

Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants

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The relative roles of temperature and day length in driving spring leaf unfolding are known for few species, limiting our ability to predict phenology under climate warming^{1,2}. Using experimental data, we assess the importance of photoperiod as a leaf-out regulator in 173 woody species from throughout the Northern Hemisphere, and we also infer the influence of winter duration, temperature seasonality, and inter-annual temperature variability. We combine results from climate- and light-controlled chambers with species' native climate niches inferred from georeferenced occurrences and range maps. Of the 173 species, only 35% relied on spring photoperiod as a leaf-out signal. Contrary to previous suggestions, these species come from lower latitudes, whereas species from high latitudes with long winters leafed out independent of photoperiod. The strong effect of species' geographic-climatic history on phenological strategies complicates the prediction of community-wide phenological change.

Understanding the environmental triggers of leaf-out and leaf senescence is essential for forecasting the effects of climate change on temperate zone forest ecosystems^{2–4}. Correlation analyses suggest that warmer springs are causing earlier leaf emergence, leading to an extended growing season^{5,6} and increased carbon uptake⁷. A continuing linear response to spring warming, however, is not expected because stimuli, such as photoperiod^{1,8–10} and chilling^{11–13}, additionally trigger dormancy release.

Photoperiod limitation refers to the idea that plant sensitivity to day length protects leaves against frost damage by guiding budburst into a safe time period¹. Experiments have shown that day-length-sensitive species react to spring temperatures only once day length increases¹⁰. Because day length will not change under climate warming, photosensitive species may be less responsive to warmer temperatures^{1,9,14,15}.

Experiments addressing the relative importance of photoperiod versus temperature for dormancy release have been carried out in about 40 species^{8–12}, and among them a few species, most strikingly *Fagus sylvatica*, exhibited strong photoperiodism^{8–10,12,16–19}. Results are often equivocal, perhaps in part reflecting experimental difficulties in adequately modifying day length when working with trees^{9,11,12,20,21}.

Why species differ in their relative reliance on photoperiod and spring temperature as leaf-out signals is largely unknown. This prevents the development of mechanistic models for predicting spring phenology under climate warming. The need to understand spring phenology in its geographic-climatic context is highlighted by studies suggesting that phenological strategies in long-lived woody species have evolved as adaptations to the climate in a species' native range^{22–25}. A common garden study of 495 woody species from different climates showed that species native to warmer

climates flush later than species native to colder areas, but did not investigate whether this was due to different species relying on temperature or photoperiod²⁵. If photoperiod indeed provides a safeguard against leafing out too early^{1,9}, photoperiodism should be especially important in regions with unpredictable frost events—that is, high inter-annual variability in spring temperatures (here called 'high temperature variability' hypothesis)²⁶—and in regions with oceanic climates in which temperature is a less reliable signal because the change between winter and spring temperatures is less pronounced ('oceanic climate' hypothesis)¹. A third hypothesis is that photoperiodism mirrors species' latitudinal occurrence because day-length seasonality increases towards the poles, and day length thus provides an especially strong signal at higher latitudes ('high latitude' hypothesis)³. Of these predicted correlates of photoperiod as a spring leaf-out signal, only the 'oceanic climate' hypothesis has been tested¹², with no significant relationship found.

We set out to investigate the effect of photoperiod on leaf-out timing in species from different winter temperature regimes ('high latitude' hypothesis), temperature seasonality regimes ('oceanic climate' hypothesis), and between-year spring temperature variability ('high temperature variability' hypothesis) (Fig. 1a), and to test if photoperiod-sensitive species react less to spring temperatures than do photoperiod-insensitive species. We used 173 species (in 78 genera from 39 families) from the Northern Hemisphere grown in a mid-latitude (48° N) European botanical garden and modified the day length experienced by buds on twigs cut from these species at three different times, and hence chilling levels (see Methods and Supplementary Fig. 1). To assign the species to their climate ranges, we queried georeferenced occurrence data against climate grids for winter duration (Fig. 1b), temperature seasonality (*T* seasonality), and inter-annual spring temperature variability (*T* variability). In addition, each species was also assigned to its predominant Koeppen–Geiger climate type²⁵. To achieve our second aim, we tested for correlations between species' photoperiodism (as inferred from our experiments on leaf-out in twigs under different light regimes) and their leaf-out behaviour *in situ* (as inferred from multi-annual leaf-out observations on intact trees; Fig. 2).

