Spring warming substantially advances leaf unfolding and flowering time for perennials. Winter warming, however, decreases chilling accumulation (CA), which increases the heat requirement (HR) and acts to delay spring phenology. Whether or not this negative CA-HR relationship is correctly interpreted in ecosystem models remains unknown. Using leaf unfolding and flowering data for 30 perennials in Europe, here we show that more than half (7 of 12) of current chilling models are invalid since they show a positive CA-HR relationship. The possible reason is that they overlook the effect of freezing temperature on dormancy release. Overestimation of the advance in spring phenology by the end of this century by these invalid chilling models could be as large as 7.6 and 20.0 days under RCPs 4.5 and 8.5, respectively. Our results highlight the need for a better representation of chilling for the correct understanding of spring phenological responses to future climate change.
Spring phenology (e.g., budburst, leaf-out, and flowering) of perennials has advanced in recent decades around the middle and high latitudes (north of 30° N) of the Northern Hemisphere. Shifts in spring phenology have essential implications for ecosystems and the climatic system, ranging from interactions among plants and their herbivores to the balance among surface carbon, energy, and water. PROJECTING FUTURE TRENDS IN SPRING PHENOLGY

We assessed 12 chilling models coded as C1–C12 (see “Methods” for a full description). The linear trends in CA during winter to early spring (previous November to April) from 1951 to 2018 were calculated for each station based on all models and E-OBS gridded temperature data set. We expected that the accumulated chilling in Central Europe has progressively decreased as the winter temperature (Previous November to February) increased significantly by 0.25 °C/decade from 1951 to 2018. The trends in CA and its spatial pattern, however, varied among the models (Fig. 2). CA for Models C1, C2, C4, C5, and C12 decreased significantly at >88% of the stations (p < 0.05) because the winter temperature exceeded the maximum effective temperature under climate warming (e.g., 5 °C for model C1). The proportion of stations reporting a significant decrease in CA for the other models only ranged from 1.0% (Model C8) to 61.5% (Model C5). The increasing trends even dominated across Central Europe for models C7–C9, possibly because the freezing temperature became effective under climate warming in these models, and the effect of this increase was higher than the effect of decrease caused by the loss of maximum effective temperature. Pearson’s r between each pair of chilling models for each station (Supplementary Fig. 4) indicated that not all chilling models were positively correlated with each other. Some models were even negatively interrelated (e.g., Model C1 and C6), suggesting that the current chilling models could not reflect a consistent trend when measuring the change in the amount of chilling.

