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1 **Day length unlikely to constrain climate-driven shifts in leaf-out times of northern**
2 **woody plants**
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21
22 **The relative roles of temperature and day length in driving spring leaf unfolding are**
23 **known for few species, limiting our ability to predict phenology under climate**
24 **warming[1,2]. Using experimental data, we assess the importance of photoperiod as a leaf-**
25 **out regulator in 173 woody species from throughout the Northern Hemisphere, and we**
26 **also infer the influence of winter duration, temperature seasonality, and inter-annual**
27 **temperature variability. We combine results from climate- and light-controlled**
28 **chambers with species' native climate niches inferred from geo-referenced occurrences**
29 **and range maps. Of the 173 species, only 35% relied on spring photoperiod as a leaf-out**
30 **signal. Contrary to previous suggestions, these species come from lower latitudes,**
31 **whereas species from high latitudes with long winters leafed out independent of**
32 **photoperiod, supporting the idea that photoperiodism may slow or constrain poleward**
33 **range expansion[3]. The strong effect of species' geographic-climatic history on**
34 **phenological strategies complicates the prediction of community-wide phenological**
35 **change.**
36
37   Understanding the environmental triggers of leaf out and leaf senescence is essential
38 for forecasting the effects of climate change on temperate zone forest ecosystems[2,3,4].
39 Correlation analyses suggest that warmer springs are causing earlier leaf emergence, leading
40 to an extended growing season[5,6] and increased carbon uptake[7]. A continuing linear response
41 to spring warming, however, is not expected because stimuli, such as photoperiod[1,8-10] and
42 chilling[11-13], additionally trigger dormancy release.
43   Photoperiod limitation refers to the idea that plant sensitivity to day length protects
44 leaves against frost damage by guiding budburst into a safe time period[1]. Experiments have
45 shown that day length-sensitive species react to spring temperatures only once day length
46 increases[10]. Because day length will not change under climate warming, photosensitive
47 species may be less responsive to warmer temperatures[1,9,14,15].
48   Experiments addressing the relative importance of photoperiod *versus* temperature
49 for dormancy release have been carried out in about 40 species[8-12], and among them a few
50 species, most strikingly *Fagus sylvatica*, exhibited strong photoperiodism[8-10,12,16-19]. Results

