

Innately shorter vegetation periods in North American species explain native–non-native phenological asymmetries

Constantin M. Zohner * and Susanne S. Renner

The length of the vegetation period (LVP), which is the time between leaf-out and leaf senescence, affects numerous ecosystem functions, including biogeochemical cycles and interspecific interactions. The evolutionary mechanisms determining LVP, however, are poorly understood, and thus, it is unknown whether innate LVPs differ between eastern North American (ENA), European and East Asian species. Here we monitored LVP in 2014–2015 in 396 Northern Hemisphere woody species grown in a common garden. We found that ENA species, under the same conditions, have three weeks (11%) shorter vegetation periods than their European and East Asian relatives, because their leaves flushed 9 ± 4 and 13 ± 4 days later and senesced 9 ± 4 and 11 ± 4 days earlier. LVPs of species introduced from Eurasia into ENA are therefore longer than those of native species, suggesting that the spread of non-natives might alter seasonal forest productivity in ENA. LVP between naturalized invasive and non-invasive species, however, did not differ, rejecting the common assumption that longer leaf presentation generally fosters invasive success. A likely explanation for the shorter LVP of ENA species is that region's uniquely high inter-annual temperature variation. These results highlight the footprint of regional climate history, which will affect forest response to climate change.

Understanding the drivers of leaf-out and leaf senescence is essential for forecasting consequences of anthropogenic climate change on temperate-zone forest ecology and economics^{1–3}. Correlative studies have shown that earlier bud burst occurs in response to climate warming, with leaf-out in woody species advancing by 3–8 days for each 1 °C increase in air temperature^{4–6}, although winter chilling also influences leaf-out^{7,8}. Spring photoperiod is an important leaf-out signal only for a few species⁹. The relative importance of the three cues mostly depends on the historical climate conditions under which species evolved, leading to latitudinal^{6,9} and longitudinal¹⁰ differences in leaf-out strategies. How climate change affects the timing of the end of the growing season remains unresolved^{5,11}. Different from spring phenology, leaf senescence in the fall appears to be under strong photoperiod control, with temperature having a modulating role¹², but investigations have been limited to a few species¹³. To forecast lengths of vegetation period (LVPs) under climate warming, information on a broad sample of species from different biomes and clades is needed. This need can be met by taking advantage of the thousands of non-native woody species growing in botanical gardens^{6,10,14,15}. Senescence and leaf-out strategies are largely genetically determined¹⁶, and the phenological responses in woody plants growing permanently outdoors in botanical garden are expected to reflect adaptations to temperature, day length, humidity and precipitation in their native biomes.

Here we first address the timing of leaf senescence in woody species from across the Northern Hemisphere and infer how autumn phenology interacts with spring leaf-out to affect overall LVP. Specifically, we combined multiyear data on spring leaf-out and autumn senescence times for individuals from 396 tree and shrub species grown under the same environmental conditions in the Munich Botanical Garden and applied hierarchical Bayesian models for leaf phenology accounting for shared evolutionary history. Such phylogenetically informed approaches are needed to account for the lack of statistical independence owing to the strong evolutionary

signal in LVP (Pagel's $\lambda = 0.85$ for the phylomatic tree and 0.80 for the gene tree; Supplementary Fig. 1). We also detected a negative non-linear association between a species' LVP and its maximum height ($R^2 = 0.22$; Supplementary Fig. 2b). To control for this, our hierarchical Bayesian analyses include species' maximum attainable heights as a fixed effect.

Given substantial variation among species and regions in LVP, we also investigated whether phenological strategies contribute to invasion success^{8,17–20} and consequently to the asymmetric invasion patterns in the Northern Hemisphere. Notably, 56% of woody invasive species originating from East Asia are invasive in eastern North America (ENA), whereas only 10% of woody invaders from ENA are invasive in East Asia²¹. Studies of both individual species and communities have suggested that innately long growing seasons may confer an advantage on invasive species, especially with continued climate warming. For example, *Berberis thunbergii*, which is native to Japan and invasive in ENA, leafs out approximately one month before native ENA shrubs and therefore benefits from spring sunlight in the understory¹⁸; shrubs from Europe or East Asia that are invasive in Concord, USA, leaf out earlier and have weaker winter-chilling requirements than native shrubs⁸; and another study in ENA found that non-native understory shrub species retained their leaves significantly longer than did native species¹⁹. We therefore used our data on LVP in 396 species from across the Northern Hemisphere to test whether invasiveness is related to early leaf-out, low winter-chilling requirements or extended LVP.

