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## LETTER

# Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change

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### Abstract

A well-timed phenology is essential for plant growth and reproduction, but species-specific phenological strategies are still poorly understood. Here, we use a common garden approach to compare biannual leaf-out data for 495 woody species growing outdoors in Munich, 90% of them not native to that climate regime. For three species, data were augmented by herbarium dates for 140-year-long time series. We further meta-analysed 107 temperate-zone woody species in which leaf-out cues have been studied, half of them also monitored here. Southern climate-adapted species flushed significantly later than natives, and photoperiod- and chilling-sensitive species all flushed late. The herbarium method revealed the extent of species-specific climate tracking. Our results forecast that: (1) a northward expansion of southern species due to climate warming will increase the number of late flushers in the north, counteracting documented and expected flushing time advances; and (2) photoperiod- and chilling-sensitive woody species cannot rapidly track climate warming.

### Keywords

Chilling, forcing, leaf-out, phenology, photoperiod, temperature.

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## INTRODUCTION

Understanding, and hence being able to predict, plant phenological events, such as leaf-out, flowering, fruiting and leaf senescence, is essential for agriculture and forestry, and is the basis for forecasting how these processes may change with a changing climate. In the Northern Hemisphere, phenological monitoring has focused on spring phenology, especially flushing and flowering (Fitter *et al.* 1995; Sparks & Carey 1995; Menzel 2000; Wolkovich *et al.* 2012; Mazer *et al.* 2013). While the signals and physiological mechanisms triggering dormancy release are little understood, it is clear that in the temperate zones they involve spring temperatures ('forcing'), photoperiod (day length relative to night length) and preceding periods of chilling (Heide 1993a,b; Körner 2006; Ghelardini *et al.* 2010; Polgar & Primack 2011; Basler & Körner 2012; Laube *et al.* 2014; Polgar *et al.* 2014). Because spring temperatures vary strongly from year to year, sensitivity to photoperiod protects plants from the potentially fatal consequences of simply tracking temperatures (Körner & Basler 2010). In long-lived species, photoperiodism is a population-level trait that helps stabilise dormancy release, while temperature signals play a modulating role (Körner & Basler 2010).

Because species' reliance on photoperiod and/or temperature thresholds evolved over evolutionary time, it is difficult to predict how the phenology of plant communities will change with the ongoing climate warming and its accompanying floristic change (already seen at mid-elevations: Peñuelas & Boada 2003; Lenoir *et al.* 2010). Warming springs are advancing bud break in species relying entirely or mostly on temperature cues (Menzel *et al.* 2006), but for other species

the roles of photoperiod and perhaps unmet chilling requirements as winters become shorter, remain controversial (Heide 1993b; Myking & Heide 1995; Caffarra & Donnelly 2011; Vitasse *et al.* 2011; Laube *et al.* 2014; Polgar *et al.* 2014). So far, leaf-out phenology has been studied in a tiny proportion of the World's woody species, and many potentially important factors, such as the precipitation regime are rarely analysed. For those species for which there are data, analyses have focused on bifactorial correlations, although twig-cutting experiments are beginning to add much-needed experimental insights (Heide 1993a,b; Basler & Körner 2012; Laube *et al.* 2014; Polgar *et al.* 2014).

One approach for finding out species' phenological strategies (short of experiments) is to study individuals outside the native range, for example, in common gardens. As long as the individuals are acclimated but had no chance for evolutionary adaptation, their leaf-out times will reflect their native thresholds for chilling, forcing and photoperiod. Depending on which species were included, the approach would also allow predicting how the phenology of a community may change under floristic change. Unexpectedly, such a 'botanical garden approach' in which phenological strategies would be grouped by species' native biomes does not seem to have been used. In disregarding evolutionary adaptation, the approach differs from analyses of wide-ranging species' phenology along N-S gradients as that of Borchert *et al.* (2005), who studied bud break in some 40 species of trees and shrubs at 10 locations ranging from 44°N south to 10°N, to investigate how far south temperature controls leaf-out. While temperature and photoperiodic regimes both change with latitude, they do not do so exactly in parallel because of altitude, landscape topology, proximity to large water bodies and the earth's

angle relative to the sun. The rule of 1 °C increase in temperature leading to a 5- to 7-day advance in bud break time (Menzel & Fabian 1999; Chmielewski & Rötzer 2001) therefore does not hold at lower latitudes (Borchert *et al.* 2005).

Here, we use biannual leaf-out data for almost 500 woody species growing in the botanical garden of Munich to compare leaf-out strategies among species originating from different temperature, precipitation and photoperiod regimes. Climate data came from the recently revised Köppen–Geiger system (Kottek *et al.* 2006; Peel *et al.* 2007), which is available on a 0.5-degree latitude/longitude grid with monthly resolution from the Climatic Research Unit of the University of East Anglia and the Global Precipitation Climatology Centre located at the German Weather Service. Of the monitored species, 90% are not native to Germany. Instead, they come from warmer, more seasonal, or colder, more or less humid climates. Many do not set fruit, and there is no natural reproduction of these woody species in the garden, which was laid out and planted 100 years ago (most trees were planted much later than that).

The first hypothesis we wanted to test, using biannual leaf-out data for 495 species (the ‘botanical garden approach’) was that species adapted to more southern climates leaf out later than native species. This expectation was based on southern species probably requiring higher heat sums than northern species (Sanz-Perez *et al.* 2009; for Mediterranean oak species; Olson *et al.* 2013; for *Populus balsamifera* populations), which in Munich might be reached later than in their native regions. The opposite expectation has recently been put forward by Polgar *et al.* (2014), who suggest that trees and shrubs from more southern locations, which might have lower chilling requirements, would be able to enter the increasing ‘early season niche’ which is expected from global climate warming. The second hypothesis we wanted to test with the garden data was that photoperiod- and chilling-sensitive species leaf out later than purely spring temperature-reliant species. This was based on the assumption that sensitivity to these cues provides a safety mechanism against flushing during early warm spells and thus helps avoid damage to young leaves by late freezing events (Körner 2006; Körner & Basler 2010). Therefore, we conducted a meta-analysis of woody species in which phenological cues have been studied, including many also monitored in our study.

Dates on herbarium specimen labels have been widely used to infer past flowering times (Borchert 1996; Primack *et al.* 2004; Lavoie & Lachance 2006), but leaf-out dates from herbaria have never been used. Such longer time series would be valuable to compare leaf-out in particular years in the past as long as one also had the relevant temperature records. To explore this approach, we decided to include leaf-out data from herbarium collections for three species, the phenological strategies of which differ, namely, Norway maple (*Acer platanoides*), hornbeam (*Carpinus betulus*) and beech (*Fagus sylvatica*). The long-term (up to 140 years) records also allow testing whether decreased periods of chilling during the winter lead to an increase in the heat sum required to induce budburst. This has been inferred from cut twigs placed in climate chamber (Heide 1993a,b; Ghelardini *et al.* 2010; Caffarra & Donnelly 2011; Laube *et al.* 2014; Polgar *et al.* 2014) and

from the behaviour of trees along an altitudinal gradient, which served as a proxy for a changing climate (Vitasse & Basler 2013), but never *in situ*. Our study presents the first use of herbarium specimens for assessing long-term leaf-out times and the first use of a botanical garden to compare species-specific leaf-out patterns across species from many native biomes.