51 are often equivocal, perhaps in part reflecting experimental difficulties in adequately
52 modifying day length when working with trees[9,11,12,20,21].
53   Why species differ in their relative reliance on photoperiod and spring temperature as
54 leaf-out signals is largely unknown. This prevents the development of mechanistic models for
55 predicting spring phenology under climate warming. The need to understand spring
56 phenology in its geographic-climatic context is highlighted by studies suggesting that
57 phenological strategies in long-lived woody species have evolved as adaptations to the
58 climate in a species' native range[22-25]. A common garden study of 495 woody species from
59 different climates showed that species native to warmer climates flush later than species
60 native to colder areas, but did not investigate whether this was due to different species relying
61 on temperature or photoperiod[25]. If photoperiod indeed provides a safeguard against leafing
62 out too early[1,9], photoperiodism should be especially important (i) in regions with
63 unpredictable frost events, i.e., high inter-annual variability in spring temperatures (here
64 called 'high temperature variability' hypothesis)[26] and (ii) in regions with oceanic climates in
65 which temperature is a less reliable signal because the change between winter and spring
66 temperatures is less pronounced ('oceanic climate' hypothesis)[1]. A third hypothesis is that
67 photoperiodism mirrors species' latitudinal occurrence because day-length seasonality
68 increases towards the poles, and day length thus provides an especially strong signal at higher
69 latitudes ('high latitude' hypothesis)[3]. Of these predicted correlates of photoperiod as a spring
70 leaf-out signal, only the 'oceanic climate' hypothesis has been tested[12], with no significant
71 relationship found.
72   We set out to (i) investigate the relative effect of photoperiod on leaf-out timing in
73 species from different winter temperature regimes ('high latitude' hypothesis), temperature
74 seasonality regimes ('oceanic climate' hypothesis), and between-year spring temperature
75 variability ('high temperature variability' hypothesis) [Fig. 1a], and to (ii) test if photoperiod-
76 sensitive species react less to spring temperatures than do photoperiod-insensitive species. We
77 used 173 species (in 78 genera from 39 families) from the Northern Hemisphere grown in a
78 mid-latitude (48°N) European Botanical Garden and modified the day length experienced by
79 buds on twigs cut from these species at three different times and hence chilling levels (see
80 Methods and Supplementary Fig. 1). To assign the species to their climate ranges, we queried
81 geo-referenced occurrence data against climate grids for winter duration (Fig. 1b),
82 temperature seasonality (T seasonality), and inter-annual spring temperature variability (T
83 variability). In addition, each species was also assigned to its predominant Koeppen-Geiger
84 climate type[25]. To achieve our second aim, we tested for correlations between species'
85 photoperiodism (as inferred from our experiments on leaf-out in twigs under different light
86 regimes) and their leaf-out behaviour *in situ* (as inferred from multi-annual leaf-out
87 observations on intact trees; Fig. 2).
88   With low chilling (twig-collection in December), 61 (35%) of the 173 species leafed
89 out later under short day conditions than under long days, while the remaining 112 species did
90 not react differently regardless of short and long days. Increased chilling reduced species'
91 sensitivity to photoperiod: Under intermediate chilling conditions (twig-collection in
92 February), 16 (9%) of the 173 species showed delayed budburst under short days. Under long
93 chilling conditions (twig-collection in March), only 4 (2%) species, namely *Fagus crenata, F.*
94 *orientalis, F. sylvatica,* and *Carya cordiformis*, leafed out later under short days. Based on the
95 current results, constraints on the climate-warming-driven advance of leaf-out[15] likely will be
96 twofold in photosensitive species: (i) reduced winter chilling *per se* will cause plants to
97 require more forcing in the spring and (ii) reduced chilling additionally will cause higher
98 photoperiod requirements. The latter constraint will become more significant, as springs will
99 arrive ever earlier (i.e., at ever shorter photoperiods) in the future.
100   Where do the species that rely on photoperiodism as a leaf-out trigger come from?
101 Our data reject all three suggested correlates of photoperiodism (i.e., the 'high latitude', 'high