Results and discussion

Continental-scale differences in LVP. The growing seasons of ENA species were, on average, three weeks (18 ± 8 days (9%) or 24 ± 6 days (12%); means \pm 95% confidence intervals) shorter than those of East Asian or European species (Fig. 1). These differences could be attributed to both later spring leaf unfolding and earlier autumn chlorophyll breakdown (Fig. 1b). This continental effect

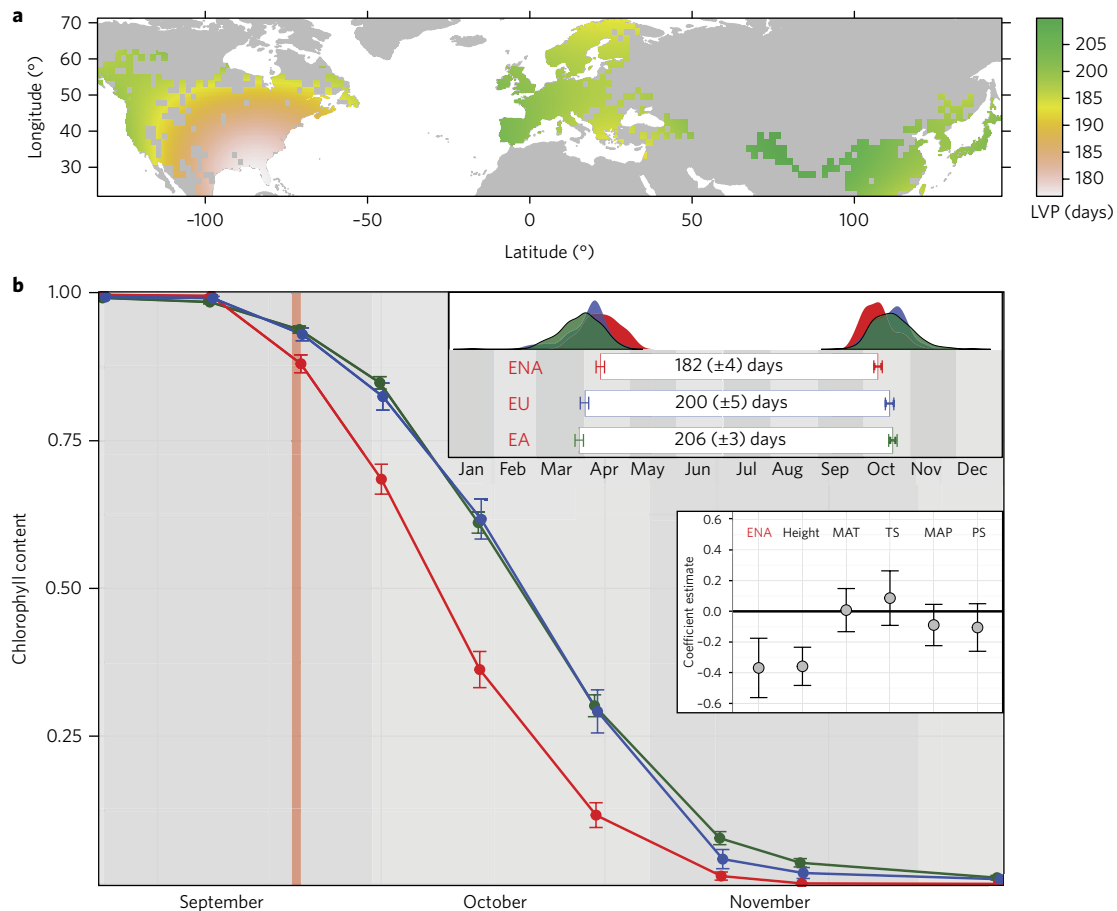


Fig. 1 | LVP of ENA, European and East Asian species. **a**, Genetic inertia in the biogeography of LVP: regional differences in LVP of temperate woody species grown under uniform conditions in the Munich Botanical Garden. Note that this map does not show any phenotypic differences expressed as a result of environmental parameters when the same species are growing in their native habitats. Non-native trees and shrubs grown in the Munich Botanical Garden were mostly obtained by exchange with other gardens, more rarely wild-collected, therefore the exact provenance of individuals was unknown for most species. **b**, Relative leaf chlorophyll degradation (mean \pm s.e.m. chlorophyll content) in autumn for ENA ($n = 73$), East Asian (EA; $n = 222$) and European (EU; $n = 63$) species, observed in 2015 in the Munich Botanical Garden. Vertical red line indicates the autumn equinox. Top inset, density plots and mean ($\pm 95\%$ confidence interval) for the date of spring leaf-out and the date of 50% chlorophyll loss in autumn, relative to peak chlorophyll reading per species, for ENA, East Asian and European species, pooled across 2014 and 2015 growing seasons. ENA species flushed 9 ± 4 or 13 ± 4 days later than European or East Asian species and broke down their chlorophyll 9 ± 4 days or 11 ± 4 days earlier than European or East Asian species, respectively (Kruskal-Wallis test: $P < 0.001$). Numbers within bars depict the mean LVP ($\pm 95\%$ confidence interval). Bottom inset, coefficient values (mean $\pm 95\%$ confidence interval) for the effect of biogeographic origin (ENA ($n = 66$ versus East Asian and Europe ($n = 217$)), species' maximum attainable growth height (height), median mean annual temperature (MAT), temperature seasonality (TS), mean annual precipitation (MAP) and precipitation seasonality (PS) in a species' native range on species-specific LVP estimated from a hierarchical Bayesian model including phylogenetic autocorrelation.