## MATERIAL AND METHODS

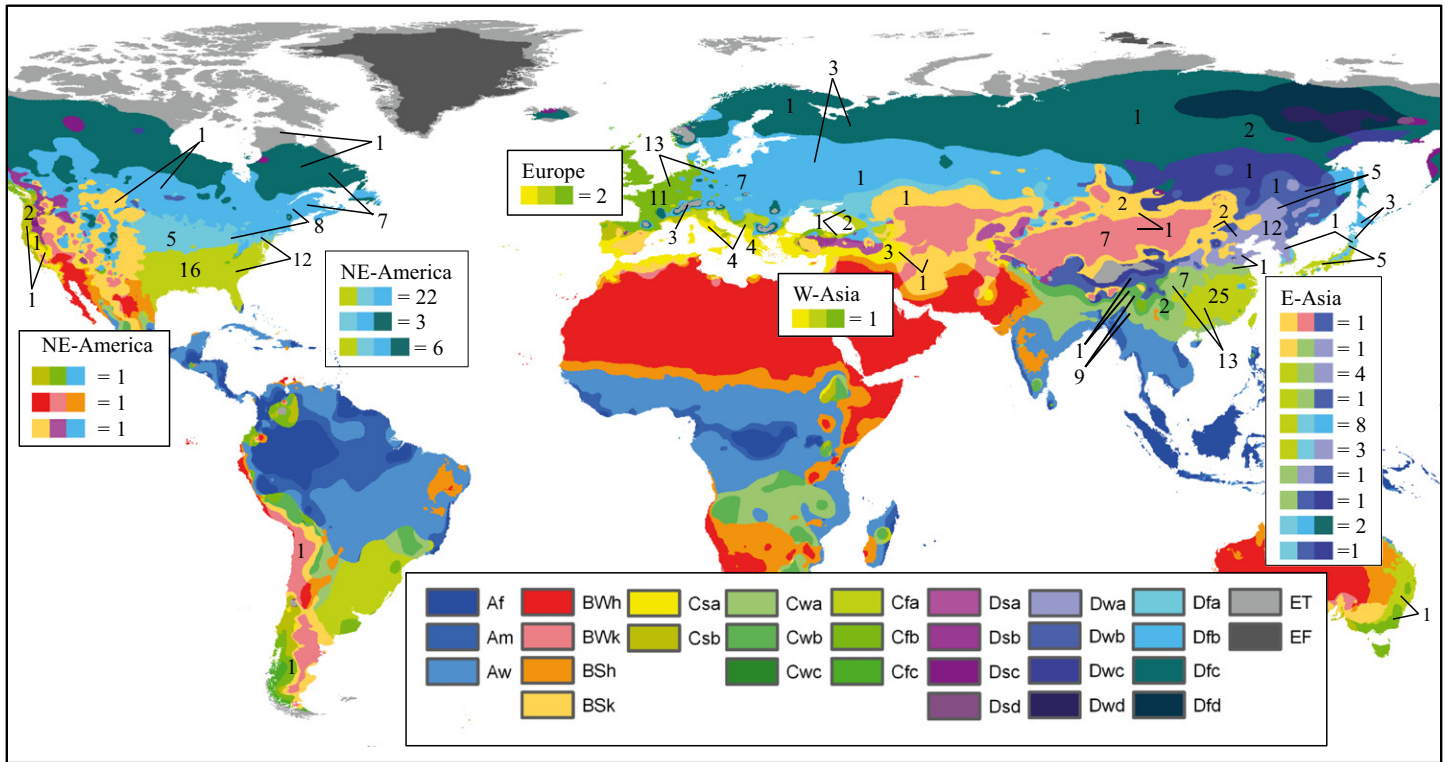
### Study site, species and climate data

The Munich Botanical Garden is located at 501 m a.s.l. and 48°09'45" N, 11°30'06" E. It opened in its current location in May 1914. Leaf-out (recorded as day of the year = DOY) of woody plant species growing permanently outdoors without winter protection was monitored twice a week, with 495 species observed in 2012 and 462 in 2013, because some species are no longer maintained in cultivation (Appendix Table S1). For the three species (*Acer platanoides*, *Carpinus betulus* and *Fagus sylvatica*) for which we inferred long-term data by using herbarium specimens (see below), we additionally observed the 2014 leaf-out dates. Following the International Phenological Gardens of Europe (IPGE 1960), the day when 3–4 branches on a plant had leaves pushed out all the way to the petiole was considered that species' leaf-out date. The monitoring included deciduous and evergreen shrubs, trees and vines in 61 families from 24 orders, with usually one individual per species. The geographic break-down of the 495 (2012) species is as follows: Northern Asia 5 species (1%), Eastern Asia 224 (45.3%), Southern Asia 10 (2%), Western Asia 17 (3.4%), Central Asia 7 (1.4%), Northern America 105 (21.2%), Southern America 2 (0.4%), Europe 77 (15.6%), Australia 1 (0.2%) and hybrids 47 (9.5%).

Daily mean temperatures from 18 stations between 300 and 650 m a.s.l. in the vicinity of Munich and 1 in the Nymphenburg district where the botanical garden is located (at 501 m) were downloaded from Deutscher Wetterdienst, Offenbach, Germany, via WebWerdis ([https://werdis.dwd.de/werdis/start\\_js\\_JSP.do](https://werdis.dwd.de/werdis/start_js_JSP.do)). They include daily mean temperatures between 1 November and 30 April from 1879 to 2014. Heat sums (= forcing time) were calculated as day degrees from 1 January to the date of leafing out, using 5 °C as the base temperature (see for instance Vitasse & Basler 2013). Chill days were calculated as days with mean air temperature < 5 °C between 1 November and leaf-out (Vitasse & Basler 2013; Laube *et al.* 2014).

### Native climate and phenological strategy assignments

To score species' native climates, we used the recently revised Köppen–Geiger system, which groups climates according to a region's seasonal precipitation and seasonal temperature, and is available as a GIS shape file and for use in GoogleEarth (Kottek *et al.* 2006; Peel *et al.* 2007; see <http://koeppen-geiger.vu-wien.ac.at> and <http://people.eng.unimelb.edu.au/mpeel/koppen.html>). It employs a three-letter system, in which the first letter indicates the so-called main climate, the second, the annual distribution of precipitation, and the third, temperature parameters (Fig. 1). The current climate of Munich is a



**Figure 1** The climate zones represented in the sample of woody species monitored in Munich (Köppen–Geiger map adapted from Peel *et al.* 2007). Numbers refer to the total numbers of species originating from the respective climate zone; numbers of species occurring in adjacent climate zones are shown next to lines to those and also in the five insets, one for each biogeographic region. Legend for the Köppen system shown in the bottom inset: Main climate: A = Tropical, B = Arid, C = Temperate, D = Cold, E = Polar; precipitation regime: f = Rainforest, m = Monsoon, w = Savanna, W = Desert, S = Steppe, s = Dry summer, w = Dry winter, f = fully humid; temperature regime: h = Hot, k = Cold, a = Hot summer, b = Warm summer, c = Cold summer, d = Very cold winter; T = Tundra, F = Frost.

Dfb climate, i.e. cold, fully humid, and with warm summers (Peel *et al.* 2007), and there is evidence of Munich currently shifting to a warmer Cfa or Cfb climate (Rubel & Kottke 2010).

To assign species to climates, we determined their natural distribution, using <http://linnaeus.nrm.se/flora/welcome.html>, <http://www.euforgen.org/distributionmaps.html>, <http://www.efloras.org> and <http://plants.usda.gov/java/>. Species occurring in more than one climate were scored for the climate predominant in >75% of their distribution area. Climates covering < 10% of a species' range were disregarded. Where none of two or more climate zones was predominant, we scored the species for only those Köppen letters common to all occupied climates. For example, a species occurring in climates Dfa, Dfb, Dw b would be scored only for the letter D (cold climate). Figure 1 shows the climate distribution of all species that could be scored. The 47 hybrids in our data sets were not assigned to a native climate zone. Correlations of species' leaf-out dates and accumulated heat sums in 2012 and 2013 with their native climate were analysed with difference-of-means tests (Fig. 2).