102   temperature variability', and 'oceanic climate' hypotheses) and instead reveal that it is the
103   species from shorter winters (i.e., lower, not higher latitudes) that rely on photoperiodism (P
104   < 0.05; Table 1; Fig. 1). Of the 173 species, the 22 that come from regions with long winters
105   (> 7 months with an average temperature below 5°C), such as alpine and subarctic regions are
106   photoperiod-insensitive, while the 14 species with high photoperiod requirements are
107   restricted to regions with shorter winters (not exceeding six months with an average
108   temperature below 5°C; Fig. 1). In a hierarchical Bayesian model that controlled for possible
109   effects of shared evolutionary history and species' growth height, winter duration remained
110   negatively correlated with species' photoperiodism (Fig. 1a). Analyses that used the
111   Koeppen-Geiger climate classification yielded the same results as analyses that used the
112   climate grids, namely that most photoperiod-sensitive species are native to warm climates
113   with mild winters (Supplementary Fig. 2).
114   Why is there a negative correlation between species' reliance on day length as a leaf-
115   out signal and the winter duration in their native ranges? There are two possible mechanisms
116   on how photoperiod perception in plants may interact with forcing requirements: (i) Either
117   plants need to reach a fixed photoperiod threshold before they perceive forcing temperatures
118   or (ii) forcing requirements gradually decrease with increasing photoperiod. The first
119   mechanism would require that plants from regions with long winters have higher photoperiod
120   thresholds because in these areas days are already long (>14-h) when minimum temperatures
121   cross the freezing threshold (see also Way & Montgomerey[21]: Fig. 1). The second mechanism
122   would require that the relative use of photoperiod as a budburst regulator decreases towards
123   regions with long winters because days in spring become long before the risk of encountering
124   freezing temperatures has passed. Experimental results from *Fagus sylvatica* show a gradual
125   response to photoperiod independent of the latitudinal origin of the experimental plants:
126   Forcing requirements decrease with increasing day length up to about 16-h, with further
127   increase of daylight having little additional effect[8,10]. This supports the second mechanism.
128   The second mechanism is also supported by *F. sylvatica* leafing out earlier at regions with
129   long winter duration than photo-insensitive species and therefore operating at a smaller
130   'safety margin' against late frosts[27,28]. The hypothesis that Northern woody species evolved
131   photoperiod-independent leaf-out strategies because at high latitudes day length increase in
132   spring occurs too early for frost to be safely avoided needs to be tested with further
133   experiments addressing the physiological mechanisms of photoperiod perception in different
134   taxonomic groups.
135   That photosensitive species are restricted to regions with relatively short winters
136   supports the idea that photoperiodism may slow or constrain poleward range expansion[3]. With
137   a warming climate, however, the last day with night frost occurs ever earlier (in Germany,
138   between 1955 – 2015, the last frost on average advanced by 2.6 days per decade;
139   Supplementary Fig. 3), and photoperiod-sensitive species might do well at higher latitudes or
140   elevations.
141   The leaf-out dates showed that those species with high photoperiod requirements had
142   lower between-year variance in leaf-out dates than species lacking photoperiodism.
143   Accordingly, in photoperiod-sensitive species, accumulated thermal time until budburst
144   showed greater variation among years than that of photoperiod-insensitive species ($P < 0.01$;
145   Fig. 2). Leaf unfolding in species that rely on day length is thus less responsive to temperature
146   increase, and in these species photoperiod will constrain phenological responses to climate
147   warming, with possible consequences for carbon gain, the local survival of populations and
148   community composition[2,4]. The extent to which species' phenological strategies are
149   influenced by their climatic histories highlights the need for a broader geographic sampling in
150   global-change studies[29].
151   Our results do not support previous ideas about phenological strategies in temperate
152   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, many species – mostly from lineages with a warm-temperate or subtropical background, e.g., *Fagus*[30] – additionally rely on photoperiodism. Therefore, only in regions with shorter winters, photoperiod may be expected to constrain climate change-driven shifts in the phenology of spring leaf unfolding.

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231
232 **Acknowledgements**

239
240 **Author contributions**

241 C.M.Z. and S.S.R. designed the study. C.M.Z. conducted the experiments and leaf-out
242 observations. C.M.Z. and B.M.B. performed the analyses. C.M.Z. and S.S.R. led the writing
243 with inputs from the other authors.
244
245 **Additional information**
246 Supplementary information is available in the online version of the paper. Reprints and
247 permissions information is available online at www.nature.com/reprints. Correspondence and
248 requests for materials should be addressed to C.M.Z.
249
250 **Competing financial interests**
251 The authors declare no competing financial interests.
252
253
254

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, c. 40 cm-long twigs were collected at three different dormancy stages (on 21 Dec, 10 Feb, and 21 Mar) 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 (~100 μmol s^{-1} 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), re-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 microg/l; Sigma–Aldrich, Germany)[9,10]. We used 60 replicate twigs per species (10 twigs per treatment, 3x2 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, i.e. the proportion of buds flushed over the total number of buds on the twigs, was not recorded. Treatment effects (long vs. short days at three different dormancy stages) on the response variable (accumulated degree days >0°C outside and in climate chamber from 21 Dec 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 Dec (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 Dec 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 Feb (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 degree 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 study[12] that used the same experimental approach to detect species' photoperiod requirements, allowing us to apply the same definition of photoperiod categories to their 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, viz. 2012–2015, available from the Munich botanical garden. The 2012 and 2013 data come from our earlier study[25], and the same individuals were monitored again in 2014 and 2015. A species' leaf-out date was

