) from each other [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

1° increase in spring temperature led to an increase in DD required to leaf-out of 37.7 in *Fagus* and of 15.2–24.3 in *Acer*, *Carpinus* and *Prunus*; and an increase by 1 WD led to a decrease of 2.6 DD to leaf-out in *Fagus* and of 1.3–1.7 in *Acer*, *Carpinus* and *Prunus* (Figure 2b).

In agreement with these results, the strongest effect of latitude on safety margins against late frosts was found in *Fagus* (Figure 3): with each 1° increase in latitude, the frost safety margin of this species decreased by 1.8 days (Figure 3). No decrease in the safety margin with latitude was detected in *Carpinus*, while in *Acer* and *Prunus*, safety margins in northern ecotypes decreased by 1.0–0.5 days. This latitudinal pattern is best explained by a gradient in winter duration

(winter days). Per additional WD, the frost safety margin decreased by 0.48 days in *Fagus* but only by 0.25–0.32 days in the other species (Figure 3). To ensure that year of collection did not affect the latitudinal patterns reported above, we ran the analyses in Figures 2 and 3 with year included as an additional effect term.

The effect of CD on leaf phenology and frost safety margins was similar to that of WD (Supporting Information Figures S1 and S2): *Fagus* showed the smallest leaf-out response to winter chilling (Supporting Information Figure S1) and accordingly the strongest decline in frost safety margins with increasing duration of winter chilling (Supporting Information Figure S2). The predictive power of



**FIGURE 3** Species-specific effects of latitude, spring temperature and winter duration on safety margins against the last spring frost. Plots show linear regression lines and 95% confidence limits. Dots refer to data from herbarium specimens of known location and leaf-out time ( $n = 84$  *Fagus sylvatica*, 136 *Prunus spinosa*, 82 *Carpinus betulus* and 90 *Acer platanoides*). Data for the spring temperature and winter-days analyses (middle and right panels) were averaged at the 1-degree pixel scale (Figure 2). To control for a possible temporal bias in the analysis of latitude, we ran multivariate linear regression models including year as an additional effect term to extract partial  $R^2$  values, slopes and  $p$  values for the effect of latitude (left panels). For *F. sylvatica*, temperatures  $< -3$  °C were considered as frosts, for the other species, temperatures  $< -5$  °C. \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$  [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

CD was generally lower than that of WD, with the number of CD explaining 24 and 11% of the spatial variation in leaf-out dates and frost safety margins across the four species (Supporting Information Figures S1 and S2), whereas the number of WD explained 55 and 27%, respectively (see Figures 2 and 3; percentages represent explained variation inferred from partial  $R^2$  values of linear regression models controlling for species).

## 4 | DISCUSSION

This study supports the hypothesis that ecotypes of widespread European trees differ in their phenological safety margins against spring frost damage, with populations from cold, high-latitude regions having narrower safety margins than populations from warmer regions (Figure 3). To our knowledge, this phenomenon has never been quantified and placed in an adaptive physiological context before. Relevant to understanding our finding are experiments showing that warming requirements (degree-day accumulation) to leaf-out in temperate trees decrease with increasing duration of winter chilling and day length (Harrington & Gould, 2015; Heide, 1993; Laube et al., 2014; Zohner, Benito, Fridley, Svenning, & Renner, 2017; Zohner, Benito, Svenning, & Renner, 2016). Effective winter chilling, however, does not linearly increase with winter duration because negative temperatures are less effective than temperatures slightly above zero (Harrington, Gould, & St.Clair, 2010; Körner et al., 2016; Vitasse et al., 2018). In our data, winter duration (i.e., the number of WD <5 °C) explained 55 and 27% of the spatial variation in leaf-out dates and frost safety margins across the four species (Figures 2 and 3), while effective chilling (temperatures between 0 and 5 °C) explained only 24 and 11%, respectively (Supporting Information Figures S1 and S2). This indicates that it is the length of winter per se, not the physiologically relevant chilling range, that best explains the observed latitudinal differences in phenology, pointing towards day-length and adaptive mechanisms.