Relationship between CA and HR. We calculated CA (from 1 November in the previous year to the date of onset of spring events) for each species, station, and year using the 12 chilling models to determine if the models met the physiological assumption of Fig. 1. Also, HR was calculated based on a commonly used forcing model (integrating daily mean temperatures >0 °C from 1 January to the date of onset of spring events). The correlations between CA and HR varied among the chilling models for all species. Figure 3 shows an example of leaf-out for *Betula pendula*. Five chilling models (C1, C2, C4, C5, and C12) that predicted decreasing trends in CA exhibited significant negative correlations between CA and HR, and the other models exhibited positive correlations. Twenty-nine of the 30 species had significantly negative Pearson’s r between HR and CA based on the above five models (Supplementary Fig. 5). We therefore classified models C1, C2, C4, C5, and C12 as valid models, because they met the physiological assumption in Fig. 1. No or only a few species had negative CA–HR relationships in the other seven models (Supplementary Fig. 5), which were thus classified as invalid models. We also analyzed the station-level relationship between CA and HR for all stations with at least 15-years of records. Few stations (<10% for all species) had significantly negative Pearson’s r between CA and HR when using the invalid models, but >30% of the stations (for most of the species) had significantly negative r between CA and HR when using the valid models (Supplementary Fig. 6). Since we only used one forcing model (Model F1, see the equations in “Methods”) to calculate HR, we further validated the chilling models by correlating them with HR based on the other seven forcing models (Models F2–F8). The percentage of stations with significantly negative Pearson’s r between CA and HR was larger for the valid than the invalid models, regardless of the forcing model chosen (Supplementary Fig. 7). Thus, the performance of the chilling models was not affected by the choice of forcing models. Although some of the invalid models were calibrated specifically for fruit and nut trees (e.g., Model C7 and C9), they still did not perform better than the valid models for *Prunus avium* (a fruit tree supplying edible cherry).
Phenological trends based on chilling models. We tested the impact of the choice of the chilling model on past and predicted future trends in spring phenology by developing a process-based model incorporating the relationship between CA and HR. First, we assessed whether different chilling models could reproduce spatial gradients of spring events across warm and cold regions in Europe. Most of the species showed a similar result, so here we only show an example of leaf out for *B. pendula* (Supplementary Fig. 10). Across different locations, the simulated mean date correlated significantly with the observed mean dates with $R^2$ ranging from 0.65 and 0.72 ($p < 0.01$) for all the models. However, when comparing the root-mean-square error (RMSE), the valid models (RMSE = 4.2–6.9 days) were overall more accurate than the invalid model (RMSE = 6.5–10.7 days), because the invalid models produce an earlier leaf-out date than observation in cold regions but later leaf-out date in warm regions. Second, we assessed whether different chilling models could reproduce the observed temporal trends of spring events in Europe. Across all species and locations, the different models reproduced similar trends with the observed data from 1980 to 2018, but the invalid models simulated an earlier spring event compared to the observed data from the 1990s to the 2010s (Fig. 4a). Also, we compare the simulated and observed trends from 1980 to 2018 at different locations for the leaf out of *B. pendula* (Supplementary Fig. 11). For all models, the simulated and observed data exhibited consistently earlier trends at most locations. However, the valid model ($R^2 = 0.15–0.17$, RMSE = 0.18–0.20 days year$^{-1}$) performed better than the invalid models ($R^2 = 0.02–0.09$, RMSE = 0.22–0.34 days year$^{-1}$) when comparing the $R^2$ and RMSE between the simulated and observed trends. The invalid model seemed to overestimate the past earlier trends in the leaf-out date (Supplementary Fig. 11).

Based on the daily future climate data, the predicted advance in spring phenology during the 2020s to the 2090s was generally stronger for the invalid than the valid chilling models for all species in scenarios for Representative Concentration Pathways (RCPs) 4.5 and 8.5 (Supplementary Figs. 12 and 13). Averaged from all species, the date of onset of spring events gradually and *Corylus avellana* (widely grown hazelnut plants for commercial nut production) (Supplementary Fig. 7).

In order to assess the scale effect caused by large grid size of E-OBS data set (about 10 km) and the non-uniform cover of plants and temperature in the grid cells, we compared the HR and CA based on E-OBS data set and a station-based Global Historical Climatology Network (GHCN) data set. The results showed that CA or HR calculated by these two data sets was significantly correlated, and the CA–HR relationship was stable among two data sets (see the example of *B. pendula* in Supplementary Fig. 8). Thus, the scale effect did not affect the relationship between CA and HR. We also evaluate the difference caused by the different starting dates of temperature accumulation. Compared to temperature accumulated since 1 January, the later starting date (15 January and 1 February) would result in less HR (based on Model F1), especially for areas with a warm winter (see the example of *B. pendula* in Supplementary Fig. 9). Although the starting dates of heat accumulation altered the slope of HR against CA (based on Model C1), the significantly negative correlation between HR and CA remained.

**Fig. 1 Conceptual scheme of the relationship between HR and CA.** Previous studies (Supplementary Table 1) found that saplings and twigs of 91 perennials need less heat for budburst (or leaf-out and flowering) if they receive more or longer chilling in natural or controlled environments. A chilling accumulation (CA) is linearly or nonlinearly (the figure only shows a nonlinear relationship) negatively correlated with heat requirement (HR). The subplot shows the number of species exhibiting such a relationship for each life form (b) and genus (c). The CA–HR relationships for each species are shown in Supplementary Fig. 1.