To compare phenological strategies of different temperate woody plants, we compiled information on species with known chilling, and/or photoperiod sensitivity from Heide (1993a,b), Borchert *et al.* (2005), Caffarra & Donnelly (2011), Basler & Körner (2012), Polgar *et al.* (2014) and Laube *et al.*

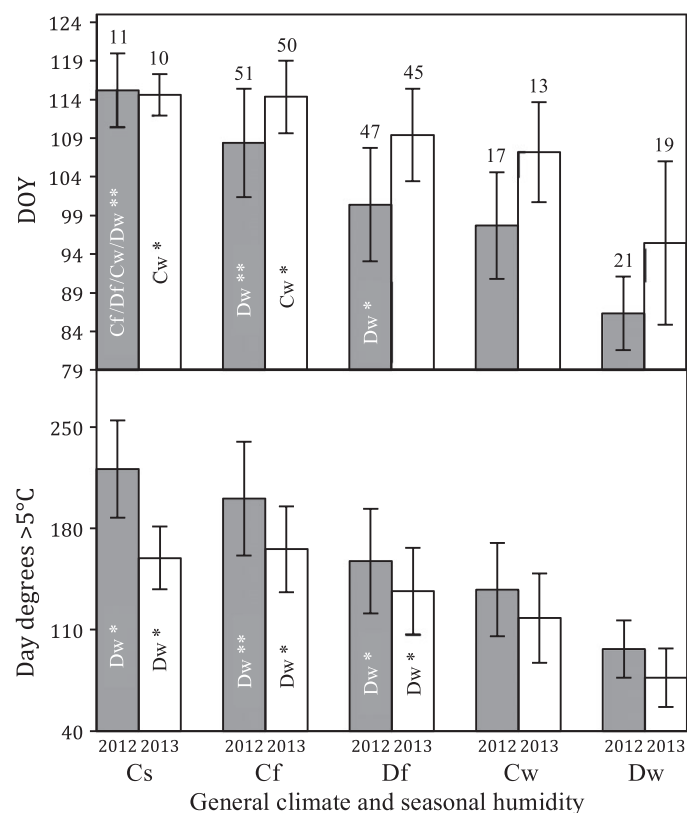
(2014). Difference-of-means tests were then used to test for correlations of leaf-out dates and accumulated heat sums in 2012 and 2013 with phenological strategies (Fig. 3).

All statistical analyses relied on R (R Core Team 2013), and Appendix Table S2 shows which tests were used on which data. An ANOVA was performed in case of homoskedastic, normally distributed vectors. In the case of two or more normally distributed heteroskedastic vectors, a Welch test or a Kruskal–Wallis H (KW) test showed if groups exhibited different means. A Wilcoxon or KW test was performed when a normal distribution could not be assumed. *Post-hoc* analyses: In the case of homoskedastic, normally distributed vectors, we used a Tukey–Kramer (TK) test. Dunnett's test (Dunnett–Tukey–Kramer pairwise multiple-comparison test adjusted for unequal variances and unequal sample sizes = DTK test; Dunnett 1980) was applied where variances were unequal. When vectors were not normally distributed, the Kruskal–Wallis method (multiple comparison after Kruskal–Wallis) was used (Siegel & Castellan 1988).

#### Herbarium data on leaf-out times over the past 141 years

Leaf-out dates of *Carpinus betulus*, *Fagus sylvatica* and *Acer platanoides*, three species that flower simultaneous with leaf-out, were inferred from label data on specimens in the Munich herbarium. Only specimens meeting the following





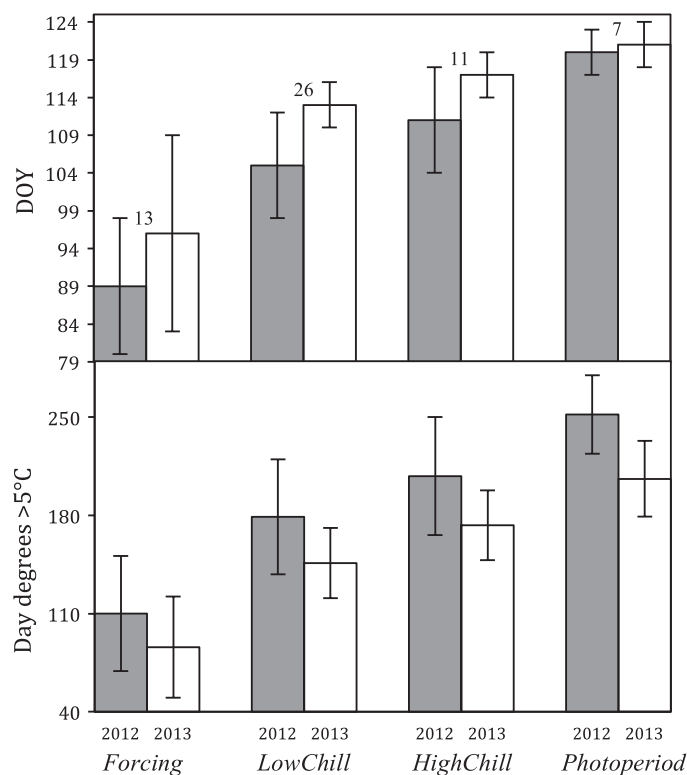
**Figure 2** Mean leaf-out dates ( $\pm$ SD) and heat sums ( $\pm$ SD) in 2012 ( $n = 147$ ) and 2013 ( $n = 137$ ) of woody species from different native climate types cultivated in Munich, with species grouped according to their main climate and seasonal precipitation regime (Cs = temperate climate with dry summer periods, Cf = temperate climate without dry seasons, Df = cold climate without dry seasons, Cw = temperate climate with dry winter periods and Dw = cold climate with dry winter periods; Fig. 1). Mean leaf-out dates (DOY) in 2012/2013: Cs climate 115/115; Cf 108/114; Df 100/109; Cw 98/107 and Dw 86/95. Letters within columns indicate which groups leafed out earlier/accumulated lower heat sums in the respective year (\*significant at  $P < 0.05$ ; \*\*significant at  $P < 0.001$ ). Sample sizes are shown above columns.

criteria were used: (1) not all leaves entirely enrolled; (2) leaves not yet full sized and (3) individuals collected in the vicinity of Munich between 300 m and 650 m a.s.l. Leaf-out dates were regressed on the respective year (Appendix Figure S6) and mean spring temperature (1 March until 30 April) between 1879 and 2014 (Fig. 4). For each herbarium specimen, we used climate data from weather stations close to the respective collection site and altitude (difference between weather station and collection site  $< 50$  m). For each of the three species, we calculated its accumulated heat sums and chill days (defined above). The relationship between heat sums required to induce budburst and accumulated number of chill days was analysed by linear regression models (Fig. 5).

## RESULTS

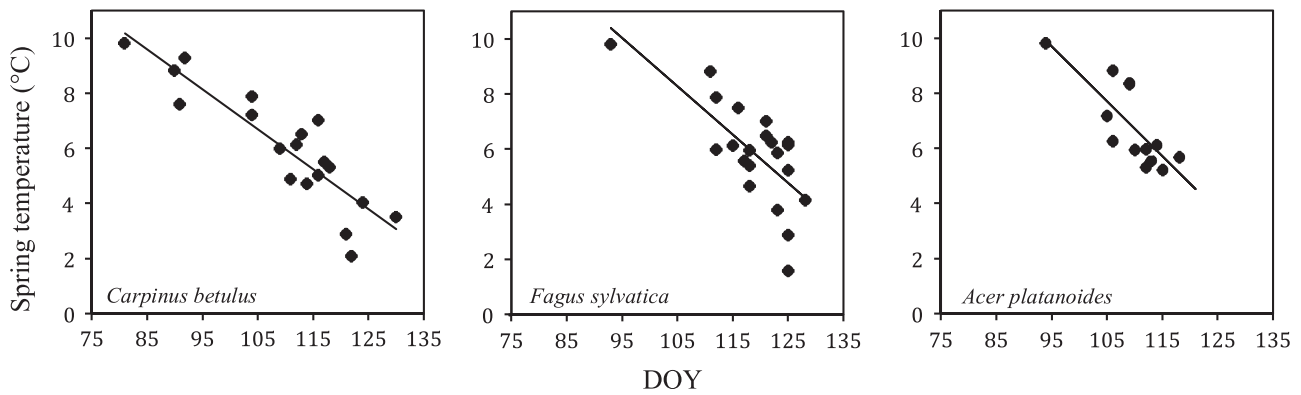
### Influence of a species' native climate on its flushing time

Over the past 100 years, mean spring temperatures (March 1 to April 30) in Munich have increased by 1.5 °C (Appendix