306   defined as the day when three branches on a plant had leaves pushed out all the way to the
307   petiole. Thermal requirements of species were calculated as the sum of growing-degree days
308   from 1 January until day of leaf-out using a base temperature of 0°C. Species names are given
309   in Appendix Table S1. To test if species with photoperiod requirements show lower variation
310   in leaf-out and higher variation in thermal requirements among years than do photo-
311   insensitive species, we applied difference-of-means tests (Fig. 2). Because vectors were not
312   normally distributed we conducted Kruskal–Wallis H tests with a *post-hoc* Kruskalmc
313   analysis (multiple comparison after Kruskal–Wallis)[32].

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

323   *Species ranges and climate characteristics*
324   To obtain species' native distribution ranges, we extracted georeferenced locations from the
325   Global Biodiversity Information Facility (GBIF; http://www.gbif.org/), using the dismo R-
326   package[33]. Cleaning scripts in R were used to filter reliable locations and exclude species with
327   unreliable records, using the following criteria: (i) only records from a species' native
328   continent were included; (ii) coordinate duplicates within a species were removed; (iii)
329   records based on fossil material, germplasm, or literature were removed; (iv) records with a
330   resolution >10 km were removed; and (v) only species with more than 30 georeferenced
331   GBIF records within their native continent were included. After applying these filtering
332   criteria, we were left with distribution data for 144 of the 173 species.
333   We then derived species-specific climate ranges from querying georeferences against
334   climate grids of three bioclimatic variables: T seasonality (BIO7; Temperature difference
335   between warmest and coldest month), T variability (inter-annual spring T variability
336   calculated as the standard deviation of March, April, and May average T from 1901 – 2013),
337   and winter duration (defined as the numbers of months with an average T below 5°C). A grid
338   file for the winter duration was based on global monthly weather data available at
339   www.worldclim.org[34], from which we calculated the number of months with an average
340   temperature below 5°C for the global land surface (see Fig. 1b). T seasonality was based on
341   gridded information (2.5-arc minute spatial resolution data) about the annual temperature
342   range derived from the WorldClim dataset (bioclim7)[34]. T variability was calculated as the
343   standard deviation of spring (March, April, and May) average temperatures from 1901 to
344   2013 (see Supplementary Fig. 5). Data on monthly average temperatures during this period
345   were available from the CRU database (5-arc minute spatial resolution data)[35]. For each
346   bioclimatic variable we determined three species-specific measures: the upper and lower
347   limits and the median which were obtained from the bioclimatic data covering a species range
348   at the 0.95, 0.05, and 0.50 quantile, respectively.
349   As an alternative approach that allowed us to infer the predominant climate of 171 of
350   the 173 species, we used the Koeppen-Geiger system[36]. Information on species-specific
351   Koeppen-Geiger climate types was available from our earlier study[25] in which each species'
352   natural distribution was determined using information from range maps and range
353   descriptions: http://linnaeus.nrm.se/flora/welcome.html and
354   http://www.euforgen.org/distribution-maps/ for the European flora,
355   http://plants.usda.gov/java/ and http://esp.cr.usgs.gov/data/little/ for North America, and
356   http://www.efloras.org for Asia. As a proxy for a species' native winter temperature regime, it