was of similar magnitude in shrubs and trees (Supplementary Fig. 3). In a phylogenetic hierarchical Bayesian model, the effect of continent (ENA compared to Europe or East Asia) on LVP was highly significant (lower inset in Fig. 1b), and in line with this, in the 12 families containing both ENA and Eurasian species (at least two species per family and region), ENA species had a shorter LVP (between 4 and 35 days) than Eurasian species (Supplementary Fig. 4a). Similarly, in 11 out of 12 genera containing both ENA and Eurasian species, ENA species had a shorter LVP (between 1 and 22 days) than Eurasian species (Supplementary Fig. 4b).

Why do ENA species have such a short growing season? Mean annual temperature and temperature seasonality are unlikely to be the explanation (see small effect sizes in Fig. 1b). Moreover, mean annual temperature and temperature seasonality in ENA and East Asia are similar, whereas Europe has a cooler, but less seasonal climate. A unique feature of the modern ENA climate is high inter-annual temperature variability. Leaf-out in species from regions

where spring temperatures are less predictable (defined as a high standard deviation of mean minimum temperatures for the March–May period between 1901 and 2013) is substantially delayed compared to regions with more predictable springs (see Fig. 1c from ref. ¹⁰). Unstable and/or varying temperatures (relative to Europe and East Asia) have existed in ENA over a geologically long time^{22–24}, probably selecting for conservative growth strategies²⁵.

With ever-warmer mean annual temperatures, can we expect the regional differences in LVP among the Northern Hemisphere woody species analysed here to increase or decrease? The pronounced chilling requirements of ENA species serve as a safeguard against precocious bud break¹⁰, and shortened winters with insufficient chilling may therefore at some point prevent further advances of leaf unfolding. By contrast, in East Asia, where the onset of spring is less variable, woody species require little winter chilling and are better able to track spring warming^{10,26}. In the fall, many East Asian and European species began degrading leaf chlorophyll in response