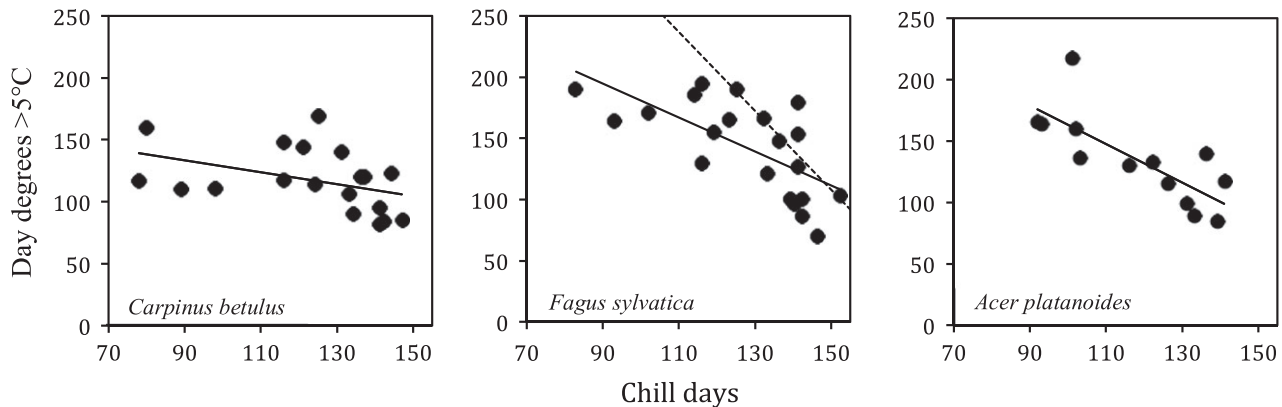


**Figure 3** Mean leaf-out dates ( $\pm$ SD) and heat sums ( $\pm$ SD) in 2012 and 2013 for species requiring signals from photoperiod as well as long chilling for their dormancy release (*Photoperiod*), photoperiod-independent species with high chilling requirements (*HighChill*), photoperiod-independent species with low chilling requirements (*LowChill*), and species relying entirely on forcing temperatures (*Forcing*), cultivated and monitored in Munich. Mean leaf-out dates (DOY) in 2012/2013: strategy *Forcing* 89/96, *LowChill* 105/113, *HighChill* 111/117 and *Photoperiod* 120/121. In 2012 and 2013, species relying entirely on spring temperature (strategy *Forcing*) flushed earlier and accumulated lower heat sums than species from any other group ( $P < 0.05$ ). Sample sizes are shown above columns.

Figure S1), whereas chill days ( $< 5$  °C) have decreased by 19 days (Appendix Figure S2). For the 147 species restricted to a single main climate and precipitation regime (regimes Cs, Cf, Cw, Df, Dw spelled out in Fig. 1), a difference-of-means test revealed a significant effect of native climate and precipitation regime on leaf-out times ( $P < 0.001$ ; Fig. 2 and Appendix Table S2). In 2012, species native to a temperate climate with dry summer periods (Cs) leafed out significantly later than species from any other climate. Species from temperate or cold regions without dry seasons (Cf, Df) leafed out significantly later than species native to cold regions with dry winter periods (Dw). In 2013, species from a warm, dry summer or fully humid climate (Cs, Cf) leafed out significantly later than species from a cold, dry winter climate (Dw). A species' native climate and precipitation regime had a significant influence on its forcing requirements ( $P < 0.001$ ; Fig. 2 and Appendix Table S2). In both years, species from a cold, dry winter climate (Dw) accumulated significantly fewer heat sums until budburst than species from Cs, Cf and Df climates.



**Figure 4** Correlation between mean spring temperature (1 March until 30 April) and leaf-out dates (DOY) for *Carpinus betulus*, *Fagus sylvatica* and *Acer platanoides* in Munich, Germany, between 1884 and 2014. The solid lines represent the best fit via ordinary least squares regression (*C. betulus*: Slope =  $-0.15$ ,  $R^2 = 0.79$ ,  $F(1, 17) = 50.2$ ,  $P < 0.001$ ,  $n = 19$ ; *F. sylvatica*: Slope =  $-0.18$ ,  $R^2 = 0.52$ ,  $F(1, 19) = 19.3$ ,  $P < 0.001$ ,  $n = 21$ ; *A. platanoides*: Slope =  $-0.2$ ,  $R^2 = 0.63$ ,  $F(1, 11) = 18.4$ ,  $P = 0.001$ ,  $n = 13$ ).



**Figure 5** Correlation between accumulated chill days (days  $< 5$  °C from 1 Nov until budburst) and heat sums (day degrees  $> 5$  °C from 1 Jan until budburst) for *Carpinus betulus*, *Fagus sylvatica* and *Acer platanoides*. Data from herbarium specimens and *in situ* monitoring between 1882 and 2014. Linear models were fitted to the three species: *C. betulus*: Slope =  $-0.48$ ,  $R^2 = 0.17$ ,  $F(1, 17) = 3.5$ ,  $P = 0.08$ ,  $n = 19$ ; *F. sylvatica*: Slope =  $-1.4$ ,  $R^2 = 0.41$ ,  $F(1, 19) = 13.0$ ,  $P = 0.002$ ,  $n = 21$ , dashed line from Vitasse & Basler 2013 (Slope =  $-3.2$ ); *A. platanoides*: Slope =  $-1.8$ ,  $R^2 = 0.60$ ,  $F(1, 11) = 16.3$ ,  $P = 0.002$ ,  $n = 13$ .

For the 196 species restricted to a single main climate, but with within-species variation in precipitation and summer temperature regimes, there still was a significant effect of native climate on leaf-out time ( $P < 0.001$ ; Appendix Figure S3 and Table S2). Species native to temperate zones (C) leafed out significantly later than species from cold (D) or arid habitats (B). A total of 204 species were restricted to a particular precipitation regime, for example, dry winter climates (Köppen letter w; Fig. 1), and a Kruskal–Wallis test showed that seasonal humidity alone also affects leaf-out ( $P < 0.001$ ; Appendix Figure S4 and Table S2). Species native to regions with dry winter periods (w) leafed out significantly earlier than species from regions without any dry period (f) or with a dry summer (s). Finally, in the 150 species restricted to a particular temperature regime (Köppen codes a = hot, b = warm, c = cold), summer temperature affected leaf-out times ( $P = 0.004$ ; Appendix Figure S5 and Table S2). Species native to hot summer climates (a) leafed out significantly later than species native to cold summer climates (c).

### Results from the meta-analysis

External leaf-out cues are well documented for 107 woody species, 51% of them also monitoring in this study (Table 1 including our data). Of these, 18 species in 9 genera and 6 families require long chilling and photoperiods for their dormancy release (subsequently called strategy *Photoperiod*); 19 species in 13 genera and 11 families are photoperiod independent, but require long chilling (strategy *HighChill*); 52 species in 34 genera and 21 families are photoperiod independent and have short chilling requirements (strategy *LowChill*); and 13 species in 10 genera and 8 families rely entirely on forcing temperatures (strategy *Forcing*). We could add five plants to the last category, namely, *Buddleja albiflora*, *Buddleja alternifolia*, *Lonicera × notha*, *Lonicera × salicifolia* and *Prinsepia sinensis* (Table 1) in which bud development occurred whenever there were a few warm days, even in January. Leaf-out times and heat sums required for flushing differed significantly among the four leaf-out strategies ( $P < 0.01$ ; Fig. 3 and Appendix Table S2).