With low chilling (twig collection in December), 61 (35%) of the 173 species leafed out later under short day conditions than under long days, while the remaining 112 species did not react differently regardless of short and long days. Increased chilling reduced species' sensitivity to photoperiod: Under intermediate chilling conditions (twig collection in February), 16 (9%) of the 173 species showed delayed budburst under short days. Under long chilling conditions (twig collection in March), only four (2%) species, namely *Fagus crenata*, *F. orientalis*, *F. sylvatica*, and *Carya cordiformis*, leafed out later under short days. Based on these results, constraints on the climate-warming-driven advance of

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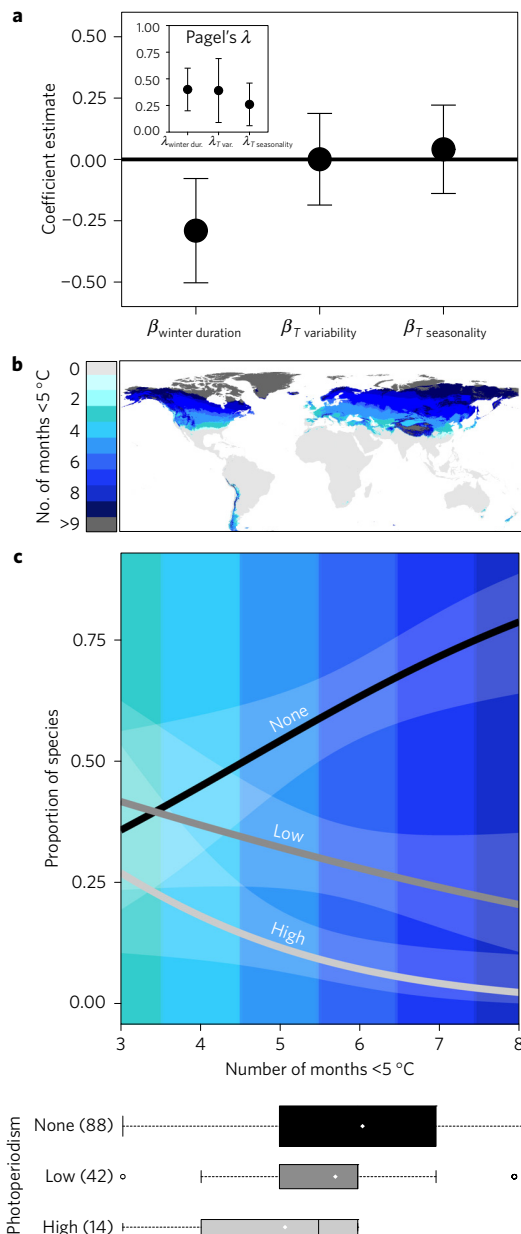


Figure 1 | Relationship between species' spring photoperiodism and the maximum winter duration in their native ranges. **a**, Coefficient estimates (effective posterior means β and 95% credible intervals) for the effect of day length sensitivity on maximum winter duration, median T variability, and maximum T seasonality. Models control for phylogenetic autocorrelation and species' maximum growth height. See Supplementary Methods for a detailed description of regression components. Values reflect standardized data and can be interpreted as relative effect sizes. The inset shows fitted values of phylogenetic signal (Pagel's λ , mean and 95% CIs) for species' maximum winter duration, median T variability, and maximum T seasonality (dependent variables), respectively. **b**, Winter duration, calculated as the number of months with mean air temperature below 5 °C. **c**, Proportion of species with a given level of photoperiod sensitivity as a function of maximum winter duration (0.95 quantile) in a species' native range (ordinal logistic regression model; $P < 0.01$; Table 1). Colours as in **b**. Envelopes around each line show 95% confidence intervals. Boxplots for species' maximum winter duration when they were grouped according to photoperiod requirements are shown below the graph. Photoperiod requirements: None, No sensitivity; Low, Sensitivity to day length during early dormancy; High, Sensitivity to day length also in late dormancy (see Supplementary Fig. 1).

leaf-out¹⁵ will probably be twofold in photosensitive species: reduced winter chilling *per se* will cause plants to require more warming in the spring, and reduced chilling additionally will cause higher photoperiod requirements. The latter constraint will become more significant, as springs will arrive ever earlier (that is, at ever shorter photoperiods) in the future.