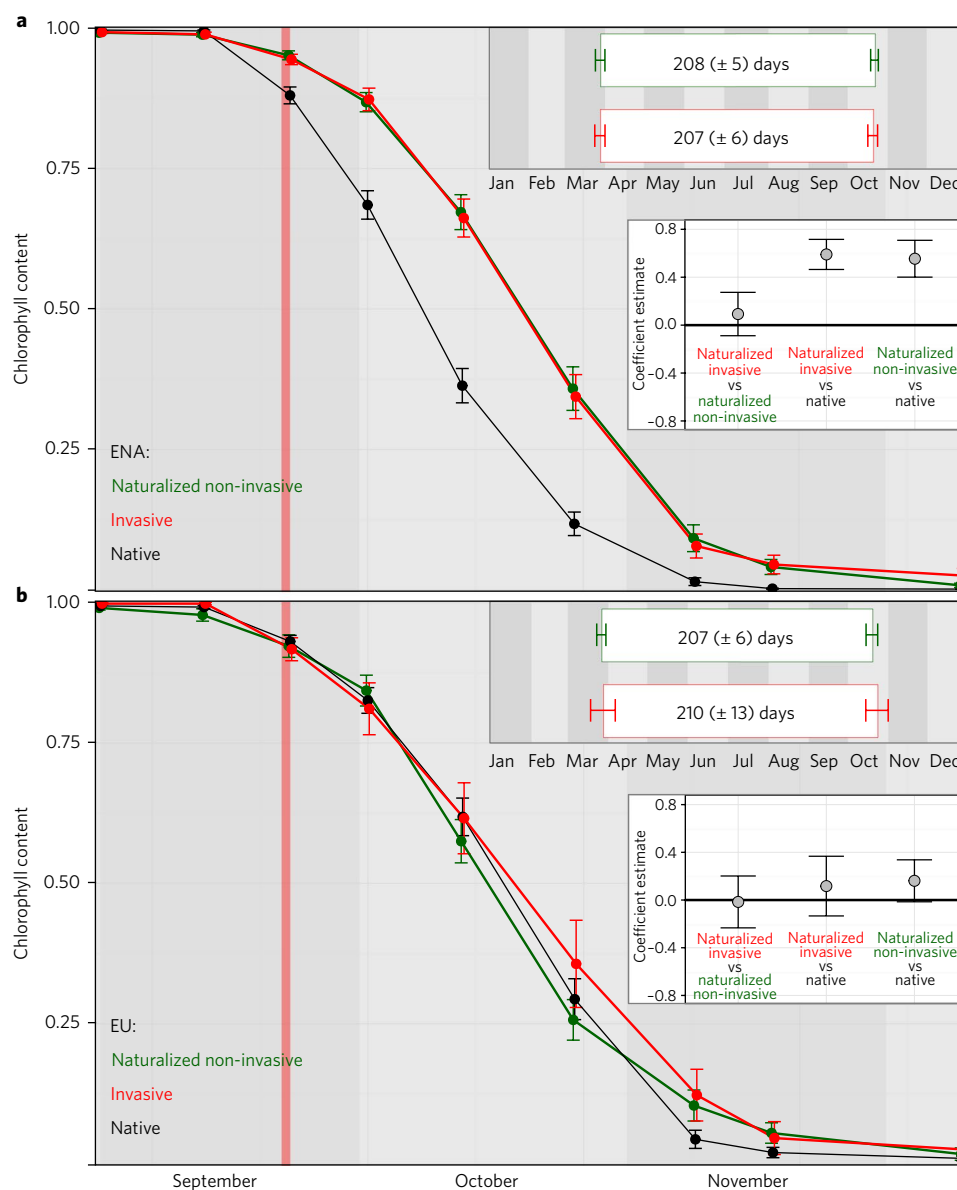


Fig. 2 | LVP of naturalized non-invasive, invasive and native species in ENA and Europe. a, ENA; b, Europe. a, b, Relative leaf chlorophyll degradation (mean \pm s.e.m. chlorophyll content) in autumn for naturalized non-invasive, invasive and native species in ENA (**a**; $n=58, 51,$ and $73,$ respectively) and Europe (**b**; $n=51, 14,$ and 63) observed in 2015 in the Munich Botanical Garden. Top insets, mean ($\pm 95\%$ confidence interval) for the date of spring leaf-out and the date of 50% chlorophyll loss in autumn, relative to peak chlorophyll reading per species, for naturalized non-invasive and invasive species in the respective continent, pooled across 2014 and 2015 growing seasons. Numbers within bars depict the mean LVP ($\pm 95\%$ confidence interval). Bottom insets, coefficient values (mean $\pm 95\%$ confidence intervals) for differences in LVP for the ‘naturalized non-invasive versus invasive’, ‘invasive versus native’, and ‘naturalized non-invasive versus native’ comparisons, estimated from hierarchical Bayesian models including phylogenetic autocorrelation and a fixed effect for species’ maximum attainable growth height. Sample sizes: 51 invasive, 58 naturalized non-invasive, 73 ENA native species (**a**); 14 invasive, 51 naturalized non-invasive, 63 European native species (**b**).

to pronounced drops in temperature, whereas many ENA species began chlorophyll breakdown earlier and independent of temperature drops (Fig. 1b and Supplementary Fig. 5), suggesting a greater photoperiod determination in ENA species. Satellite observations of forest spring and autumn colour change tend to confirm the lower temperature sensitivity of growing season duration in ENA compared to East Asia and Europe²⁶. Future studies will be needed to address the effect of stress factors, such as changes in the amount and frequency of precipitation, on growing season duration. In this study, precipitation as a factor determining growing season duration was controlled for, because the plants in the Munich Botanical Garden were continuously supplied with sufficient water.

LVP in naturalized non-invasive, invasive and native species in ENA and Europe. Studies that have investigated possible links between vegetative phenology and invasion success have contrasted the phenologies of invasive and native species and found that leaf-out times^{8,18} and leaf senescence times¹⁹ differ between ENA natives and invasive species from East Asia or Europe. However, such ‘invasive versus native’ comparisons cannot detect the effect of phenological strategy on invasion success, because this requires contrasting phenological behaviours for naturalized species that are either invasive or not (‘invasive versus naturalized-only’ approach)²⁷. Of the 396 species for which we have LVP data, 51 are invasive in ENA and 59 are naturalized but

non-invasive in ENA. Another 14 are invasive in Europe and 51 are naturalized but non-invasive in Europe. For the ENA native and non-native species, LVP differed markedly (lower inset of Fig. 2a). Among both shrubs and trees, native species had 18 ± 8 and 25 ± 9 days (mean \pm 95% confidence interval) shorter growing seasons than non-native species when grown under the same conditions, because of their later spring leaf unfolding and earlier chlorophyll breakdown (Supplementary Fig. 6). The differences between native and non-native species were of similar magnitude in understory shrubs and canopy trees (Supplementary Fig. 6). These results support the prediction²⁸ that continuing invasions of East Asian species in ENA may extend the LVP in ENA deciduous forests, affecting forest productivity and carbon balances¹⁹. For the European native and non-native species, we found no difference in LVP (lower inset in Fig. 2b), suggesting that introduced species will have little effect on forest productivity in Europe.