**Fig. 10.** Across different locations, the simulated mean date correlated significantly with the observed mean dates with $R^2$ ranging from 0.65 and 0.72 ($p < 0.01$) for all the models. However, when comparing the root-mean-square error (RMSE), the valid models (RMSE = 4.2–6.9 days) were overall more accurate than the invalid model (RMSE = 6.5–10.7 days), because the invalid models produce an earlier leaf-out date than observation in cold regions but later leaf-out date in warm regions. Second, we assessed whether different chilling models could reproduce the observed temporal trends of spring events in Europe. Across all species and locations, the different models reproduced similar trends with the observed data from 1980 to 2018, but the invalid models simulated an earlier spring event compared to the observed data from the 1990s to the 2010s (Fig. 4a). Also, we compare the simulated and observed trends from 1980 to 2018 at different locations for the leaf out of *B. pendula* (Supplementary Fig. 11). For all models, the simulated and observed data exhibited consistently earlier trends at most locations. However, the valid model ($R^2 = 0.15–0.17$, RMSE = 0.18–0.20 days year$^{-1}$) performed better than the invalid models ($R^2 = 0.02–0.09$, RMSE = 0.22–0.34 days year$^{-1}$) when comparing the $R^2$ and RMSE between the simulated and observed trends. The invalid model seemed to overestimate the past earlier trends in the leaf-out date (Supplementary Fig. 11).

Based on the daily future climate data, the predicted advance in spring phenology during the 2020s to the 2090s was generally stronger for the invalid than the valid chilling models for all species in scenarios for Representative Concentration Pathways (RCPs) 4.5 and 8.5 (Supplementary Figs. 12 and 13). Averaged from all species, the date of onset of spring events gradually
advanced until the 2060s and then remains stable under RCP 4.5 but continuously advanced under RCP 8.5 (Fig. 4). The phenological change matched the warming trends of two climate scenarios (Supplementary Fig. 14). The advance in spring events under RCP 4.5 from the 2010s to the 2090s averaged for all species was 11.2–13.7 days for the valid models but 16.8–22.5 days for the invalid models (Fig. 4c). The advances in spring events under RCP 8.5 by the end of this century averaged 20.0 days larger for the invalid than the valid models (Fig. 4d).

Discussion
An earlier leaf-out date can increase the photosynthetic production of forests, so using an invalid chilling model to predict the start of the growing season would likely overestimate terrestrial photosynthesis and carbon uptake in spring. In addition to predicting future phenological change, the chilling models were used to estimate the chilling requirement of commercially important fruit and nut trees, such as apples, pears, and cherries. The cultivars selected based on the amount of winter

Fig. 2 Spatial patterns of the linear trends in chilling accumulation based on 12 chilling models. The chilling accumulation from 1 November to 30 April was calculated using the 12 chilling models. a–l Models C1–C12. Dark blue circles, significant and negative slopes (two-sided F-test, \( p < 0.01 \), \( n = 68 \) years). Light blue circles, insignificant and negative slopes (two-sided F-test, \( p > 0.05 \), \( n = 68 \) years). Dark red circles, significant and positive slopes (two-sided F-test, \( p < 0.05 \), \( n = 68 \) years). Light red circles, insignificant and positive slopes (two-sided F-test, \( p > 0.05 \), \( n = 68 \) years).
chilling at their production sites would likely fail to grow normally in another location if an invalid model was used to estimate the adaptative capacity of CA. In this study, the amount of chilling based on invalid models even increase at mid- and high latitudes under climatic warming (Fig. 2), possibly because in these areas the daily mean temperature during the coldest period of winter was below 0 °C, which did not contribute to CA for most of the invalid chilling models (e.g., Model C3 regarded that only the temperature between 0 and 5 °C was effective). Due to winter warming, the number of days with temperature below 0 °C reduced, causing an increase in the amount of chilling. If using the invalid models to estimate the amount of chilling, the increased trends in the amount of chilling would continue at mid- and high latitudes in scenarios of future climatic warming, so growers in these regions may miss the opportunity to adapt to climate change, e.g., by breeding tree cultivars for lower chilling requirements.