Where do the species that rely on photoperiodism as a leaf-out trigger come from? Our data reject all three suggested correlates of photoperiodism (that is, the 'high latitude', 'high temperature variability', and 'oceanic climate' hypotheses) and instead reveal that it is the species from shorter winters (that is, lower, not higher latitudes) that rely on photoperiodism ($P < 0.05$; Table 1 and Fig. 1). Of the 173 species, the 22 that come from regions with long winters (>7 months with an average temperature below 5 °C), such as alpine and subarctic regions, are photoperiod-insensitive, while the 14 species with high photoperiod requirements are restricted to regions with shorter winters (not exceeding six months with an average temperature below 5 °C; Fig. 1). In a hierarchical Bayesian model that controlled for possible effects of shared evolutionary history and species' growth height, winter duration remained negatively correlated with species' photoperiodism (Fig. 1a). Analyses that used the Koeppen–Geiger climate classification yielded the same results as analyses that used the climate grids—namely, that most photoperiod-sensitive species are native to warm climates with mild winters (Supplementary Fig. 2).

Why is there a negative correlation between species' reliance on day length as a leaf-out signal and the winter duration in their native ranges? There are two possible mechanisms on how photoperiod perception in plants may interact with warming requirements: either plants need to reach a fixed photoperiod threshold before they perceive spring temperatures, or forcing requirements gradually decrease with increasing photoperiod. The first mechanism would require that plants from regions with long winters have higher photoperiod thresholds because in these areas days are already long (>14 h) when minimum temperatures cross the freezing threshold (see also Way & Montgomery²¹; Fig. 1). The second mechanism would require that photoperiod as a budburst regulator is less important in regions with long winters because days in spring become long before the risk of encountering freezing temperatures has passed. Experimental results from *Fagus sylvatica* show a gradual response to photoperiod independent of the latitudinal origin of the experimental plants: Forcing requirements decrease with increasing day length up to about 16 h, with further increase of daylight having little additional effect^{8,10}. This supports the second mechanism. *Fagus sylvatica* therefore leafs out earlier in regions with long winter duration than photo-insensitive species, and operates at a smaller 'safety margin' against late frosts^{27,28}. The hypothesis that northern woody species evolved photoperiod-independent leaf-out strategies because at high latitudes day-length increase in spring occurs too early for frost to be safely avoided needs to be tested with further experiments addressing the physiological mechanisms of photoperiod perception in different taxonomic groups.

That photosensitive species are restricted to regions with relatively short winters supports the idea that photoperiodism may slow or constrain poleward range expansion³. With a warming climate, however, the last day with night frost occurs ever earlier (in Germany, between 1955–2015, the last frost on average advanced by 2.6 days per decade; Supplementary Fig. 3), and photoperiod-sensitive species might then do well at higher latitudes or elevations.

The leaf-out dates showed that those species with high photoperiod requirements had lower between-year variance in leaf-out dates than species lacking photoperiodism. Accordingly, in photoperiod-sensitive species, accumulated thermal time until budburst showed greater variation among years than it did in photoperiod-insensitive species ($P < 0.01$; Fig. 2). Leaf unfolding in species that rely on day length is thus less responsive to temperature

Table 1 | Global relationships between species' photoperiod requirements and duration of winter, inter-annual spring temperature variability (T variability), and T seasonality in their native range for 144 temperate woody species.

	ANOVA	OLR	Multiv. OLR	Random forest	HB model
	F values	Weight _{AIC}	Estimate \pm CI	MDA	EPM \pm CI
Winter duration	$F(1, 142) = 9.5^*$	0.90*	$-0.47 \pm 0.28^*$	33.7	-1.1 ± 0.5
T variability	$F(1, 142) = 0.3$	0.05	0.99 ± 1.17	22.9	-0.3 ± 0.5
T seasonality	$F(1, 142) = 1.9$	0.05	0.00 ± 0.01	20.8	-0.2 ± 0.5

Five comparative measures were used: the F value from univariate analysis of variance (ANOVA), Akaike weights from bivariate regressions using ordinal logistic regression (OLR) models, parameter estimates and 95% confidence intervals (CI) based on multivariate OLR models, mean decrease in accuracy values (MDA) from random forest analysis, and coefficient values (effective posterior means (EPM) and 95% CIs) from a hierarchical Bayesian (HB) model controlling for phylogenetic autocorrelation and species' maximum growth height. For each single climatic parameter we initially considered the upper limit (0.95 quantile), median (0.5 quantile), and lower limit (0.05 quantile) across each species' range and kept the variable that yielded the lower Akaike information criterion (AIC) according to OLR models (that is, we kept the 0.95 quantile for winter duration and T seasonality, and the 0.5 quantile for T variability). Sample size: No photoperiod requirements, 88 species; Low, 42 species; High, 14 species. * $P < 0.01$.