Based on the trade-off between growing season length and frost avoidance (Figure 1), one expects genetic differences between high- and low-latitude ecotypes: evolution should favour late-flushing ecotypes with high spring warming requirements at low latitudes, while favouring early flushing ecotypes with low warming requirements at high latitudes because early leaf-out maximizes growing season length. Such latitudinal clines in warming requirements might be enhanced by parallel clines in day-length sensitivity (Gauzere et al., 2017; Zohner et al., 2016). Indeed, using common garden experiments, Vitasse, Delzon, Bresson, et al. (2009) showed that northern *F. sylvatica* individuals leaf-out earlier than southern ones, and for the congeneric *F. crenata*, Osada et al. (2018) suggest that this is due to northern ecotypes having lower spring warming, chilling and day-length requirements than southern ecotypes.

The latitudinal differences in leaf-out warming requirements reported here have implications for species range shifts and assisted migration efforts (also Alberto et al., 2013). Under rapid climate

warming, the optimal warming sums required by high-latitude ecotypes to leaf-out will likely increase as a result of warmer/longer growing seasons (see Figure 1), perhaps leading to the local leaf-out times becoming increasingly mismatched with the occurrence of frost (Renner & Zohner, 2018). Such possible disequilibria could be counteracted by poleward range expansions as occurred during other Holocene warm periods (Petit & Hampe, 2006). Assisted migration strategies using low-latitude individuals with high spring warming requirements might, therefore, help to restore optimal leaf-out timing in managed populations, minimizing late frost risk, and maximizing carbon capture.

Our results also pinpoint taxonomic differences in the latitudinal variation in spring phenology and frost safety margins. For each 1-day increase in winter duration, frost safety margins decrease by 0.48 days in *Fagus*, but only by 0.25–0.32 days in *Carpinus*, *Acer* and *Prunus* (Figure 3). The most likely proximate explanation for these differences is the high chilling and day-length sensitivity of *Fagus* (Heide, 1993; Laube et al., 2014; Zohner et al., 2016). Accordingly, we find that winter duration has the most pronounced effect on warming requirements to leaf-out in *Fagus*, with each increase of one winter day reducing warming requirements by 2.6 DD, but only by 1.3–1.7 DD in the three other species (Figure 2). The most likely ultimate explanation for the strong latitudinal differences in frost safety margins in *Fagus* is the large dependence on long growing seasons for wood formation and tissue maturation in this species (Lenz, Vitasse, Hoch, & Körner, 2014).

## 5 | CONCLUSION

Here, based on the trade-off between late flushing and a long growing season, we present evidence for a new concept explaining why frost safety margins should become narrower at high-latitude regions with short vegetation periods—at least in species such as *F. sylvatica* that require a long growing season for tissue maturation. Because our findings are based on a small sample size—not fully balanced across time and space—more individuals will need to be studied in the future, which will require data on how leaf-out changes per degree latitude, per degree temperature and per extra chilling day in thousands of trees from 40° to 60° latitudes. Such data are not available from any database, and ongoing attempts to merge the Pan European Phenology (PEP725) database (Templ et al., 2018), covering mainly Germany Austria, and Switzerland, with phenological data from southern Europe and Scandinavia have not yet come to fruition. An analysis of herbarium material was therefore the only approach to test our new hypothesis for why phenological strategies should differ among populations, such that high-latitude populations show minimized spring warming requirements. To further deepen our understanding of the interplay among phenology, climate adaptation, and species range limits, merging of databases will need to be paralleled by climate chamber experiments targeted at tree individuals of different provenances, with the environmental parameters then modified to test specific expectations.

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## AUTHOR CONTRIBUTIONS

CMZ and SSR designed the study. CMZ and VS collected the herbarium data. CMZ and LM performed analyses. CMZ and SSR wrote the manuscript.

## DATA AVAILABILITY STATEMENT

Data used in the study are available in Supporting Information Table S1.

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## SUPPORTING INFORMATION

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

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