The effect of freezing temperatures is the most important structural difference between valid and invalid chilling models (Supplementary Fig. 15). The rate of chilling (the effectiveness of different temperatures on dormancy break) for the invalid models is zero or low for temperatures <0 °C. The rate of chilling for the valid models, however, is still effective even for temperatures <−5 °C. For example, if using Model C1 (temperature <5 °C is effective) to measure the amount of chilling, winter warming would lead to more number of days with the daily mean temperature higher than 5 °C, and thus decrease the CA. However, for Model C3 (temperature between 0 and 5 °C is effective), this effect would be counteracted by the increase in the number of days with temperature >0 °C. Considering the increased HR of spring phenology in Europe, Model C1 would produce a negative relationship between CA and HR, but Model C3 may produce an opposite result. Thus, our study suggested that the valid models, which considered the effect of freezing temperatures during dormancy, could better explain the CA–HR mechanism. Further experiments, however, are necessary to confirm this assumption, such as giving saplings or twigs a treatment of different chilling temperatures of the same duration and then a test of regrowth under the same forcing conditions.

However, the effectiveness of temperatures <0 °C is rarely tested before, because plants cannot survive if they are exposed to freezing temperatures immediately at the end of the growing season. Tolerance to freezing under natural conditions gradually increases with exposure to low temperatures (a process known as cold acclimation), which allows plants to survive winter conditions. Sudden exposure to freezing temperatures could extensively damage plant tissues due to the lack of cold acclimation (by frost cavitation). More complex experiments are needed to understand the multifaceted nature of chilling accumulation.
Therefore necessary to confirm the effect of freezing temperatures on the rate of chilling, e.g., by using gradually decreasing temperatures to simulate cold acclimation in situ. Furthermore, acclimation in plants may alter the HR of plants. The acclimation could be accounted for by using different slopes and interceptions to describe the CA–HR relationship for individuals growing at different climatic conditions. However, when comparing the CA–HR relationship between low latitude (lower than 50.65° N) and high latitude (higher than 50.65° N), we did not find a significant difference in CA–HR relationship (Supplementary Fig. 16). Thus, we did not consider the impact of acclimation in this study.

Overall, the advance in budburst and leaf formation of perennials in recent decades were associated with spring warming. Due to the negative relationship between CA and HR, the reduced winter chilling slowed the spring phenological advance. We report that the majority of the current chilling models failed to represent the negative relationship between CA and HR, using 2,493,644 phenological records for 30 species from 1951 to 2018, potentially because these models were developed for limited species in specific geographic regions and did not consider the effectiveness of freezing temperature. If these invalid chilling models are used to predict future phenological change, the advance in spring phenology at the end of this century would be twice as early as predicted using the valid models, and future spring terrestrial net carbon uptake would consequently be overestimated.

Methods

Phenological and climatic data. We used data from the Pan-European Phenology Project (PEP725)39, an open-access database with long-term plant phenological observations across 25 European countries (http://www.pep725.eu/). The regional/national network partners of PEP725 are following a consistent guideline for phenological observations29 and prepare the data for submission to the PEP725 database curators29. We selected 30 species for which sufficient observational data were available: 21 deciduous broadleaved trees or shrubs, 6 herbaceous perennials, 2 evergreen coniferous trees, and 1 deciduous coniferous tree (Supplementary Table 3). Particularly, our data set included one fruit tree (Prunus avium) and one nut tree (Corylus avellana) since some of the chilling models are specifically developed for fruit and nut trees. A total of 2,493,644 individual records from 15,533 phenological stations were used. The stations were mainly distributed in moderate climates in Central Europe (Supplementary Fig. 3). Four spring events based on the BBCH code were investigated: BBCH 10, 11, 60, and 69, representing first leaves separated, first leaves unfolded, first flowers open, and end of flowering, respectively31.

We used the E-OBS v19.0eHOM data set32 with a spatial resolution of 0.1° × 0.1° for 1950–2018 for calculating CA and HR of the in situ phenological records. This
data set is provided by the European Climate Assessment & Data set project and includes homogenized series of daily mean, minimum, and maximum temperatures. We also use the daily maximum and minimum temperature data from the GHCN data set to assess the scale effect. The GHCN data set contains station-based measurements from over 90,000 land-based stations worldwide, but only parts of PEP725 stations match with the GHCN stations.