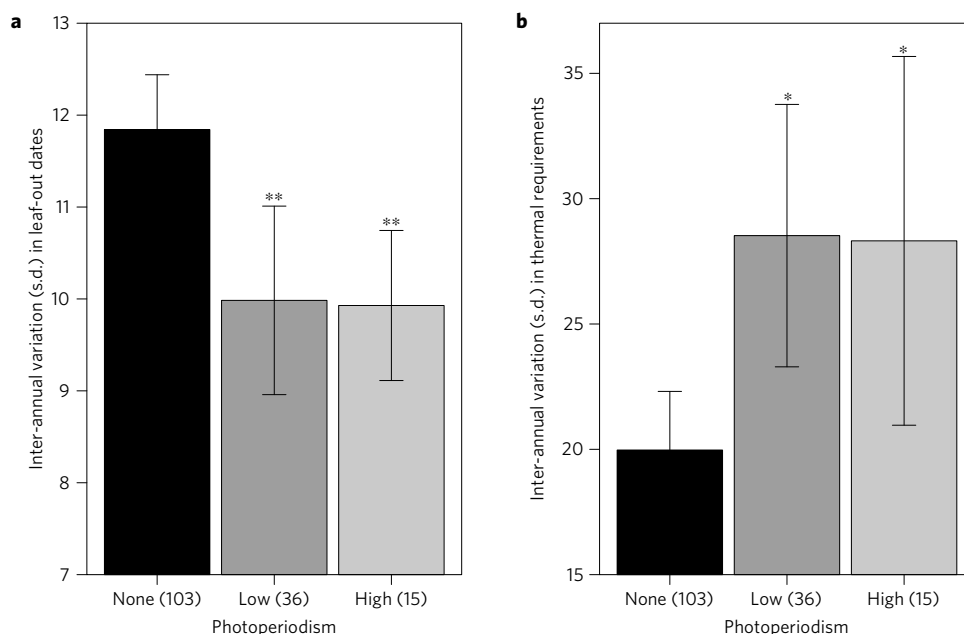


Figure 2 | Effect of day length sensitivity on inter-annual variability in leaf-out. a, b, Photoperiod-dependent leaf-out strategies lead to low inter-annual variability in leaf-out dates (**a**) and high inter-annual variability in thermal time until budburst (**b**). For each species ($n = 154$) the s.d. in leaf-out dates and thermal requirements was calculated on the basis of leaf-out dates available from the Munich Botanical Garden from 2012 to 2015. We show the mean \pm 95% confidence interval for each group. Thermal time was calculated as the sum of growing-degree days from 1 January until the day of leaf-out in the respective species using 0°C as base temperature. Asterisks above bars indicate which group differed significantly from the group of species with no photoperiod requirements (* $P < 0.05$, ** $P < 0.01$).

increase, and in these species photoperiod will constrain phenological responses to climate warming, with possible consequences for carbon gain, the local survival of populations and community composition^{2,4}. The extent to which species' phenological strategies are influenced by their climatic histories highlights the need for a broader geographic sampling in global-change studies²⁹.

Our results do not support previous ideas about phenological strategies in temperate woody species (the 'high temperature variability' hypothesis; the 'oceanic climate' hypothesis; the 'high latitude' hypothesis^{1,3,26}). In regions with long winters, trees appear to rely on cues other than day length, such as winter chilling and spring warming. By contrast, in regions with short winters, some species—mostly from lineages with a warm-temperate or subtropical background, for example, *Fagus*³⁰—additionally rely on photoperiodism. Therefore, photoperiod may be expected to constrain climate-driven shifts in spring leaf unfolding only at lower latitudes.

Methods

Methods and any associated references are available in the [online version of the paper](#).

Received 7 December 2015; accepted 19 September 2016; published online 17 October 2016; corrected online 14 November 2016

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Acknowledgements

We thank V. Sebald and M. Wenn for help with conducting the twig-cutting experiments. B.M.B. acknowledges funding by Aarhus University and the Aarhus University Research Foundation under the AU IDEAS programme (Centre for Biocultural History) and J.-C.S. support from by the European Research Council (ERC-2012-StG-310886-HISTFUNC). The study was part of the KLIMAGRAD project sponsored by the 'Bayerisches Staatsministerium für Umwelt und Gesundheit'.

Author contributions

C.M.Z. and S.S.R. designed the study. C.M.Z. conducted the experiments and leaf-out observations. C.M.Z. and B.M.B. performed the analyses. C.M.Z. and S.S.R. led the writing with inputs from the other authors.

Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to C.M.Z.