**Table 1** Leaf-out requirement in 107 woody species for which the main external cues have been investigated: *Photoperiod* = Photoperiod + High chilling + Forcing, *HighChill* = High chilling + Forcing, *LowChill* = Low chilling + Forcing

Leaf-out requirements	2012 leaf-out (DOY)	Source
<b>Photoperiod</b>		
<i>Abies alba</i> (Pinaceae)	124 (1)	Basler & Körner (2012)
<i>Acer pseudoplatanus</i> (Sapindaceae)	–	Laube <i>et al.</i> (2014)
<i>Aesculus hippocastanum</i> (Sapindaceae)	113 (1)	Laube <i>et al.</i> (2014)
<i>Celtis laevigata</i> (Cannabaceae)	124 (3)	Borchert <i>et al.</i> (2005)
<i>C. occidentalis</i>	122 (0)	Borchert <i>et al.</i> (2005)
<i>C. reticulata</i>	–	Borchert <i>et al.</i> (2005)
<i>Fagus sylvatica</i> (Fagaceae)	115 (–3)	Heide (1993a); Caffarra & Donnelly (2011); Basler & Körner (2012); Laube <i>et al.</i> (2014)
<i>F. grandifolia</i>	–	Borchert <i>et al.</i> (2005)
<i>Picea abies</i> (Pinaceae)	118 (7)	Basler & Körner (2012); Laube <i>et al.</i> (2014)
<i>Populus tremula</i> (Salicaceae)	–	Laube <i>et al.</i> (2014)
<i>Quercus bicolor</i> (Fagaceae)	124 (–2)	Laube <i>et al.</i> 2014
<i>Q. germana</i>	–	Borchert <i>et al.</i> (2005)
<i>Q. michauxii</i>	–	Borchert <i>et al.</i> (2005)
<i>Q. palustris</i>	–	Borchert <i>et al.</i> (2005)
<i>Q. petraea</i>	–	Basler & Körner (2012)
<i>Q. stellata</i>	–	Borchert <i>et al.</i> (2005)
<i>Q. virginiana</i>	–	Borchert <i>et al.</i> (2005)
<i>Tilia cordata</i> (Malvaceae)	–	Caffarra & Donnelly (2011); Basler & Körner (2012)

(continued)

#### Leaf-out dates from herbarium specimens over the past 141 years

For *Carpinus betulus*, 16 leaf-out dates from herbarium specimens and three from living trees observed in 2012, 2013 and 2014 cover the period from 1886 to 2014, or 128 years (Appendix Figure S6). The latest leaf out occurred on 10 May 1965, the earliest on 22 March 2014, a difference of 49 days (SD = 13.1). *Carpinus betulus* is leafing out 18 days earlier than it did 100 years ago ( $P = 0.001$ ; Appendix Figure S6) or 7 days per 1 °C increase in spring temperature, indicating high sensitivity to temperature ( $P < 0.001$ ; Fig. 4). For *Fagus sylvatica*, 19 leaf-out dates from herbarium specimens and three from 2012, 2013 and 2014 *in situ* monitoring cover the period from 1872 to 2014, or 142 years (Appendix Figure S6). The latest leaf-out occurred on 8 May 1982, the earliest on 3 April 2014, a difference of 35 days (SD = 7.7). Leaf-out dates of beech advanced by 9 days over the last 100 years ( $P = 0.01$ ; Appendix Figure S6) or 6 days per 1 °C temperature increase ( $P < 0.001$ ; Fig. 4). For *Acer platanoides*, 11 herbarium specimens and the 2012, 2013 and 2014 *in situ* data cover the period from 1873 to 2014, or 141 years (Appendix Figure S6). The latest leafing out occurred on 1 May 1873, the earliest on 4 April in 2014, a

**Table 1.** (continued)

Leaf-out requirements	2012 leaf-out (DOY)	Source
<b>HighChill</b>		
<i>Acer negundo</i> (Sapindaceae)	98 (10)	Laube <i>et al.</i> (2014)
<i>Acer pseudoplatanus</i>	–	Basler & Körner (2012)
<i>Acer saccharinum</i>	122 (–6)	Polgar <i>et al.</i> 2014
<i>Acer saccharum</i>	114 (5)	Polgar <i>et al.</i> (2014); Laube <i>et al.</i> (2014)
<i>Betula pubescens</i> (Betulaceae)	–	Heide (1993b)
<i>B. pendula</i>	102 (1)	Basler & Körner (2012); Laube <i>et al.</i> (2014)
<i>Juglans ailantifolia</i> (Juglandaceae)	124 (–8)	Laube <i>et al.</i> 2014
<i>Juglans cinerea</i>	–	Laube <i>et al.</i> (2014)
<i>Larix decidua</i> (Pinaceae)	86 (19)	Basler & Körner (2012); Laube <i>et al.</i> (2014)
<i>Lindera benzoin</i> (Lauraceae)	109 (10)	Polgar <i>et al.</i> (2014)
<i>Nyssa sylvatica</i> (Cornaceae)	124 (–2)	Polgar <i>et al.</i> (2014)
<i>Populus tremula</i> (Salicaceae)	–	Heide (1993b)
<i>Prunus avium</i> (Rosaceae)	–	Laube <i>et al.</i> (2014)
<i>Pseudotsuga menziesii</i> (Pinaceae)	–	Laube <i>et al.</i> (2014)
<i>Quercus rubra</i> (Fagaceae)	122 (3)	Borchert <i>et al.</i> (2005); Laube <i>et al.</i> (2014)
<i>Quercus robur</i>	118 (1)	Laube <i>et al.</i> (2014)
<i>Sassafras albidum</i> (Lauraceae)	128 (–2)	Polgar <i>et al.</i> (2014)
<i>Smilax rotundifolia</i> (Smilacaceae)	–	Polgar <i>et al.</i> (2014)
<i>Symphoricarpos albus</i> (Caprifoliaceae)	–	Laube <i>et al.</i> (2014)

(continued)

difference of 27 days (SD = 6.6). Per 1 °C increase in spring temperature *A. platanoides* flushed 5 days earlier ( $P = 0.001$ ; Fig. 4) and there was a change in leaf-out times over the past 100 years of 8 days ( $P = 0.02$ ; Appendix Figure S6).

For *F. sylvatica* and *A. platanoides* there was a correlation between accumulated chill days and heat sums, whereas for *C. betulus* we could not find a significant relationship (Fig. 5). Over the past 100 years, forcing requirements in beech and Norway maple have increased by 30-day degrees, plausibly related to a decrease in chill days of 19 days (see Appendix Figure S2). If the number of chill days until 2050 were to decrease linearly as it has over the past 50 years (see inset Appendix Figure S2), the average plant in Munich would experience 73 chill days, and forcing requirements in beech and maple would further increase by, respectively, 46- and 52-day degrees.

#### Inter-annual variation

In both years (2012 and 2013), leafing out occurred over a period of 9 weeks (disregarding the outlier *Prinsepia sinensis*; below). The order of leafing out and accumulated heat sums was essentially the same in both years (leaf-out dates:  $R^2 = 0.54$ ,  $F(1, 460) = 545.8$ ,  $P < 0.001$ ; heat days:  $R^2 = 0.77$ ,  $F(1, 460) = 1559$ ,  $P < 0.001$ ;  $n = 462$ ; Appendix Figure S7).