The idea that early leaf-out or late leaf senescence may explain invasion success^{8,19} is not supported by our data. For the ENA flora, the average LVP of naturalized non-invasive species was 208 ± 5 days and the LVP of invasive species was 207 ± 6 days (Fig. 2a). Similarly, the hierarchical Bayesian model revealed no difference in LVP between naturalized non-invasive and invasive species (lower inset of Fig. 2a). Even when we included only understory shrubs in the analyses, which have been thought to benefit particularly from an extended growing season^{19,29–31}, we detected no differences in the timing of spring leaf-out and autumn senescence between naturalized non-invasive and invasive species (Supplementary Fig. 6). Similarly, in the European flora we detected no difference between both groups: the average LVP of naturalized non-invasive species was 207 ± 6 days, of invasive species 210 ± 13 days (Fig. 2b). For both the ENA and the European floras, chilling requirements also did not differ between naturalized non-invasive and invasive species (χ^2 test: $P=0.49$ and 0.73 ; Supplementary Fig. 7a and b, respectively). These results suggest that vegetative phenology alone is a poor predictor of invasion success.

Conclusion

Overall, the discovery that, when grown under identical conditions, the growing seasons of ENA trees and shrubs are on average three weeks shorter than the growing seasons of their Eurasian relatives stresses the importance of regional history in the functioning of continental-scale biomes^{21,32}. The differences that we found involved the phenologies of numerous trans-Beringian plant clades of different ages, yet ENA and Eurasian species in the same genera have different LVPs (Supplementary Fig. 4). We hypothesize that the late spring leaf-out and early autumnal chlorophyll breakdown in ENA species detected here result from extremely variable climates in ENA allowing long-term survival of only those trees and shrubs with conservative phenological strategies.

Methods

Study site and temperature conditions. The study was carried out between January 2014 and December 2015 in the Munich Botanical Garden ($48^\circ 09' N$, $11^\circ 30' E$; 501 m above sea level). The year 2014 was characterized by a very warm spring (the mean March–April temperature was $9.6^\circ C$; or $2.5^\circ C$ warmer than the 1960–2013 average; see Supplementary Fig. 8), a ‘normal’ summer (mean June–August temperature of $18.3^\circ C$; or $0.2^\circ C$ warmer than the average) and a warm autumn (mean September–October temperature of $13.6^\circ C$; or $1.3^\circ C$ warmer than the average). The year 2015 was characterized by a mild spring ($8.1^\circ C$; or $1.0^\circ C$ warmer than the average), a very warm summer ($20.8^\circ C$; or $2.7^\circ C$ warmer than the average) and a cold autumn ($11.6^\circ C$; or $0.7^\circ C$ colder than the average).

Leaf-out monitoring, chilling requirements and leaf chlorophyll measurements.

Information on the chilling requirements in 215 woody species came from twig cutting experiments¹⁰. Leaf-out and leaf senescence were observed in two consecutive years (2014 and 2015) in 396 woody species growing permanently outdoors without winter protection. Non-native trees and shrubs grown in the Munich Botanical Garden were mostly obtained by exchange with other gardens, more rarely wild-collected, therefore the exact provenance of individuals was

unknown for most species. Leaf-out was monitored twice a week during spring (three individuals per species were monitored). Following common definitions^{33,34}, a plant's leaf-out date was defined as the day when at least three branches on that plant had unfolded leaves pushed out all the way to the petiole. For the same individuals, autumn leaf senescence was monitored weekly between 1 September and 15 December. We obtained species-specific senescence levels by visually assessing the percentage of leaf colouring and abscission. Leaf senescence was defined as the day when 50% of leaves had changed their colour or had abscised as a result of low temperatures and/or shorter day lengths^{35,34}. Individuals that showed senescence symptoms as a result of stress-related factors (for example, diseases and drought) were excluded from subsequent analyses (however, note that plants in the Munich Botanical Garden are irrigated if necessary, ruling out drought-related discolouring as an important factor).

To obtain species-level leaf-out and senescence dates, we first calculated the mean of all individual leaf-out–senescence dates for the respective species in each year (2014 and 2015) and then the average between the two years. Species-specific growing season length (LVP) was calculated as the period (in days) from leaf-out until leaf senescence. When averaged across all 396 study species, LVP was 208 days in 2014 and 193 days in 2015. The order of LVP among species was similar in both study years. Thus, the between-species variation in LVP observed in 2014 explained 64% of the variation observed in 2015 ($R^2=0.64$; Supplementary Fig. 2a). LVP (average of 2014 and 2015) was normally distributed (Shapiro–Wilk normality test: $P>0.05$) with an average of 200 days (6.5 months) and a s.d. of 20 days. The three species with the shortest LVP (<160 days) were *Cercis canadensis* (from ENA, LVP = 160 days), *Gymnocladus dioica* (ENA, 155) and *Gleditsia sinensis* (East Asia, 153); the species with the longest LVP (>255 days) were *Cotoneaster franchetii* (East Asia, 257), *Prinsepia sinensis* (East Asia, 265) and *Ribes maximowiczii* (East Asia, 261). See Supplementary Table 1 for information on the LVP of all 396 species. The mean daily temperature along with the temporal distribution of leaf-out and senescence dates for the two study years is shown in Supplementary Fig. 5.