Competing financial interests

The authors declare no competing financial interests.

Methods

Twig-cutting experiments. We conducted twig-cutting experiments on 144 temperate woody species growing permanently outdoors without winter protection in the botanical garden of Munich to test for an effect of day length on dormancy release and subsequent leaf unfolding (see Supplementary Table 1 for species names). Twig cuttings have been shown to precisely mirror the phenology of donor trees because dormancy release is controlled at the bud level and not influenced by hormonal signals from other parts of a tree, such as the stem or the roots^{10,31}. In winter 2013/2014, twigs approximately 40 cm in length were collected at three different dormancy stages (on 21 December, 10 February and 21 March) for each species. After collection, we transferred the cut twigs to climate chambers and kept them under short (8 h) or long day (16 h) conditions. Temperatures in the climate chambers were held at 14 °C during the night and 18 °C during the day (see Supplementary Fig. 4 for a description of the temperature regime outside and in the climate chambers). Illuminance in the chambers was about 8 klux ($\sim 100 \mu\text{mol s}^{-1} \text{m}^{-2}$). Relative air humidity was held between 40% and 60%.

Immediately after cutting, we disinfected the twigs with sodium hypochlorite solution (200 ppm active chlorine), cut them a second time, and then placed them in 0.5 l glass bottles filled with 0.4 l cool tap water enriched with the broad-spectrum antibiotics gentamicin sulfate ($40 \mu\text{g l}^{-1}$; Sigma-Aldrich, Germany)^{9,10}. We used 60 replicate twigs per species (10 twigs per treatment, 3×2 full factorial experiment) and monitored bud development every second day. For each treatment, we recorded the leaf-out dates of the first eight twigs that leafed out. A twig was scored as having leafed out when three buds had their leaves pushed out all the way to the petiole. Flushing rate, that is, the proportion of buds flushed over the total number of buds on the twigs, was not recorded. Treatment effects (long versus short days at three different dormancy stages) on the response variable (accumulated degree days $> 0^\circ\text{C}$ outside and in climate chamber from 21 December until leaf-out) were assessed in ANOVAs. We defined three categories to describe a species' photoperiodism: none = No response to day length, low = sensitivity to day length during early dormancy, high = sensitivity to day length also during late dormancy. Species whose twigs when cut on 21 December (early dormancy stage) showed no statistical difference between 8-h and 16-h photoperiod treatments were categorized as having no photoperiod requirements. Species whose twigs when cut on 21 December leafed out significantly later when they were exposed to 8-h day length compared to 16-h days were categorized as having low photoperiod requirements. Species whose twigs when cut on 10 February (advanced dormancy stage) still leafed out later under short days (8 h) than under 16-h days were categorized as having high photoperiod requirements. When twigs were cut on 21 March, only three *Fagus* species and *Carya cordiformis* reacted differently to 8-h and 16-h photoperiods, and we categorized them as having high photoperiod requirements. In addition to the ANOVA assessment, a day-length effect was only considered significant if the forcing requirements under 8-h day length were $> 50^\circ$ days higher than under 16-h day length and if the additional forcing requirement was $> 10\%$ larger than required under long days (see Supplementary Fig. 1 for species-specific treatment effects). Information on the photoperiod requirements of 29 additional species came from a previous study¹² that used the same experimental approach to detect species' photoperiod requirements, allowing us to apply the same definition of photoperiod categories to these authors' data. This resulted in photoperiod data for a total of 173 woody species in 78 genera from 39 families.

In situ leaf-out observations. For 154 of the 173 species with information on photoperiod requirements (previous section), we have four years of observations of leaf-out dates (2012–2015) available from the Munich Botanical Garden. The 2012 and 2013 data come from our earlier study²⁵, and the same individuals were monitored again in 2014 and 2015. A species' leaf-out date was defined as the day when three branches on a plant had leaves pushed out all the way to the petiole. Thermal requirements of species were calculated as the sum of growing-degree days from 1 January until day of leaf-out using a base temperature of 0°C . Species names are given in Supplementary Table 1. To test if species with photoperiod requirements show lower variation in leaf-out and higher variation in thermal requirements among years than do photo-insensitive species, we applied difference-of-means tests (Fig. 2). Because vectors were not normally distributed we conducted Kruskal–Wallis H tests with a *post hoc* kruskalmc analysis (multiple comparison after Kruskal–Wallis)³².