357   was scored for the first Koeppen-Geiger letter (D-climate = coldest month average below -
358   3°C, C-climate = coldest month average above -3°C). For species' summer temperature, the
359   third Koeppen-Geiger letter was used (a-climate = warmest month average above 22°C with
360   at least four months averaging above 10°C; b-climate = warmest month average below 22 °C
361   but with at least four months averaging above 10 °C, c-climate = warmest month average
362   below 22°C with three or fewer months with mean temperatures above 10 °C). The second
363   letter in the Koeppen system refers to precipitation regime and was disregarded in the
364   analyses. Species were scored for the predominant conditions in their native range; for
365   example, a species occurring in 40% Cfa, 30% Dfa, and 30% Dfb climates would be scored as
366   "D" and "a".
367
368   *Data analysis*
369   The quantiles (0.05, 0.5, and 0.95) of each climate parameter (winter duration, T
370   seasonality, and T variability) were highly correlated among each other (Pearson correlation,
371     $r > 0.5$). To avoid multicollinearity in our models, we included only one quantile for each
372   climate parameter. For each climate parameter, we kept the quantile that gave the best
373   prediction of species-level variation in photoperiodism. We fitted univariate logistic
374   regression models to our data and, for each climate parameter, kept the variable with the
375   lower Akaike information criterion (AIC), i.e., we kept the 0.95 quantile of winter duration,
376   0.95 quantile of T seasonality, and 0.5 quantile of T variability. We tested for
377   multicollinearity among the retained predictor variables by using variance inflation factors
378   (VIF). All VIF were smaller than 5, indicating sufficient independence of the predictor
379   variables. ANOVA and ordinal logistic regression (OLR) were used to separately test for
380   correlations among predictor variables and species-specific photoperiod sensitivity (see Table
381   1, Fig. 1c, and Supplementary Fig. 6). To examine the relative contribution of each climate
382   variable to explain species-specific photoperiod sensitivity, we applied multivariate OLR,
383   random forest[37,38], and hierarchical Bayesian models. The hierarchical Bayesian models
384   allowed us to control for phylogenetic signals in our data (Supplementary Fig. 7) using the
385   Bayesian phylogenetic regression method[39] (next section). We analysed correlations between
386   species' native climates as inferred from the Koeppen-Geiger system[36] and their photoperiod
387   requirements by applying contingency analyses (Fisher's test) and hierarchical Bayesian
388   models (next section).
389
390   *Data analysis including the phylogenetic structure*
391   To account for possible effects of shared evolutionary history, we applied hierarchical
392   Bayesian models. The phylogenetic signal in trait data was estimated using Pagel's λ[40], with
393   the 'phylosig' function in the R package 'phytools' v0.2-1[41]. The phylogenetic tree for our
394   173 target species came from Panchen et al.[42] and was assembled using the program
395   Phylomatic[43] (Supplementary Fig. 7). Its topology reflects the APG III phylogeny[44], with a
396   few changes based on the Angiosperm Phylogeny Website[45]. We manually added about 10
397   missing species to the tree. Branch lengths of the PHYLOMATIC tree are adjusted to reflect
398   divergence time estimates based on the fossil record[46,47]. Besides controlling for phylogenetic
399   signal λ[40] of traits, the hierarchical Bayesian approach allowed us to control for possible
400   effects of growth height on species-level photoperiod requirements and climate ranges, by
401   including species' mature growth height as a fixed effect in the models. Mature growth height
402   is a significant functional trait that is related to species' growth phenology[42] as well as climate
403   ranges[48]. Slope parameters across traits are estimated simultaneously without concerns of
404   multiple testing or P-value correction.
405   To determine which climate parameter best explains species-level differentiation in
406   photoperiodism, we treated species' photoperiod requirements (ordinal data) as a dependent
407   variable. Three climate variables (species-specific maximum winter duration, 0.95 quantile;

408   max. T seasonality; 0.95 quantile; and median T variability, 0.5 quantile) and species' mature

409   growth height were used as predictor variables (Table 1 and Supplementary Fig. 8).

410   Regression components are of the form:

411   ordered logit($photoperiod_i$) = $\beta_{\text{max winter duration}}$ x *max winter duration$_i$*

412   + $\beta_{\text{median T variability}}$ x *median T variability$_i$*

413   + $\beta_{\text{max T seasonality}}$ x *max T seasonality$_i$*

414   + $\beta_{\text{growth height}}$ x *growth height$_i$*

415   β refers to the estimated slopes of the respective variable. In an alternative model, we

416   used species' Koeppen winter and summer temperature types and mature growth height as

417   predictor variables (Supplementary Fig. 9):

418   ordered logit($photoperiod_i$) = $\beta_{\text{winter temp}}$ x *winter temp$_i$*