For future climatic data (2019–2099), we used daily minimum and maximum temperatures simulated by the HADGEM2-ES model (with a spatial resolution of 0.5°×0.5°) under two climatic scenarios (RCP 4.5 and RCP 8.5). These data have been bias-corrected by applying the method used in the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP), which were available on the ISIMIP server (https://esg.pik-potsdam.de/projects/isimip2b/).

**Chilling models.** We used 12 chilling models to measure the amount of chilling. One type of chilling model is based on several specific temperature thresholds. The most commonly used model, developed in the 1930s and 1940s for peach, calculates the number of hours or days with temperatures <7.2 or ≥7°C. Another commonly used upper-temperature threshold for chilling is 5°C. Some studies, however, have suggested that subfreezing temperatures were effective,

\[ \text{CU}_i = \begin{cases} 1 & T \leq 5 \\ 0 & T > 5 \end{cases} \quad (1) \]

\[ \text{CU}_2 = \begin{cases} 1 & -10 < T < 5 \\ 0 & T \geq 5 \end{cases} \quad (2) \]

\[ \text{CU}_3 = \begin{cases} 1 & 0 < T \leq 5 \\ 0 & T > 5 \end{cases} \quad (3) \]

\[ \text{CU}_4 = \begin{cases} 1 & T \leq 7 \\ 0 & T > 7 \end{cases} \quad (4) \]

\[ \text{CU}_5 = \begin{cases} 1 & -10 < T < 7 \\ 0 & T \geq 7 \end{cases} \quad (5) \]

\[ \text{CU}_6 = \begin{cases} 1 & 0 < T \leq 7 \\ 0 & T > 7 \end{cases} \quad (6) \]

where \( \text{CU}_i \) is the rate of chilling for Model \( C_i \) and \( T \) is the daily mean temperature (°C).

Model \( C_7 \) is also known as the Utah Model,

\[ \text{CU}_7 = \begin{cases} 0 & T \leq 1.4 \\ 0.4 & 1.4 < T \leq 2.4 \\ 1 & 2.4 < T \leq 9.1 \\ 0.5 & 9.1 < T \leq 12.4 \\ 0 & 12.4 < T \leq 15.9 \\ 0 & T > 15.9 \end{cases} \quad (7) \]

where \( \text{CU}_i \) is the rate of chilling for Model \( C_i \) and \( T \) is the daily mean temperature (°C). Model \( C_8 \) is a dynamic model developed for peach in Israel and South Africa and now adopted for apricot cultivars. The most important characteristic of Model \( C_8 \) was that a previous intermediate product affected the rate of chilling in the current hour or day. We did not provide equations for Model \( C_9 \) for simplicity (see the equation in Luudelings et al.).

Harrington et al. summarized published results for chilling units and constructed a chilling function based on a three-parameter Weibull distribution, coded as Model \( C_{90} \) (Eq. (9)). Model \( C_{10} \) has a triangular form, which was fitted by Hänninen using previous experimental results for Finnish birch seedlings (Eq. (10)). Zhang et al. recently fitted observational data to the triangular model for 24 plant species and found that a mean optimal chilling temperature of 0.2°C and an upper limit of the chilling temperature of 6.9°C were most effective. Model \( C_{12} \), therefore, uses the triangular form with parameters of 0.2 and 6.9°C (Eq. (11)).
were not under other stresses.

\[
FU_i = \begin{cases} 
0 & T < T_i \text{ or } T > T^*_i \\
\frac{2 \pi L}{T_i - T^*_i} \left(1 + \cos\left(\frac{2 \pi (T - T_i)}{T_i - T^*_i}\right)\right) & T_i < T < T^*_i
\end{cases}
\]

(19)

where \(FU_i\) is the rate of forcing for Model \(F_i\), \(T\) is the daily mean temperature (°C), \(T_i = 4\), \(T^*_i = 25\), and \(T^*_i = 36\).

**Analysis**

We assessed the ability of each chilling model to represent long-term trends in the chilling conditions by calculating CA using each chilling model for each station for 1951–2018. CA was calculated as the sum of \(CU_i\) from 1 January to the date of onset of spring events using Model \(F_i\), and the performances of the other forcing models (\(F_i - F_6\)) were also tested. We also compared 1 January with the other two starting dates of temperature accumulation (15 January and 1 February) to test for potential difference causing by the date when temperature accumulation begins.

