

Forests synchronize their growth in contrasting Eurasian regions in response to climate warming

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Forests play a key role in the carbon balance of terrestrial ecosystems. One of the main uncertainties in global change predictions lies on how the spatiotemporal dynamics of forest productivity will be affected by climate warming. Here we show an increasing influence of climate on the spatial variability of tree growth during the last 120 years, ultimately leading to unprecedented temporal coherence in ring-width records over wide geographical scales (spatial synchrony). Synchrony in growth patterns across cold-(central Siberia) and drought-constrained (Spain) Eurasian conifer forests have peaked in the early twenty-first century at subcontinental scales (~1,000 km). Such enhanced synchrony is similar to that observed in trees co-occurring within a stand. In Boreal forests, the combined effects of recent warming and increasing intensity of climate extremes are enhancing synchrony through an earlier start of wood formation and a stronger impact of year-to-year fluctuations of growing-season temperatures on growth. In Mediterranean forests, the impact of warming on synchrony is mainly related to an advanced onset of growth and the strengthening of drought-induced growth limitations. Spatial patterns of enhanced synchrony represent early-warning signals of climate change impacts on forest ecosystems at subcontinental scales.

tree rings | spatial synchrony | global warming | boreal forests | Mediterranean forests

Introduction

Understanding how climate change affects forests across multiple spatiotemporal scales is important for anticipating its impacts on terrestrial ecosystems. Increases in atmospheric CO₂ concentration and shifts in phenology (1–3) could favor tree growth by enhancing photosynthesis and extending the effective growing period, respectively (4). Conversely, recent warming could increase respiration rates and, together with increasing heat and drought stresses, exert negative impacts on forest productivity (5, 6). As it is unclear to what extent enhanced carbon uptake could be offset by the detrimental effects of warming on tree performance, the actual consequences of climate change on forest carbon cycling are still under debate. Notably, climate change has a stronger impact on forests constrained by climatic stressors such as suboptimal temperatures or water shortage (7). As high-resolution repositories of biological responses to the environment, dendrochronological archives can be used to monitor this impact (8).

The concept of spatial synchrony in tree growth refers to the extent of coincident changes in ring-width patterns among geographically disjunct tree populations (9). Climatic restrictions tend to strengthen growth-climate relationships resulting in enhanced common ring-width signals (i.e. more synchronous tree growth). Thus, regional bioclimatic patterns can be delineated by identifying groups of trees whose growth is synchronously driven by certain climatic constraints (10, 11). A number of synthesis studies provide evidence for globally coherent multispecies responses to climate change in natural systems, including forests,

with a focus on the role of increasingly warmer temperatures (12, 13). Indeed, climate has changed markedly over the last decades, prompting an array of physiological reactions in trees that could strengthen growth-climate relationships, hence enhancing spatial synchrony. Such tree responses may be linked to global shifts in the timing of plant activity (2), drought stress in mid latitudes (6, 14), or uncoupling of air and soil thermal regimes in the early growing season (15) and direct heat stress (16) in high latitudes, among others. Changing tree growth patterns associated to enhanced synchrony in response to warming have been reported at small geographical scales (<150 km) (14–18, but see 19). However, an extended examination of synchrony patterns is currently lacking for large (i.e. subcontinental) areas.

To determine whether climate warming and increased variability (1) lead to more synchronous tree growth, we examine changes in spatial synchrony for the last 120 years across subcontinental areas by using a comprehensive network of 93 ring-width chronologies from six different conifer species across two climatically contrasting Eurasian biomes: Boreal forests in central Siberia ($n = 45$ chronologies) and Mediterranean forests in Spain ($n = 48$ chronologies; *SI Appendix*, Fig. S1 and Table S1). Central Siberia has a severe continental climate with a prolonged cold season, large intra-annual temperature variations and moderate precipitation. Spain is dominated by a typical Mediterranean climate with mild (coast) to cool (inland) wet winters and summer drought. Thus, temperature exerts the main climatic control over

Significance

Forests dominate carbon fluxes in terrestrial ecosystems. We demonstrate how an intensified climatic influence over tree growth during the last 120 years has increased spatial synchrony in annual ring-width patterns within contrasting (Boreal and Mediterranean) Eurasian biomes and on broad spatial scales. Current trends in tree growth synchrony are related to regional changes in climate factors controlling productivity, overriding local and taxonomic imprints on forest carbon dynamics. Enhanced synchrony is becoming a widespread, although regionally dependent, phenomenon that is related to warmer springs and increased temperature variability in high latitudes and to warmer winters and drier growing seasons in mid latitudes.