419   + $\beta_{\text{summer temp}}$ x *summer temp$_i$*

420   + $\beta_{\text{growth height}}$ x *growth height$_i$*

421   These models do not statistically account for phylogenetic structure by allowing

422   correlations to vary according to the phylogenetic signal λ, because λ estimation is not

423   possible for ordinal (or logistic) models. To nevertheless account for data non-independence

424   due to shared evolutionary history of species (see Supplementary Fig. 7), we inserted genus

425   and family random intercept effects in the model. To examine relative effect sizes of predictor

426   variables, we standardized all variables by subtracting their mean and dividing by 2 SD before

427   analysis[49]. The resulting posterior distributions are a direct statement of the influence of each

428   parameter on species-level differentiation in photoperiod requirements. The effective

429   posterior means (EPM) for the relationships between winter duration, temperature seasonality,

430   and spring temperature variability and species-specific photoperiodism are shown in

431   Supplementary Fig. 8, and the EPMs for relationships between Koeppen-Geiger climates and

432   photoperiod requirements are shown in Supplementary Fig. 9.

433   The hierarchical Bayesian model strongly preferred winter duration to T seasonality

434   and T variability as an explanatory variable for species' photoperiodism. Likewise, the model

435   using the Koeppen system preferred the Koeppen winter climate to the summer climate as a

436   predictor of species' photoperiodism. To validate these results, instead of treating

437   photoperiodism as dependent variable, we tested two other models. The first compared the

438   distribution of covariates (max. winter duration, max. T seasonality, and median T variability)

439   between the different photoperiod categories. Species' values for max. winter duration, max.

440   T seasonality, and median T variability can be treated as continuous characters, which

441   allowed us to incorporate phylogenetic distance matrices to control for shared evolutionary

442   history of species (Pagel's λ values: max. winter duration = 0.40; max. temp. seasonality =

443   0.39; median temp. variability = 0.26; see inset Fig. 1a). This model included three dependent

444   variables that were normally distributed with mean μ, variance σ^2, and correlation structure Σ

445   (Fig. 1a):

446   *max winter duration$_i$* ~ $N(\mu_{\text{max winter duration } i},\ \sigma^2_{\text{max winter duration}}, \Sigma)$

447   *median T variability$_i$* ~ $N(\mu_{\text{median T variability } i},\ \sigma^2_{\text{median T variability}}, \Sigma)$

448   *max T seasonality$_i$* ~ $N(\mu_{\text{max T seasonality } i},\ \sigma^2_{\text{max T seasonality}}, \Sigma)$

449   Regression components are of the form:

450         $\mu_{\text{max winter duration } i}$ = $\alpha_1 + \beta_{\text{winter dur}}$ x *photoperiodism$_i$* + β_1 x *mature growth height$_i$*

451         $\mu_{\text{median T variability } i}$ = $\alpha_3 + \beta_{\text{T variability}}$ x *photoperiodism$_i$* + β_2 x *mature growth height$_i$*

452          $\mu_{\text{max T seasonality } i}$ = $\alpha_2 + \beta_{\text{T seasonality}}$ x *photoperiodism$_i$* + β_3 x *mature growth height$_i$*

453   The other model, based on species' Koeppen climate letters as outcome, included two binary

454   dependent variables that capture whether species are native to regions with mild or cold

455   winters (KW; Koeppen C or D climate) and warm or cold summers (KS; Koeppen a or b

456   climate) [Supplementary Fig. 2]:

457   *winter temp* ~ $Bernoulli(WT_i)$

458   *summer temp* ~ $Bernoulli(ST_i)$

459 Regression components are of the form:

$$\text{logit}(WT_i) = \alpha_1 + \beta_1 \times photoperiodism_i + \beta_3 \times maximum\ growth\ height_i$$

$$\text{logit}(ST_i) = \alpha_2 + \beta_2 \times photoperiodism_i + \beta_4 \times maximum\ growth\ height_i$$