CA was calculated as the sum of \(CU_i\) from 1 November in the previous year to the date of onset of spring events. We chose 1 November as the start date for CA because the endodormancy of temperate trees began around 1 November. We only tested the linear relationship because the data were better fitted by the linear regression than the exponential model (Fig. 3), even though CA was linearly or nonlinearly negatively correlated with \(HR\). Pearson’s \(r\) between CA and HR for all records was calculated for each species, with a significantly negative Pearson’s \(r\) \((p < 0.05)\) indicating that the chilling model met the physiological assumption. We also analyzed the relationship between CA and HR at all stations with at least 15-year records to determine if the results were robust at the station level.

The above analysis is based on the E-OBS data set. Given the large grid size of the E-OBS data set (about 10 km) and the non-uniform cover of plants and temperature-chilling models, we assessed the scale effect by comparing the HR and CA based on E-OBS data set with GHCN data set. We only retained the phenological station where a corresponding meteorological station (distance and altitude difference should be less than 5 km and 100 m, respectively) existed in the GHCN data set and compared the HR, CA, and their relationship.

We developed an empirical model based on the linear regression function between CA and HR (e.g., the linear fitted line in Fig. 3) to simulate the past and future spring phenological change. We calculated CA (from the previous 1 November to the current date) and heat accumulation (from 1 January to the current date) for each species in each year using a daily step. HR for the current date was calculated using the predefined linear regression function between HR and CA. The day when heat accumulation began to be larger than HR was determined as the date of onset of spring events. Compared to our empirical models, in current terrestrial biosphere models, the simulation of leaf onset is usually only based on GDDs (e.g., Model \(F_1\) and \(F_2\) in this study), while only one chilling model (ORCHIDEE) consider the effect of chilling (Model \(C_1\) in this study).

Thus, at least currently, the CA–HR representation of vegetation phenology in terrestrial biosphere models.

We predicted the annual spring phenological change (2019–2099) for each species using the above process-based models under RCP 4.5 and RCP 8.5. To produce consistent phenological time series from past to future, we simulated the past spring phenological change from 1980 to 2018 by using the E-OBS v19.0eHOM data set, which was resampled to the same spatial resolution (0.5 × 0.5°) with the climatic data projected by HADGEM2-ES. First, we assessed whether different chilling models could reproduce spatial gradients of spring events across warm and cold regions in Europe. For each species, the simulated mean date (1980–2018) was correlated to the observed mean dates across grids with the observation data. Second, we assessed whether different chilling models could reproduce temporal trends of spring events in Europe. For each grid with at least 15-year observation data, the simulated and observed trends were estimated as the slope of the linear regression of spring phenology against year. At last, we compared the simulated trends estimated by each chilling model with the observed trends.

**Reporting summary**

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

**Data availability**

Phenological data can be accessed from https://www.ecad.eu/download/ensembles/download.php. GHCN data set can be accessed from https://www.ncdc.noaa.gov/data-access/land-based-station-data/

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**Code availability**

All Matlab scripts, from the initial processing of data sets to final analyses, are archived online at https://ww2.mathworks.cn/matlabcentral/fileexchange/74606-code-for-chilling-and-forcing-model.

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Acknowledgements

This work was funded by the National Key R&D Program of China (Grant No. 2018YFA0606102), National Natural Science Foundation of China (Grant No. 41871032), Youth Innovation Promotion Association, CAS (Grant No. 2018070), and Program for ‘Keqen’ Excellent Talents in IGSNRR, CAS (Grant No. 2018RC101). PC and JP were supported by ERC Synergy grant ERC-SyG-2013-610028 IMBALANCE-P.

Author contributions

H.W., C.W., and Q.G. designed the research. H.W. analyzed the data and wrote the first draft of the paper. C.W., J.P., and P.C. extensively revised the writing. All the authors contributed to writing the paper.

Competing interests

The authors declare no competing interests.

Additional information

**Supplementary information** is available for this paper at https://doi.org/10.1038/s41467-020-18743-8.

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**Peer review information** *Nature Communications* thanks the anonymous reviewers for their contributions to the peer review of this work. Peer review reports are available.

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