**Table 1.** (continued)

Leaf-out requirements	2012 leaf-out (DOY)	Source
<b>LowChill</b>		
<i>Acer rubrum</i> (Sapindaceae)	103 (11)	Polgar <i>et al.</i> 2014
<i>Acer tataricum</i>	–	Laube <i>et al.</i> (2014)
<i>Alnus glutinosa</i> (Betulaceae)	90 (18)	Heide (1993b)
<i>Alnus incana</i>	90 (18)	Heide (1993b)
<i>Alnus serrulata</i>	–	Polgar <i>et al.</i> (2014)
<i>Aronia arbutifolia</i> (Rosaceae)	–	Polgar <i>et al.</i> (2014)
<i>Betula lenta</i> (Betulaceae)	<b>120</b> (–5)	Polgar <i>et al.</i> (2014)
<i>Betula papyrifera</i>	–	Polgar <i>et al.</i> (2014)
<i>Betula populifolia</i>	98 (10)	Polgar <i>et al.</i> (2014)
<i>Carpinus betulus</i>	90 (19)	Heide (1993a); Laube <i>et al.</i> (2014); this study
<i>Carya glabra</i> (Juglandaceae)	–	Polgar <i>et al.</i> (2014)
<i>Cephalanthus occidentalis</i> (Rubiaceae)	<b>130</b> (–4)	Polgar <i>et al.</i> (2014)
<i>Clethra alnifolia</i> (Clethraceae)	–	Polgar <i>et al.</i> (2014)
<i>Comptonia peregrina</i> (Myricaceae)	–	Polgar <i>et al.</i> (2014)
<i>Cornus alba</i> (Cornaceae)	90 (17)	Laube <i>et al.</i> (2014)
<i>Cornus amomum</i>	–	Polgar <i>et al.</i> (2014)
<i>Cornus mas</i>	102 (7)	Laube <i>et al.</i> (2014)
<i>Corylus americana</i> (Betulaceae)	<b>118</b> (–2)	Polgar <i>et al.</i> (2014)
<i>Corylus avellana</i>	88 (19)	Heide (1993b); Laube <i>et al.</i> (2014)
<i>Euonymus alatus</i> (Celastraceae)	<b>111</b> (4)	Polgar <i>et al.</i> (2014)
<i>Fraxinus americana</i> (Oleaceae)	<b>126</b> (–4)	Polgar <i>et al.</i> (2014)
<i>Fraxinus chinensis</i>	<b>122</b> (–3)	Laube <i>et al.</i> (2014)
<i>Fraxinus excelsior</i>	<b>124</b> (–5)	Basler & Körner (2012); Laube <i>et al.</i> (2014)
<i>Gaylussacia baccata</i> (Ericaceae)	–	Polgar <i>et al.</i> (2014)
<i>Hamamelis virginiana</i> (Hamamelidaceae)	109 (6)	Polgar <i>et al.</i> (2014)
<i>Juglans regia</i> (Juglandaceae)	108 (7)	Laube <i>et al.</i> (2014)
<i>Kalmia angustifolia</i> (Ericaceae)	–	Polgar <i>et al.</i> (2014)
<i>Kalmia latifolia</i>	–	Polgar <i>et al.</i> (2014)
<i>Myrica pensylvanica</i> (Myricaceae)	–	Polgar <i>et al.</i> (2014)
<i>Pinus nigra</i> (Pinaceae)	–	Laube <i>et al.</i> (2014)
<i>P. strobus</i>	–	Laube <i>et al.</i> (2014)
<i>P. sylvestris</i>	–	Laube <i>et al.</i> (2014)
<i>P. wallichiana</i>	–	Laube <i>et al.</i> (2014)
<i>Populus grandidentata</i> (Salicaceae)	–	Polgar <i>et al.</i> (2014)
<i>Prunus avium</i> (Rosaceae)	–	Basler & Körner (2012)
<i>P. padus</i>	87 (17)	Heide (1993b)
<i>P. serotina</i>	89 (20)	Polgar <i>et al.</i> (2014); Laube <i>et al.</i> (2014)
<i>Quercus alba</i> (Fagaceae)	<b>126</b> (0)	Polgar <i>et al.</i> (2014)
<i>Rhamnus frangula</i> (Rhamnaceae)	<b>115</b> (0)	Polgar <i>et al.</i> (2014)
<i>Rhus typhina</i> (Anacardiaceae)	–	Polgar <i>et al.</i> (2014)
<i>Robinia pseudoacacia</i> (Fabaceae)	<b>119</b> (0)	Laube <i>et al.</i> (2014)
<i>Rubus idaeus</i> (Rosaceae)	–	Heide (1993b)
<i>Salix x smithiana</i> (Salicaceae)	–	Caffarra & Donnelly (2011)
<i>Sorbus aucuparia</i> (Rosaceae)	98 (11)	Heide (1993b); Basler & Körner (2012)

(continued)

**Table 1.** (continued)

Leaf-out requirements	2012 leaf-out (DOY)	Source
<i>Spiraea latifolia</i>	–	Polgar <i>et al.</i> (2014)
<i>Syringa vulgaris</i> (Oleaceae)	85 (19)	Basler & Körner (2012); Laube <i>et al.</i> (2014)
<i>Ulmus americana</i> (Ulmaceae)	98 (10)	Polgar <i>et al.</i> (2014)
<i>Vaccinium angustifolium</i> (Ericaceae)	100 (9)	Polgar <i>et al.</i> (2014)
<i>Vaccinium corymbosum</i>	–	Polgar <i>et al.</i> (2014)
<i>Vaccinium pallidum</i>	–	Polgar <i>et al.</i> (2014)
<i>Viburnum recognitum</i> (Adoxaceae)	–	Polgar <i>et al.</i> (2014)
<i>Vitis aestivalis</i> (Vitaceae)	–	Polgar <i>et al.</i> (2014)
<b>Forcing</b>		
<i>Amorpha fruticosa</i> (Fabaceae)	<b>121</b> (5)	Laube <i>et al.</i> (2014)
<i>Berberis thunbergii</i> (Berberidaceae)	82 (10)	Polgar <i>et al.</i> (2014)
<i>B. vulgaris</i>	91 (15)	Polgar <i>et al.</i> (2014)
<i>Buddleja albiflora</i> (Scrophulariaceae)	86 (19)	This study
<i>Buddleja alternifolia</i>	90 (17)	This study
<i>Celastrus orbiculatus</i> (Celastraceae)	–	Polgar <i>et al.</i> (2014)
<i>Elaeagnus umbellata</i> (Elaeagnaceae)	87 (15)	Polgar <i>et al.</i> (2014)
<i>Fraxinus pensylvanica</i> (Oleaceae)	<b>122</b> (–3)	Laube <i>et al.</i> (2014)
<i>Ligustrum compactum</i> (Oleaceae)	–	Polgar <i>et al.</i> (2014)
<i>L. ibota</i>	88 (14)	Polgar <i>et al.</i> (2014)
<i>Lonicera mackii</i> (Caprifoliaceae)	93 (15)	Polgar <i>et al.</i> (2014)
<i>L. subsessilis</i>	–	Polgar <i>et al.</i> (2014)
<i>L. × notha</i>	93 (–26)	This study
<i>L. × salicifolia</i>	79 (–9)	This study
<i>Malus domestica</i> (Rosaceae)	–	Polgar <i>et al.</i> (2014)
<i>Prinsepia sinensis</i> (Rosaceae)	68 (–32)	This study
<i>Rosa multiflora</i> (Rosaceae)	88 (–)	Polgar <i>et al.</i> (2014)
<i>Sambucus canadensis</i> (Adoxaceae)	–	Polgar <i>et al.</i> (2014)

For species included in our monitoring, the 2012 leaf-out dates are shown and printed in bold if they post-date day > 110, our cut-off for late flushing. The number of days that a species flushed later in 2013 than in 2012 is shown in brackets.

Mean air temperature between 1 March and 30 April 2012 exceeded that during the same period in 2013 by 2.9 °C (Appendix Figure S8). Year 2012 had a 102 chill days and 2013 a 116 (= days <5 °C from 1 November to 30 April). On average, species leafed out 10 days earlier (2012: DOY 98; 2013: DOY 108) and accumulated 28-day degrees more in 2012 than in 2013 (Appendix Figure S9). In general, the later a species leafed out, the higher its inter-annual variation in heat sum accumulation and the smaller its inter-annual variation in leaf-out time (Appendix Figure S7). The latest leafing out occurred almost on the same day (DOY 130 in 2012 and 133 in 2013). In 2012, this was *Cephalanthus occidentalis* from a warm Cfa climate (North America); in 2013, it was the conifers *Picea glehnii* from a cold Dfb climate (Russia and Japan) and *P. omorica* from a warm Cfb climate (Balkan Peninsula). In both years, *Prinsepia sinensis* from a cold Dwb climate (Eastern Russia and Northern China) was the first species to put out leaves (DOY 68 in 2012 and 32 in 2013).



## DISCUSSION

### The two new approaches introduced here

This study uses two novel approaches for studying leaf-out dates across temperate-zone woody species. The first involves long time series for local leaf-out from the herbarium linked to chilling and spring temperatures in the years in which the specimens had been collected. Obviously, this only works for species in which leaf-out and flowering are simultaneous because botanists do not usually collect sterile plants or plants with immature leaves. Such species include maples, birches and many other temperate shrubs and trees. The herbarium approach opens the possibility of studying species-specific and even within-species phenological variation along latitudinal gradients and to compare climate tracking in species with different phenological strategies. The second new approach is to use the phenological behaviour of species in a common garden (where they are kept under optimal conditions but not allowed to evolve) to study leaf-out strategies from different climates and thus to forecast how leaf-out may change as community floristic composition changes. In our case, the floristic change of interest would be plants from warmer, more seasonal or drier climates extending their ranges northwards, analogous to altitudinal range extensions documented in Spain, France and Switzerland (Peñuelas & Boada 2003; Lenoir *et al.* 2010).