Temporal occurrence of last frost events. Weather data were downloaded from Deutscher Wetterdienst, Offenbach, Germany, via WebWerdis (https://werdis.dwd.de/werdis/start_js_JSP.do) to gather information on the relative occurrence date and temporal shifts of the last frost (daily minimum temperature below 0°C). Information on the occurrence of the last frost from 1955 to 2015 for German locations differing in their winter duration is given in Supplementary Fig. 3. On average, across all stations, the last freezing event advanced by 2.6 days per decade.

Species ranges and climate characteristics. To obtain species' native distribution ranges, we extracted georeferenced locations from the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org>), using the dismo R package³³. Cleaning scripts in R were used to filter reliable locations and exclude species with unreliable records, using the following five criteria: only records from a species' native continent were included; coordinate duplicates within a species were removed; records based on fossil material, germplasm, or literature were removed; records with a resolution $> 10 \text{ km}$ were removed; and only species with more than 30 georeferenced GBIF records within their native continent were included. After applying these filtering criteria, we were left with distribution data for 144 of the 173 species.

We then derived species-specific climate ranges from querying georeferences against climate grids of three bioclimatic variables: *T* seasonality (BIO7; temperature difference between warmest and coldest month), *T* variability (inter-annual spring temperature variability calculated as the standard deviation of March, April, and May average temperature from 1901–2013), and winter duration (defined as the numbers of months with an average *T* below 5°C). A grid file for the winter duration was based on global monthly weather data available at www.worldclim.org³⁴, from which we calculated the number of months with an average temperature below 5°C for the global land surface (see Fig. 1b). *T* seasonality was based on gridded information (2.5-arcmin spatial resolution data) about the annual temperature range derived from the WorldClim data set (bioclim7)³⁴. *T* variability was calculated as the standard deviation of spring (March, April, and May) average temperatures from 1901 to 2013 (see Supplementary Fig. 5). Data on monthly average temperatures during this period were available from the CRU database (5-arcmin spatial resolution data)³⁵. For each bioclimatic variable we determined three species-specific measures: the upper and lower limits and the median, which were obtained from the bioclimatic data covering a species range at the 0.95, 0.05 and 0.50 quantile, respectively.

As an alternative approach that allowed us to infer the predominant climate of 171 of the 173 species, we used the Koeppen–Geiger system³⁶. Information on species-specific Koeppen–Geiger climate types was available from our earlier study²⁵ in which each species' natural distribution was determined using information from range maps and range descriptions: <http://linnaeus.nrm.se/flora/welcome.html> and <http://www.euforgen.org/distribution-maps> for the European flora, <http://plants.usda.gov/java> and <http://esp.cr.usgs.gov/data/little> for North America, and <http://www.efloras.org> for Asia. As a proxy for a species' native winter temperature regime, it was scored for the first Koeppen–Geiger letter (D-climate = coldest month average below -3°C , C-climate = coldest month average above -3°C). For species' summer temperature, the third Koeppen–Geiger letter was used (a-climate = warmest month average above 22°C with at least four months averaging above 10°C ; b-climate = warmest month average below 22°C but with at least four months averaging above 10°C ; c-climate = warmest month average below 22°C with three or fewer months with mean temperatures above 10°C). The second letter in the Koeppen system refers to precipitation regime and was disregarded in the analyses. Species were scored for the predominant conditions in their native range; for example, a species occurring in 40% Cfa, 30% Dfa, and 30% Dfb climates would be scored as 'D' and 'a'.

Data analysis. The quantiles (0.05, 0.5, and 0.95) of each climate parameter (winter duration, *T* seasonality, and *T* variability) were highly correlated among each other (Pearson correlation, $r > 0.5$). To avoid multicollinearity in our models, we included only one quantile for each climate parameter. For each climate parameter, we kept the quantile that gave the best prediction of species-level variation in photoperiodism. We fitted univariate logistic regression models to our data and, for each climate parameter, kept the variable with the lower Akaike information criterion (AIC)—that is, we kept the 0.95 quantile of winter duration, 0.95 quantile of *T* seasonality, and 0.5 quantile of *T* variability. We tested for multicollinearity among the retained predictor variables by using variance inflation factors (VIF). All VIF were smaller than 5, indicating sufficient independence of the predictor variables. ANOVA and ordinal logistic regression (OLR) were used to separately test for correlations among predictor variables and species-specific photoperiod sensitivity (see Table 1 and Fig. 1c and Supplementary Fig. 6). To examine the relative contribution of each climate variable to explain species-specific photoperiod sensitivity, we applied multivariate OLR, random forest^{37,38}, and hierarchical Bayesian models. The hierarchical Bayesian models allowed us to control for phylogenetic signals in our data (Supplementary Fig. 7) using the Bayesian phylogenetic regression method³⁹ (see next section). We analysed correlations between species' native climates as inferred from the Koeppen–Geiger system³⁶ and their photoperiod requirements by applying contingency analyses (Fisher's test) and hierarchical Bayesian models (see next section).