In 2015 we additionally measured the leaf chlorophyll content between 1 September and 15 December at two-week intervals with a chlorophyll meter (SPAD-502; Soil Plant Analysis Development, Minolta Camera Co., Ltd, Tokyo, Japan) by averaging leaf chlorophyll readings from 10 branches per individual selected at random. Total chlorophyll content per individual was then calculated as:

$$\frac{\text{Chlorophyll content}}{\text{Maximum chlorophyll content}} \times (100 - \text{leaf abscission} (\%))$$

Species assignments to native biogeographic area, climate and invasive status.

Information on the native distributions (and the prevailing climate conditions there) for the 396 species for which we have leaf-out and senescence data came from ref. ¹⁰. We grouped species according to their native region: eastern North America (ENA), western North America (WNA), South America, Europe, West Asia and East Asia. Species native to more than one of these regions were assigned to their main distribution area. WNA, South America and West Asia were not included in the continent comparisons, because there were only 11, 16 and 2 species, respectively, from these regions.

Georeferenced occurrences (from the Global Biodiversity Information Facility (<http://www.gbif.org/>); see also ref. ¹⁰) of the 396 species were queried against grid files (2.5 arc minute spatial resolution data) for mean annual temperature, temperature seasonality, mean annual precipitation and precipitation seasonality from the Worldclim dataset (BIO 1, 7, 12, and 15)^{35,36}. For each species, we determined the climate optimum by calculating its 0.5 quantile (median) for the respective climate variable.

For the 396 species, we gathered information on their non-native occurrence in ENA, Europe or East Asia using various databases. We defined as ‘naturalized’ those species introduced to a region that can sustain self-replacing populations without human intervention²¹. Information on naturalization status came from refs ^{21,37} for ENA and ref. ³⁸ for Europe. We defined an invasive species as a non-native, naturalized species with a marked impact and management concern in its introduced community^{28,39}. Species with native and non-native populations in a continent were considered native in the respective continent. Information on invasive species in ENA came from refs ^{21,40} and the Center for Invasive Species and Ecosystem Health (<http://www.invasive.org/>). For invasive species in Europe, we used the EPPO database (http://www.eppo.int/INVASIVE_PLANTS/ias_lists.htm#IAPList), NOBANIS (<http://www.nobanis.org/>), BFIS (<http://ias.biodiversity.be/definitions#list>), info flora (<https://www.infoflora.ch/de/flora/neophyten/listen-und-infoblätter.html>), EASIN (<http://alien.jrc.ec.europa.eu/SpeciesMapper/>), LBV (http://www.lbv.de/fileadmin/www.lbv.de/Ratgeber/Haus_und_Garten/Neophyten/Neophyten_Schwarze-Liste-LBV.pdf) and refs ^{41,42}.

Data analysis. Using hierarchical Bayesian models to account for phylogenetic history in the analyses. To estimate the phylogenetic signal in species-level LVP we estimated Pagel's λ ⁴³, using the ‘phylosig’ function in the phytools R package⁴⁴. We used two phylogenies to calculate λ : (i) a phylogenetic tree¹⁶, containing all of

the study species with available LVP data except for 11 hybrids ($n=385$) but low phylogenetic resolution (Supplementary Fig. 1a) and (ii) a ‘high-resolution’ tree based on DNA-sequence information¹⁰, containing 299 species with available LVP data (hereafter referred to as gene tree; Supplementary Fig. 1b). Both trees showed similar λ values (0.85 and 0.80 for the phylomatic and gene tree, respectively) and we included the phylomatic tree in our hierarchical Bayesian models, because of its more complete species sampling.

Hierarchical Bayesian models (following refs.^{9,10,45}) were used to test for effects of continental origin and climatic parameters (lower inset in Fig. 1b), or invasive status (lower insets in Fig. 2 and Supplementary Fig. 6) on species-level differentiation in LVP. We included ENA as a binary character (species present in ENA/not present) to test whether ENA species have a shortened LVP (lower inset in Fig. 1b). The hierarchical Bayesian models allowed us to test species-level differences in LVP while controlling for phylogenetic signal, measured by λ . We also controlled for growth height by including each species’ maximum attainable growth height as a fixed effect in the models. The resulting posterior distributions are a direct statement of the effect magnitude of each biogeographic and climatic parameter on species-level differentiation in LVP. To incorporate the phylogenetic structure of the data in the hierarchical Bayesian model we used the Bayesian phylogenetic regression method of ref.⁴⁶. See refs.^{9,45} for details on phylogenetic regression in a hierarchical Bayesian model, model parameterization and prior choice.