No previous study has used a botanical garden to contrast the leaf-out behaviour of natives and non-natives, although a few transplant experiments have established local genetic phenotypes in widespread woody species (cited in Lechowicz 1984). Shortcomings of our study are the lack of replication within species and that we lack data on the flushing times of the non-German species in their native climates. However, we expect the leaf-out times of these species to reflect their native thresholds for chilling, forcing and photoperiod because the trees, shrubs and lianas in the Munich garden have had no opportunity for natural propagation, precluding evolutionary adaptation. Any change in their reaction to these environmental signals in Munich would be due to phenotypic (ontogenetic) acclimatisation.

The need for phenological forecasting to be based on a broader sample of species from different climates and clades has been underlined in recent studies (Pau *et al.* 2011; Mazer *et al.* 2013). Especially for long-lived species, this need could be met by taking advantage of the thousands of non-native woody species growing, but not evolving, in botanical gardens. Gardens located at similar or different latitudes, each with 'northern non-native' and 'southern non-native' species among its cultivated plants, would provide a powerful tool to improve our knowledge of drivers of species phenology across biomes.

### Native climate largely determines leaf-out times in a common garden

We had hypothesised that species from warmer and drier climates would put out their new leaves later than species native to the Munich climate because they have higher forcing needs compared to more northern species. This expectation was

met. The southern species flushed on average 15 days later than the natives, and many of these late-flushing species belong to *Carya*, *Diospyrus*, *Fagus*, *Juglans*, *Liquidambar*, *Liriodendron*, *Nyssa*, *Platanus* and *Tilia*, groups that originally evolved under subtropical conditions (Tiffney & Manchester 2001). These results contradict the suggestion that 'trees and shrubs from more southern locations, which might have lower chilling requirements, may also be able to enter [the] new early-season niche' opening with global climate warming (Polgar *et al.* 2014: 113). Instead, our results show that species from warmer climates all have high-forcing requirements, leading to the opposite forecast, namely, that the establishment in Germany of more species from southern regions will contribute late flushers to German woody plant communities. It is unclear how evolutionary adaptation might counteract such an effect though.

Species adapted to hot (not just warm) summers, such as *Cytisophyllum sessilifolius* (Köppen-Geiger climate Csa) or *Fraxinus ornus* (Csa, Cfa; explanation of acronyms in Fig. 1), also flushed significantly later than species native to Munich's climate. An explanation of this may be that most (80%) of the hot summer-adapted species in our sample come from Mediterranean climates (Cs/f) and have high-forcing requirements. By contrast, 90% of our cool-summer species, such as *Acer tegmentosum* or *Cornus alba*, at the same time come from climates with harsh winters (Df/w climates) and leaf out significantly earlier than German species because they have lower forcing requirements. The leaf-out dates of species from cold arid deserts or steppes (BWk or BSk), such as *Berberis actinacantha* or *Buddleja alternifolia*, resembled those of Munich natives. The associations between precipitation regimes and flushing dates deserve more attention.

### Leaf-out cues in the 107 best-studied woody plant species

As shown in this study, the native climate of species largely determines their leaf-out times, with climate of course including the cycling of humidity, temperature and day length over the entire year. Of the 107 woody species best understood in terms of their leaf-out cues (Table 1), some 93% are native to the temperate or cold, fully humid climate typical of our study region (f climate; Fig. 1), and half of them were also monitored here. Those sensitive to photoperiod and requiring high chilling flushed 31 (2012) or 25 (2013) days later than species not sensitive to these two factors, and they also required higher heat sums (Fig. 3). The costs in photosynthesis, time for growth, development, tissue maturation and nutrient uptake of flushing up to a month later than other species clearly are high and must be outweighed by the advantage of not suffering from late frosts. This can only come into play in regions with a high probability of spring frosts. More work is needed on the underlying physiological and anatomical correlates of frost sensitivity.

### Long-term leaf-out data from herbarium specimens

Herbarium data have been widely used to infer past flowering times (Borchert 1996; Primack *et al.* 2004; Lavoie & Lachance 2006), but not leaf-out dates. For woody species that flush and flower simultaneously and which botanists therefore have

placed in permanent collections, herbarium records could provide much-needed data on flushing times for the past 150 years, possibly longer. We tested this idea in the Munich herbarium, using beech (*Fagus sylvatica*), a species assumed to have high chilling requirements and to obligatorily depend on photoperiod (Heide 1993a; Borchert *et al.* 2005; Vitasse & Basler 2013; Laube *et al.* 2014), hornbeam (*Carpinus betulus*), assumed to be temperature cued with low chilling and no obligate photoperiod requirements (Heide 1993a; Laube *et al.* 2014), and Norway maple (*Acer platanoides*), with unknown leaf-out cues.

Leaf-out in the three species was highly correlated with spring temperature, and in Munich, they are leafing out 5–7 days earlier per 1 °C increase in mean spring temperature as expected based on large data sets (Menzel & Fabian 1999; Chmielewski & Rötzer 2001). In terms of chilling needs, hornbeam had the lowest requirements, whereas Norway maple had the highest (Fig. 5). Fitting with this, hornbeam, with only minor chilling requirements, showed the strongest response to spring warming (7 days per 1 °C) and featured twice the inter-annual variation in leaf-out than did beech and Norway maple, suggesting that in chilling sensitive species like beech and Norway maple, unmet chilling requirements during years with warm winters delay budburst, leading to more stabilised leaf-out dates.

For beech, a study along an altitudinal gradient (131–1604 m a.s.l.) in the Pyrenees in southern France found a strong negative linear correlation between accumulated chill days and heat sums (Vitasse & Basler 2013; also Vitasse *et al.* 2009), whereas we found a more moderate relationship (Fig. 5). Photoperiod might be an additional variable confounding the relationship between chilling and required heat sums in spring. Over 131 years in Munich and over a gradient of 1470 m in the Pyrenees, beech never flushed before a day-length of 13 h occurred (range of day-length at budburst = 13 : 03–14 : 53 h:min for Munich and 13 : 35–14 : 57 h:min for the Pyrenees), even though accumulation of thermal time started much earlier in the season in southern France than in Munich. Thus, Pyrenean lower altitude individuals probably require higher heat sums than do beeches in Munich because of the shorter day lengths that they experience at the time of heat accumulation, whereas the longer photoperiods in Munich reduce the thermal time required for leaf-out, thereby substituting for unmet chilling requirements. This explanation is in keeping with Heide (1993a) who found an exponential delay of budburst with decreasing day-length.

## CONCLUSION

Under two climate change scenarios, by 2075, the Munich region will change from its current cold, fully humid climate with warm summers (Peel *et al.* 2007; Dfb in Fig. 1) to a more seasonal climate (Rubel & Kottek 2010; Cfa or Cfb in Fig. 1), most likely leading to changes in the flora. We obtained leaf-out data for ‘candidate newcomers’ from such climates and found that they flushed later than local species (depending on climate and plant clade), which would counterbalance shifts towards advanced leafing in local temperature-tracking species. A meta-analysis of 107 woody species with

known external leaf-out cues further revealed that chilling- and photoperiod-sensitive species all leaf out late (Table 1), and the 140-year-long records from the herbarium data underline the extent of species specificity in chilling, forcing and photoperiod responses (Figs. 4 and 5). If the number of chill days until 2050 were to continue decreasing linearly, the average woody plant in Munich would experience only 73 chill days, with forcing requirements increasing accordingly. Thus, for species with high chilling requirements such as *Fagus sylvatica* (Heide 1993a; Vitasse & Basler 2013; Laube *et al.* 2014), unmet chilling may well become a factor under further winter warming.