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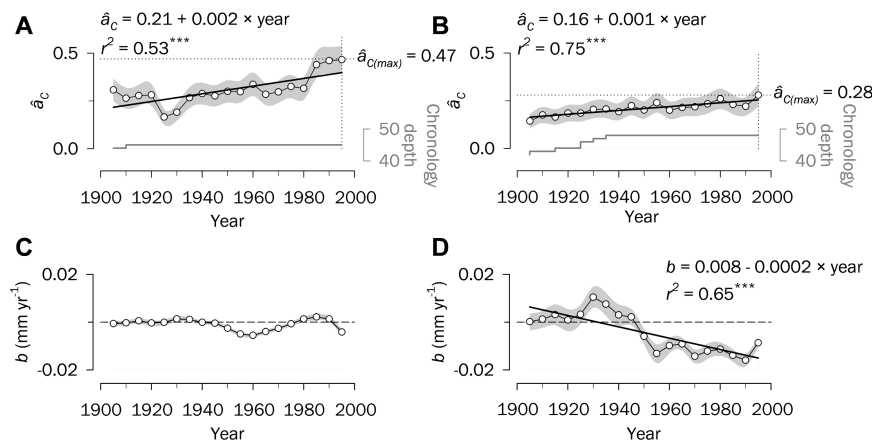


Fig. 1. Synchrony patterns and changes in absolute growth for the period 1890–2009. The spatial synchrony (\hat{a}_c) is estimated for central Siberia (A) and Spain (B) using ring-width chronologies for successive 30-year periods lagged by five years. The dotted lines indicate \hat{a}_c maxima over the study period. Grey lines represent the number of chronologies with EPS > 0.85 (chronology depth). Temporal trends in the slope (b) of growth in central Siberia (C) and Spain (D) are estimated based on raw ring-width data for the same time intervals used for synchrony. The dashed lines indicate no change in growth rate over the study period. Significant linear trends over time are depicted as black lines (***, $p < 0.001$). Shaded areas denote standard errors. Values in the x-axes correspond to the middle year of 30-year moving intervals.

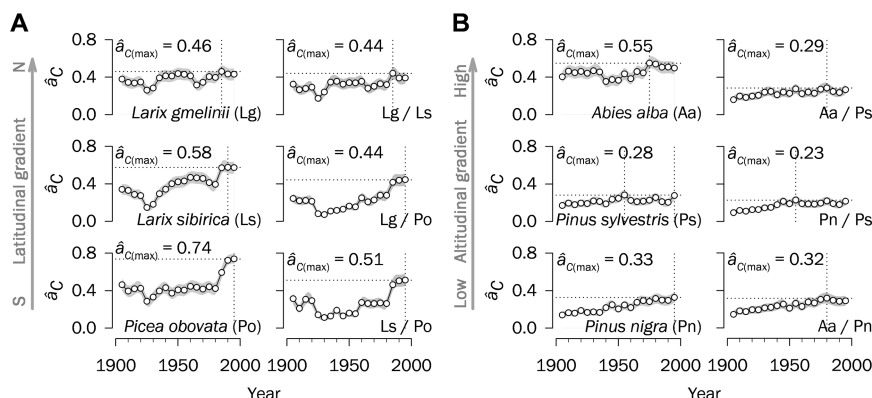


Fig. 2. Temporal trends in spatial synchrony for single and paired species for central Siberia (A) and Spain (B). Synchrony estimates (\hat{a}_c) in single species (1st and 3rd column) and species pairs (2nd and 4th column) are calculated based on ring-width chronologies using successive 30-year periods lagged by five years. The dotted lines indicate \hat{a}_c maxima over the study period in each case. Standard errors are shown as shaded areas. Values in the x-axes correspond to the middle year of 30-year moving intervals.