Spatial patterns in LVP observed in a common garden. To model regional differences in LVP of temperate woody species grown under uniform conditions in the Munich Botanical Garden we applied ordinary Gaussian process regression (kriging)⁴⁷ using the ‘krige’ function of the gstat R package⁴⁸ (Fig. 1a). Distribution data (2.5 arc minute resolution) were available for 287 species for which we had information on LVP from the Munich Botanical Garden (see ‘Leaf-out monitoring, chilling requirements and leaf chlorophyll measurements’). Before kriging, we excluded cells for which fewer than five species with LVP data were available and for the remaining cells (34,821) we averaged the LVP of all species present inside the respective cell. We fitted variogram models based on empirical data to capture the degree of local spatial dependence in our data (close-by points in geographic space are also close-by in trait space). To account for different spatial dependence in different directions (anisotropy), we separately fitted variogram models for the major axis (strongest spatial dependence) and the axis orthogonal to it (weakest spatial dependence). Cells for which the standard deviation of the kriging estimation was >10 days were excluded. Note that the obtained map (Fig. 1a) shows differences between the LVP of North American, European and Asian species when grown under uniform conditions in a common garden. This map does not show phenotypic differences expressed as a result of environmental parameters when the same species are growing in their native habitats.

All statistical analyses were conducted in R⁴⁹.

Data availability. The authors declare that all data supporting the findings of this study are available within Supplementary Table 1.

Received: 10 February 2017; Accepted: 8 August 2017;

Published online: 18 September 2017

References

- Peñuelas, J. & Filella, I. Responses to a warming world. *Science* **294**, 793–795 (2001).
- Richardson, A. D. et al. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agric. For. Meteorol.* **169**, 156–173 (2013).
- Keenan, T. F. et al. Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nat. Clim. Change* **4**, 598–604 (2014).
- Menzel, A. & Fabian, P. Growing season extended in Europe. *Nature* **397**, 659 (1999).
- Menzel, A. et al. European phenological response to climate change matches the warming pattern. *Glob. Change Biol.* **12**, 1969–1976 (2006).
- Zohner, C. M. & Renner, S. S. Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records forecasts long-term change. *Ecol. Lett.* **17**, 1016–1025 (2014).
- Laube, J. et al. Chilling outweighs photoperiod in preventing precocious spring development. *Glob. Change Biol.* **20**, 170–182 (2014).
- Polgar, C., Gallinat, A. & Primack, R. B. Drivers of leaf-out phenology and their implications for species invasions: insights from Thoreau’s Concord. *New Phytol.* **202**, 106–115 (2014).
- Zohner, C. M., Benito, B. M., Svenning, J.-C. & Renner, S. S. Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nat. Clim. Change* **6**, 1120–1123 (2016).
- Zohner, C. M., Benito, B. M., Fridley, J. D., Svenning, J.-C. & Renner, S. S. Spring predictability explains different leaf-out strategies in the woody floras of North America, Europe, and East Asia. *Ecol. Lett.* **20**, 452–460 (2017).
- Vitasse, Y. et al. Assessing the effects of climate change on the phenology of European temperate trees. *Agric. For. Meteorol.* **151**, 969–980 (2011).
- Singh, R. K., Svystun, T., AlDahmash, B., Jönsson, A. M. & Bhalerao, R. P. Photoperiod- and temperature-mediated control of phenology in trees—a molecular perspective. *New Phyt.* **213**, 511–524 (2017).
- Cooke, J. E. K., Eriksson, M. E. & Junttila, O. The dynamic nature of bud dormancy in trees: environmental control and molecular mechanisms. *Plant Cell Environ.* **35**, 1707–1728 (2012).
- Panchen, Z. A. et al. Leaf out times of temperate woody plants are related to phylogeny, deciduousness, growth habit and wood anatomy. *New Phytol.* **203**, 1208–1219 (2014).
- Panchen, Z. A. et al. Substantial variation in leaf senescence times among 1360 temperate woody plant species: implications for phenology and ecosystem processes. *Ann. Bot.* **116**, 865–873 (2015).
- Ghelardini, L. et al. Genetic architecture of spring and autumn phenology in *Salix*. *BMC Plant Biology* **14**, 31 (2014).
- Harrington, R. A., Brown, B. J. & Reich, P. B. Ecophysiology of exotic and native shrubs in southern Wisconsin. 1. Relationship of leaf characteristics, resource availability, and phenology to seasonal patterns of carbon gain. *Oecologia* **80**, 356–367 (1989).
- Xu, C. Y., Griffin, K. L. & Schuster, W. Leaf phenology and seasonal variation of photosynthesis of invasive *Berberis thunbergii* (Japanese barberry) and two co-occurring native understory shrubs in a northeastern United States deciduous forest. *Oecologia* **154**, 11–21 (2007).
- Fridley, J. D. Extended leaf phenology and the autumn niche in deciduous forest invasions. *Nature* **485**, 359–362 (2012).
- Wolkovich, E. M. et al. Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change. *Am. J. Bot.* **100**, 1407–1421 (2013).
- Heberling, J. M., Jo, I., Kozhevnikov, A., Lee, H. & Fridley, J. D. Biotic interchange in the Anthropocene: strong asymmetry in East Asian and eastern North American plant invasions. *Global Ecol. Biogeogr.* **26**, 447–458 (2017).
- Ehlers, J. & Gibbard, P. L. The extent and chronology of Cenozoic global glaciation. *Quat. Int.* **164–165**, 6–20 (2007).
- Jansson, R. Global patterns in endemism explained by past climatic change. *Proc. R. Soc. B* **270**, 583–590 (2003).
- Sandel, B. et al. The influence of Late Quaternary climate-change velocity on species endemism. *Science* **334**, 660–664 (2011).
- Dynesius, M. & Jansson, R. Evolutionary consequences of changes in species’ geographical distributions driven by Milankovitch climate oscillations. *Proc. Natl Acad. Sci. USA* **97**, 9115–9120 (2000).
- Park, T. et al. Changes in growing season duration and productivity of northern vegetation inferred from long-term remote sensing data. *Environ. Res. Lett.* **11**, 084001 (2016).
- Willis, C. G. et al. Favorable climate change response explains non-native species’ success in Thoreau’s woods. *PLoS ONE* **5**, e8878 (2010).
- Wolkovich, E. M. & Cleland, E. E. Phenological niches and the future of invaded ecosystems with climate change. *AoB Plants* **6**, plu013 (2014).
- Augspurger, C. K., Cheeseman, J. M. & Salk, C. F. Light gains and physiological capacity of understory woody plants during phenological avoidance of canopy shade. *Funct. Ecol.* **19**, 537–546 (2005).
- Gill, D. S., Amthor, J. S. & Bormann, F. H. Leaf phenology, photosynthesis, and the persistence of saplings and shrubs in a mature northern hardwood forest. *Tree Physiol.* **18**, 281–289 (1998).
- Rothstein, D. E. & Zak, D. R. Photosynthetic adaptation and acclimation to exploit seasonal periods of direct irradiance in three temperate, deciduous-forest herbs. *Funct. Ecol.* **15**, 722–731 (2001).
- Ricklefs, R. E. Community diversity: relative roles of local and regional processes. *Science* **235**, 167–171 (1987).
- Denny, E. G. et al. Standardized phenology monitoring methods to track plant and animal activity for science and resource management applications. *Int. J. Biometeorol.* **58**, 591–601 (2014).
- Phenological Observation Guide of the International Phenological Gardens* (International Phenological Gardens of Europe, Berlin, revised from original version from 1960); https://www.agrar.hu-berlin.de/en/institut-en/departments/dntw-en/agrarmet-en/phaenologie/ipp/IPG_ObsGuide.pdf
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. WorldClim high resolution global climate surfaces v.1.3. (Dryad Digital Repository, 2004); <http://datadryad.org/handle/10255/dryad.12700>
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978 (2005).
- USDA, NRCS *The PLANTS Database* (National Plant Data Center, 2016); <http://plants.usda.gov>
- European Invasive Alien Species Gateway* (DAISIE, 2016); <http://www.europe-alien.org/>