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## AUTHORSHIP

CMZ and SSR designed the study. CMZ performed the analyses. CMZ and SSR co-wrote this study.

## REFERENCES

- Basler, D. & Körner, C. (2012). Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agric. For. Meteorol.*, 165, 73–81.
- Borchert, R. (1996). Phenology and flowering periodicity of neotropical dry forest species: evidence from herbarium collections. *J. Trop. Ecol.*, 12, 65–80.
- Borchert, R., Robertson, K., Schwartz, M.D. & Williams-Linera, G. (2005). Phenology of temperate trees in tropical climates. *Int. J. Biometeorol.*, 50, 57–65.
- Caffarra, A. & Donnelly, A. (2011). The ecological significance of phenology in four different tree species: effects of light and temperature on bud burst. *Int. J. Biometeorol.*, 55, 711–721.
- Chmielewski, F.M. & Rötzer, T. (2001). Response of tree phenology to climate change across Europe. *Agric. For. Meteorol.*, 108, 101–112.
- Dunnnett, C.W. (1980). Pairwise multiple comparisons in the unequal variance case. *J. Am. Stat. Assoc.*, 75, 796–800.
- Fitter, A.H., Fitter, R.S.R., Harris, I.T.B. & Williamson, M.H. (1995). Relationships between first flowering date and temperature in the flora of a locality in central England. *Funct. Ecol.*, 9, 55–60.
- Ghelardini, L., Santini, A., Black-Samuelsson, S., Myking, T. & Falusi, M. (2010). Bud dormancy in elm (*Ulmus* spp.) clones – a case study of photoperiod and temperature responses. *Tree Physiol.*, 30, 264–274.
- Heide, O.M. (1993a). Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and long days. *Physiol. Plant.*, 89, 187–191.
- Heide, O.M. (1993b). Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. *Physiol. Plant.*, 88, 531–540.
- IPGE (1960). Phenological observation guide of the International Phenological Gardens. International Phenological Gardens of Europe, Berlin, Germany. Available at: [http://www.agrar.hu-berlin.de/fakultaeten/departments/dntw-en/agrarmet-en/phaenologie/ipg/IPG\\_ObsGuide.pdf](http://www.agrar.hu-berlin.de/fakultaeten/departments/dntw-en/agrarmet-en/phaenologie/ipg/IPG_ObsGuide.pdf). Last accessed 2 February 2014.
- Körner, C. (2006). Significance of temperature in plant life. In: *Plant Growth and Climate Change* (eds Morison, J.I.L., Morecroft, M.D.). Blackwell Publishing Ltd, Oxford, pp. 48–69.

- Körner, C. & Basler, D. (2010). Phenology under global warming. *Science*, 327, 1461–1462.
- Kottek, M., Grieser, J., Beck, C., Rudolf, B. & Rubel, F. (2006). World map of the Köppen-Geiger climate classification updated. *Meteorol. Z.*, 15, 259–263.
- Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2014). Chilling outweighs photoperiod in preventing precocious spring development. *Glob. Change Biol.*, 20, 170–182.
- Lavoie, C. & Lachance, D. (2006). A new herbarium-based method for reconstructing the phenology of plant species across large areas. *Am. J. Bot.*, 93, 512–516.
- Lechowicz, M.J. (1984). Why do deciduous trees leaf out at different times? Adaptation and ecology of forest communities. *Am. Nat.*, 124, 821–842.
- Lenoir, J., Gégout, J., Dupouey, J., Bert, D. & Svenning, J.-C. (2010). Forest plant community changes during 1989–2007 in response to climate warming in the Jura Mountains (France and Switzerland). *J. Veg. Sci.*, 21, 949–964.
- Mazer, S.J., Travers, S.E., Cook, B.I., Davies, T.J., Bolmgren, K., Kraft, N.J.B. *et al.* (2013). Flowering date of taxonomic families predicts phenological sensitivity to temperature: implications for forecasting the effects of climate change on unstudied taxa. *Am. J. Bot.*, 100, 1381–1397.
- Menzel, A. (2000). Trends in phenological phases in Europe between 1951 and 1996. *Int. J. Biometeorol.*, 44, 76–81.
- Menzel, A. & Fabian, P. (1999). Growing season extended in Europe. *Nature*, 397, 659.
- Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R. *et al.* (2006). European phenological response to climate change matches the warming pattern. *Glob. Change Biol.*, 12, 1969–1976.
- Myking, T. & Heide, O.M. (1995). Dormancy release and chilling requirement of buds of latitudinal ecotypes of *Betula pendula* and *B. pubescens*. *Tree Physiol.*, 15, 697–704.
- Olson, M.S., Levens, N., Soolanayakanahally, R.Y., Guy, R.D., Schroeder, W.R., Keller, S.R. *et al.* (2013). The adaptive potential of *Populus balsamifera* L. to phenology requirements in a warmer global climate. *Mol. Ecol.*, 22, 1214–1230.
- Pau, S., Wolkovich, E.M., Cook, B.I., Davies, T.J., Kraft, N.J.B., Bolmgren, K. *et al.* (2011). Predicting phenology by integrating ecology, evolution and climate science. *Glob. Change Biol.*, 17, 3633–3643.
- Peel, M.C., Finlayson, B.L. & McMahon, T.A. (2007). Updated world map of the Köppen-Geiger climate classification. *Hydrol. Earth Syst. Sci.*, 11, 1633–1644.
- Peñuelas, J. & Boada, M. (2003). A global change-induced biome shift in the Montseny mountains (NE Spain). *Glob. Change Biol.*, 9, 131–140.
- Polgar, C. & Primack, R.B. (2011). Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytol.*, 191, 926–941.
- Polgar, C., Gallinat, A. & Primack, R.B. (2014). Drivers of leaf-out phenology and their implications for species invasions: insights from Thoreau's Concord. *New Phytol.*, 202, 106–115.
- Primack, D., Imbres, C., Primack, R.B., Miller-Rushing, A.J. & Del Tredici, P. (2004). Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *Am. J. Bot.*, 91, 1260–1264.
- R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL. Available at: <http://www.R-project.org/>. Last accessed 2 February 2014.
- Rubel, F. & Kottek, M. (2010). Observed and projected climate shifts 1901–2100 depicted by world maps of the Köppen-Geiger climate classification. *Meteorol. Z.*, 19, 135–141.
- Sanz-Perez, V., Castro-Diez, P. & Valladares, F. (2009). Differential and interactive effects of temperature and photoperiod on budburst and carbon reserves in two co-occurring Mediterranean oaks. *Plant Biol.*, 11, 142–151.
- Siegel, S. & Castellan, N.J. (1988). *Non-Parametric Statistics for the Behavioral Sciences*. MacGraw Hill Int, New York, 213–214.
- Sparks, T.H. & Carey, P.D. (1995). The responses of species to climate over two centuries: an analysis of the Marsham phenological record, 1736–1947. *J. Ecol.*, 83, 321–329.
- Tiffney, B.H. & Manchester, S.R. (2001). The influence of physical environment on phylogeographic continuity and phylogeographic hypotheses in the Northern Hemisphere Tertiary. *Int. J. Plant Sci.*, 162, 3–17.
- Vitasse, Y. & Basler, D. (2013). What role for photoperiod in the bud burst phenology of European beech. *Eur. J. Forest Res.*, 132, 1–8.
- Vitasse, Y., Delzon, S., Dufrene, E., Pontailleur, J.Y., Louvet, J.M., Kremer, A. *et al.* (2009). Leaf phenology sensitivity to temperature in European trees: do within-species populations exhibit similar responses? *Agric. For. Meteorol.*, 149, 735–744.
- Vitasse, Y., Francois, C., Delpierre, N., Dufrene, E., Kremer, A., Chuine, I. *et al.* (2011). Assessing the effects of climate change on the phenology of European temperate trees. *Agric. For. Meteorol.*, 151, 969–980.
- Wolkovich, E.M., Cook, B.I., Allen, J.M., Crimmins, T.M., Betancourt, J.L., Travers, S.E. *et al.* (2012). Warming experiments underpredict plant phenological responses to climate change. *Nature*, 485, 494–497.

## SUPPORTING INFORMATION

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