462 The term α refers to the intercept, β to the estimated slopes of the respective variable
463 (photoperiodism and maximum growth height), and max winter duration, max temp
464 seasonality, and median temp variability refer to species values of the respective climate
465 parameters. The phylogenetic structure of the data was incorporated in the hierarchical
466 Bayesian model using the Bayesian phylogenetic regression method of de Villemereuil et
467 al.[39], by converting the 173-species ultrametric phylogeny into a scaled (0–1) variance–
468 covariance matrix (Σ), with covariances defined by shared branch lengths of species pairs,
469 from the root to their most recent ancestor[50]. We additionally allowed correlations to vary
470 according to the phylogenetic signal (λ) of climate parameters, fitted as a multiple of the off-
471 diagonal values of Σ[39]. Values of λ near 1 fit a Brownian motion model of evolution, while
472 values near zero indicate phylogenetic independence. The phylogenetic variance–covariance
473 matrix was calculated using the 'vcv.phylo' function of the ape library[51]. The resulting
474 posterior distributions are a direct statement of the influence of spring photoperiodism on
475 species-level differentiation in climate characteristics (i.e., species' max. winter duration,
476 median temp. variability, and max. temp. seasonality). Effective posterior means for the
477 respective relationships are shown in Fig. 1a.
478 To parameterize our models we used the JAGS[52] implementation of Markov chain
479 Monte Carlo methods, in the R package R2JAGS[53]. We ran three parallel MCMC chains for
480 20,000 iterations with a 5000-iteration burn-in and evaluated model convergence with the
481 Gelman and Rubin[54] statistic. Noninformative priors were specified for all parameter
482 distributions, including normal priors for α and β coefficients (fixed effects; mean = 0;
483 variance = 1000), uniform priors between 0 and 1 for λ coefficients, and gamma priors (rate =
484 1; shape = 1) for the precision of random effects of phylogenetic autocorrelation, based on de
485 Villemereuil et al.[39].
486 In table 1 we summarize the statistical results. All statistical analyses relied on R
487 3.2.2[55].

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Figure legends

Figure 1 | Relationship between species' spring photoperiodism and the maximum winter duration in their native ranges. a, Coefficient values (effective posterior means β and 95% credible intervals) for the effect of spring photoperiodism on species' 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 panel 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).

Figure 2 | 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 SD 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 ± 95% confidence interval for each group. Thermal time was calculated as the sum of growing-degree days from 1 Jan 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 (*$P < 0.05$, **$P < 0.01$).

611 **Table 1 | Global relationships between species' photoperiod requirements and duration**
612 **of winter, inter-annual spring temperature variability (T variability), and T seasonality**
613 **in their native range for 144 temperate woody species.** Five comparative measures were
614 used: the F value from univariate ANOVA, Akaike weights from bivariate regressions using
615 ordinal logistic regression (OLR) models, parameter estimates and 95% confidence intervals
616 (CI) based on multivariate OLR models, mean decrease in accuracy values (MDA) from
617 random forest analysis, and coefficient values [effective posterior means (EPM) and 95% CIs]
618 from a hierarchical Bayesian (HB) model controlling for phylogenetic autocorrelation and
619 species' maximum growth height. For each single climatic parameter we initially considered
620 the upper limit (0.95-quantile), median (0.5 quantile), and lower limit (0.05-quantile) across
621 each species' range and kept the variable that yielded the lower Akaike information criterion
622 (AIC) according to OLR models (i.e. we kept the 0.95 quantile for winter duration and T
623 seasonality, and the 0.5 quantile for T variability). Sample size: No photoperiod requirements
624 = 88 species; Low = 42 species; High = 14 species. *$P < 0.05$, **$P < 0.01$.
625

	ANOVA	**OLR**	**Multiv. OLR**	**Random forest**	**HB model**
	F values	Weight$_{AIC}$	Estimate ± CI	MDA	EPM ± CI
Winter duration	$F(1, 142) = 9.5$**	0.90**	-0.47 ± 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

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