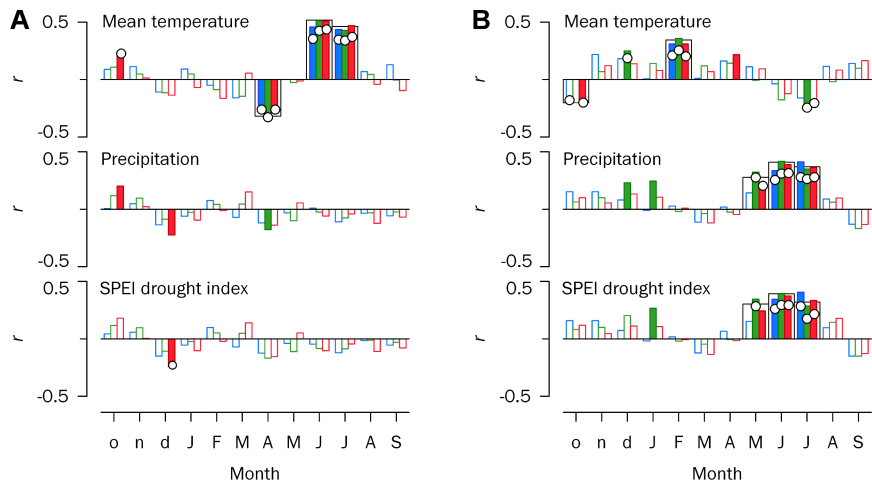


Fig. 3. Growth-climate relationships at the species and regional levels for central Siberia (A) and Spain (B). Tree growth responses to climate are based on bootstrapped correlations (indicated by bars) and response function partial regression coefficients between tree-ring indices for species or regions and monthly mean temperature, precipitation and SPEI drought index for the period 1930 to 2009. Significant correlation and partial regression coefficients ($p < 0.05$) are indicated by filled bars and white circles, respectively. Species are represented in blue (*Larix gmelinii*, *Abies alba*), green (*Larix sibirica*, *Pinus nigra*) and red (*Picea obovata*, *Pinus sylvestris*). Wide bars denote significant relationships at the regional level. Lowercase and uppercase letters in the x-axes correspond to the years before and during tree-ring formation, respectively.

productivity in Boreal forests, while Mediterranean forests are primarily water-limited (SI Appendix, section 1A).

Temporal changes in spatial synchrony (hereafter, \hat{a}_c) are quantified using a novel mixed model framework (20). This methodology has two fundamental advantages for dendrosciences (21) over other alternative approaches useful for interpreting population dynamics in ecology (22) or patterns of environmental synchrony (23): (i) it is capable of dealing with partially overlapping chronologies, yielding valid inferences of spatial synchrony for large areas in which ring-width data are available but covering different time periods; (ii) it is highly flexible to fit general statistical structures for subdivided groups

of chronologies, opening new avenues for interpreting complex spatial patterns through geographic or taxonomic stratification of a target region.

We hypothesize that climate warming triggers more synchronous tree growth at subcontinental scales owing to an amplified climatic control of growth (e.g. through higher temperatures in Siberia or decreased water availability in Spain; 1). Our objective is to interpret forest reactions to warming through an alternative approach to model-based assessments or field experimentation. Specifically, this study asks the following questions: (i) is spatial synchrony of tree growth increasing across terrestrial biomes and at what pace?, (ii) how are synchrony patterns related

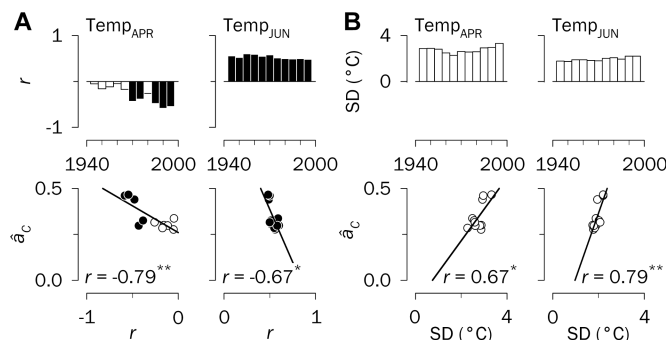


Fig. 4. Climate factors underlying changes in synchrony in central Siberia (1930–2009). (A) Moving correlation analyses (r -values) between regional tree-ring indices and April and June mean temperatures (Temp) and (B) standard deviates (SD) of April and June mean temperatures are displayed in bar diagrams for successive 30-year periods lagged by five years (upper panels). Significant correlations are indicated by filled bars in (A) ($p < 0.05$). Relationships between synchrony estimates (\hat{a}_c) and r -values or SD of climate variables are presented in scatter plots (lower panels). Note that only monthly climate factors significantly correlated to \hat{a}_c are displayed (*, $p < 0.05$; **, $p < 0.01$). The filled circles correspond to the periods with significant growth-climate relationships as indicated by moving correlation analyses in the upper panels. Displayed years in the x-axes correspond to the middle year of 30-year moving intervals.