Data analysis including the phylogenetic structure. To account for possible effects of shared evolutionary history, we applied hierarchical Bayesian models. The phylogenetic signal in trait data was estimated using Pagel's λ (ref. 40), with the

'phylosig' function in the R package 'phytools' v0.2-1 (ref. 41). The phylogenetic tree for our 173 target species came from Panchen *et al.*⁴² and was assembled using the program Phylomatic⁴³ (Supplementary Fig. 7). Its topology reflects the APG III phylogeny⁴⁴, with a few changes based on the Angiosperm Phylogeny Website⁴⁵. We manually added about 10 missing species to the tree. Branch lengths of the PHYLOMATIC tree are adjusted to reflect divergence time estimates based on the fossil record^{46,47}. Besides controlling for phylogenetic signal λ (ref. 40) of traits, the hierarchical Bayesian approach allowed us to control for possible effects of growth height on species-level photoperiod requirements and climate ranges, by including species' mature growth height as a fixed effect in the models. Mature growth height is a significant functional trait that is related to species' growth phenology⁴² as well as climate ranges⁴⁸. Slope parameters across traits are estimated simultaneously without concerns of multiple testing or P -value correction.

To determine which climate parameter best explains species-level differentiation in photoperiodism, we treated species' photoperiod requirements (ordinal data) as a dependent variable. Three climate variables (species-specific maximum winter duration, 0.95 quantile; max. T seasonality; 0.95 quantile; and median T variability, 0.5 quantile) and species' mature growth height were used as predictor variables (Table 1 and Supplementary Fig. 8).

Regression components are of the form:

$$\begin{aligned}\text{ordered logit}(\text{photoperiod}_i) = & \beta_{\text{max winter duration}} \times \text{max winter duration}_i \\ & + \beta_{\text{median } T \text{ variability}} \times \text{median } T \text{ variability}_i \\ & + \beta_{\text{max } T \text{ seasonality}} \times \text{max } T \text{ seasonality}_i \\ & + \beta_{\text{growth height}} \times \text{growth height}_i\end{aligned}$$

β refers to the estimated slopes of the respective variable. In an alternative model, we used species' Koeppen winter and summer temperature types and mature growth height as predictor variables (Supplementary Fig. 9):

$$\begin{aligned}\text{ordered logit}(\text{photoperiod}_i) = & \beta_{\text{winter temp}} \times \text{winter temp}_i \\ & + \beta_{\text{summer temp}} \times \text{summer temp}_i \\ & + \beta_{\text{growth height}} \times \text{growth height}_i\end{aligned}$$

These models do not statistically account for phylogenetic structure by allowing correlations to vary according to the phylogenetic signal λ , because λ estimation is not possible for ordinal (or logistic) models. To nevertheless account for data non-independence due to shared evolutionary history of species (see Supplementary Fig. 7), we inserted genus and family random intercept effects in the model. To examine relative effect sizes of predictor variables, we standardized all variables by subtracting their mean and dividing by 2 SD before analysis⁴⁹. The resulting posterior distributions are a direct statement of the influence of each parameter on species-level differentiation in photoperiod requirements. The effective posterior means (EPM) for the relationships between winter duration, temperature seasonality, and spring temperature variability and species-specific photoperiodism are shown in Supplementary Fig. 8, and the EPMs for relationships between Koeppen–Geiger climates and photoperiod requirements are shown in Supplementary Fig. 9.

The hierarchical Bayesian model strongly preferred winter duration to T seasonality and T variability as an explanatory variable for species' photoperiodism. Likewise, the model using the Koeppen system preferred the Koeppen winter climate to the summer climate as a predictor of species' photoperiodism. To validate these results, instead of treating photoperiodism as dependent variable, we tested two other models. The first compared the distribution of covariates (max. winter duration, max. T seasonality, and median T variability) between the different photoperiod categories. Species' values for max. winter duration, max. T seasonality, and median T variability can be treated as continuous characters, which allowed us to incorporate phylogenetic distance matrices to control for shared evolutionary history of species (Pagel's λ values: max. winter duration = 0.40; max. temp. seasonality = 0.39; median temp. variability = 0.26; see inset Fig. 1a). This model included three dependent variables that were normally distributed with mean μ , variance σ^2 , and correlation structure Σ (Fig. 1a):