39. Mack, R. N. et al. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* **10**, 689–710 (2000).
40. Fridley, J. D. Of Asian forests and European fields: Eastern U.S. plant invasions in a global floristic context. *PLoS ONE* **3**, e3630 (2008).
41. Weber, E. & Gut, D. Assessing the risk of potentially invasive plant species in central Europe. *J. Nat. Conserv.* **12**, 171–179 (2004).
42. Nehring, S., Kowarik, I., Rabitsch, W. & Essl, F. (eds) *Naturschutzfachliche Invasivitäts-Bewertungen für in Deutschland wild lebende gebietsfremde Gefäßpflanzen* (Bundesamt für Naturschutz, Bonn, 2013); <http://www.bfn.de>
43. Pagel, M. Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884 (1999).
44. Revell, L. J. Phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**, 217–223 (2012).
45. Fridley, J. D. & Craddock, A. Contrasting growth phenology of native and invasive forest shrubs mediated by genome size. *New Phytol.* **207**, 659–668 (2015).
46. de Villemereuil, P., Wells, J. A., Edwards, R. D. & Blomberg, S. P. Bayesian models for comparative analysis integrating phylogenetic uncertainty. *BMC Evol. Biol.* **12**, 102 (2012).
47. Cressie, N. Spatial prediction and ordinary kriging. *Math. Geol.* **20**, 405–421 (1988).
48. Pebesma, E. J. Multivariable geostatistics in S: the gstat package. *Comput. Geosci.* **30**, 683–691 (2004).
49. R Core Team *R: A language and environment for statistical computing* (R Foundation for Statistical Computing, 2017); <http://www.R-project.org>

Acknowledgements

The study was part of the KLIMAGRAD project sponsored by the 'Bayerisches Staatsministerium für Umwelt und Gesundheit'. We thank S. Petrone for help with the phenological observations and R. Ricklefs for comments on the manuscript.

Author contributions

C.M.Z. designed the study and performed the analyses. C.M.Z. and S.S.R. co-wrote the paper.

Competing interests

The authors declare no competing financial interests.

Additional information

Supplementary information is available for this paper at doi:10.1038/s41559-017-0307-3.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to C.M.Z.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.