$$\begin{aligned}\text{max winter duration}_i & \sim N(\mu_{\text{max winter duration}_i}, \sigma_{\text{max winter duration}_i}^2, \Sigma) \\ \text{median } T \text{ variability}_i & \sim N(\mu_{\text{median } T \text{ variability}_i}, \sigma_{\text{median } T \text{ variability}_i}^2, \Sigma) \\ \text{max } T \text{ seasonality}_i & \sim N(\mu_{\text{max } T \text{ seasonality}_i}, \sigma_{\text{max } T \text{ seasonality}_i}^2, \Sigma)\end{aligned}$$

Regression components are of the form:

$$\begin{aligned}\mu_{\text{max winter duration}_i} & = \alpha_1 + \beta_{\text{winter dur}} \times \text{photoperiodism}_i + \beta_1 \times \text{mature growth height}_i \\ \mu_{\text{median } T \text{ variability}_i} & = \alpha_3 + \beta_{T \text{ variability}} \times \text{photoperiodism}_i + \beta_2 \times \text{mature growth height}_i \\ \mu_{\text{max } T \text{ seasonality}_i} & = \alpha_2 + \beta_{T \text{ seasonality}} \times \text{photoperiodism}_i + \beta_3 \times \text{mature growth height}_i\end{aligned}$$

The other model, based on species' Koeppen climate letters as outcome, included two binary dependent variables that capture whether species are native to regions with mild or cold winters (KW; Koeppen C or D climate) and warm or cold summers (KS; Koeppen a or b climate) (Supplementary Fig. 2):

$$\text{winter temp} \sim \text{Bernoulli}(\text{WT}_i)$$

$$\text{summer temp} \sim \text{Bernoulli}(\text{ST}_i)$$

Regression components are of the form:

$$\text{logit}(\text{WT}_i) = \alpha_1 + \beta_1 \times \text{photoperiodism}_i + \beta_3 \times \text{maximum growth height}_i$$

$$\text{logit}(\text{ST}_i) = \alpha_2 + \beta_2 \times \text{photoperiodism}_i + \beta_4 \times \text{maximum growth height}_i$$

The term α refers to the intercept, β to the estimated slopes of the respective variable (photoperiodism and maximum growth height), and max winter duration, max temp seasonality, and median temp variability refer to species values of the respective climate parameters. The phylogenetic structure of the data was incorporated in the hierarchical Bayesian models using the Bayesian phylogenetic regression method of de Villemereuil *et al.*³⁹, by converting the 173-species ultrametric phylogeny into a scaled (0–1) variance–covariance matrix (Σ), with covariances defined by shared branch lengths of species pairs, from the root to their most recent ancestor⁵⁰. We additionally allowed correlations to vary according to the phylogenetic signal (λ) of climate parameters, fitted as a multiple of the off-diagonal values of Σ ³⁹. Values of λ near 1 fit a Brownian motion model of evolution, while values near zero indicate phylogenetic independence. The phylogenetic variance–covariance matrix was calculated using the 'vcv.phylo' function of the ape library⁵¹. The resulting posterior distributions are a direct statement of the influence of spring photoperiodism on species-level differentiation in climate characteristics (that is, species' max. winter duration, median temp. variability, and max. temp. seasonality). Effective posterior means for the respective relationships are shown in Fig. 1a.

To parameterize our models we used the JAGS⁵² implementation of Markov chain Monte Carlo methods in the R package R2JAGS⁵³. We ran three parallel MCMC chains for 20,000 iterations with a 5000-iteration burn-in and evaluated model convergence with the Gelman and Rubin⁵⁴ statistic. Noninformative priors were specified for all parameter distributions, including normal priors for α and β coefficients (fixed effects; mean = 0; variance = 1,000), uniform priors between 0 and 1 for λ coefficients, and gamma priors (rate = 1; shape = 1) for the precision of random effects of phylogenetic autocorrelation, based on de Villemereuil and colleagues³⁹.

In Table 1 we summarize the statistical results. All statistical analyses relied on R 3.2.2 (ref. 55).

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Erratum: Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants

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Nature Climate Change <http://dx.doi.org/10.1038/nclimate3138> (2016); published online 17 October 2016; corrected online 14 November 2016.

In the version of this Letter originally published, the last sentence should have read ‘Therefore, photoperiod may be expected to constrain climate-driven shifts in spring leaf unfolding only at lower latitudes’. This error has been corrected in all versions of the Letter.