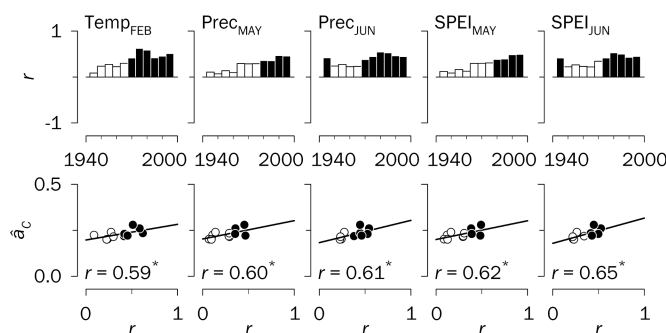


Fig. 5. Climate factors underlying changes in synchrony in Spain (1930–2009). Moving correlation analyses (r -values) between regional tree-ring indices and February mean temperatures (Temp), and May and June precipitation (Prec) and SPEI drought index in May and June are displayed in bar diagrams for successive 30-year periods lagged by five years (upper panels). Relationships between synchrony estimates (\hat{a}_c) and r -values are presented in scatter plots (lower panels). For further details see caption to Fig. 4.

to intra- and inter-specific responses to climate warming?, and (iii) what are the main climate factors underlying more synchronous forest growth? It is widely accepted in ecological theory that spatial synchrony influences metapopulation persistence and the likelihood of species extinction (24). As forests are becoming more prone to widespread mortality (25), interpreting long-term synchrony patterns of tree growth may be relevant to identify broad-scale threshold responses to climate change.

Results and Discussion

Increases in synchrony and absolute growth trends: regional patterns

Synchrony trends show that \hat{a}_c has increased during the period 1890–2009 in both study regions (Fig. 1 A and B), but at a two-fold higher pace in Siberia than in Spain ($b = 0.002 \text{ yr}^{-1}$ vs. 0.001 yr^{-1}). Whereas the increasing trend is steady over time for Spain, \hat{a}_c has experienced larger fluctuations for Siberia, with an abrupt rise observed in the last three decades. Overall, \hat{a}_c values are significantly higher after 1950 than in the first half of the twentieth century ($p = 0.001$ and $p < 0.001$ for Siberia and Spain,

respectively; one-tailed Student's test), reaching in both regions unmatched values after the 1970s.

Notably, peaks in spatial synchrony are reached in the early twenty-first century (Fig. 1 A and B). This result suggests a progressive influence of external forcing mechanisms impacting on tree performance through vast geographical areas and overriding local drivers of growth (such as topography, nutrient availability, tree competition or management, to name a few). Regional forest synchrony is currently reaching values comparable to the mean synchrony between co-occurring trees within a stand (Spain, $\hat{a}_c = 0.28 \pm 0.06$ [region] vs. 0.40 ± 0.13 [stand]; Siberia, $\hat{a}_c = 0.47 \pm 0.07$ vs. 0.49 ± 0.10 ; [mean \pm SE]). The lower mean \hat{a}_c in Spain over the study period (0.21 ± 0.02 vs. 0.32 ± 0.03 in Siberia) contrasts with the lower average distance between stands in Spain compared to Siberia ($346 \pm 195 \text{ km}$ vs. $575 \pm 331 \text{ km}$ [mean \pm SD], respectively; SI Appendix, Fig. S1). In any case, synchrony patterns in Siberia and Spain are statistically independent (SI Appendix, Tables S2 and S3), indicating that the increasing synchrony in tree growth is a widespread ecological phenomenon, although regionally dependent. Synchrony estimates could be sensitive to the number of available chronologies, and this number progressively decreases in the most recent years (SI Appendix, Table S1). However, we find a high agreement in \hat{a}_c between the complete set of chronologies and a subset that extends beyond the year 2000 (Siberia, $r = 0.90$; Spain, $r = 0.87$; $p < 0.001$ in both cases). An analysis of anomalously wide or narrow rings (i.e. “pointer years”), originating from extreme external events (26), is in agreement with the absolute peaks in synchrony found in both regions at the turn of this century (SI Appendix, section 2A and Fig. S2).

To further explore how increasing synchrony is related to regional growth patterns, we use raw ring-width records and assess shifts in growth rates over time. We notice differential paces of tree growth in Siberia and Spain for the period 1890–2009. A clear growth slowdown is observed in Spain ($b = -0.00024 \text{ mm yr}^{-2}$), whereas no significant trend appears in Siberia (Fig. 1 C and D). Such temporal changes could be affected by variations in the population age/size structure (the average chronology length is 303 ± 82 years and 247 ± 129 years for Siberia and Spain [mean \pm SD], respectively). To check for age-independent growth declines, we assess growth dynamics only for old-growth forest stands (>200 years old; $n = 43$ chronologies for Siberia; $n = 30$ chronologies for Spain). This approach minimizes temporary dynamics associated with stand development and succession. We observe a good agreement when comparing the results from this subset with the growth patterns found for the complete dataset ($r = 0.99$, $p < 0.001$ for Siberia; $r = 0.87$; $p < 0.001$ for Spain, slowdown for Spain $b = -0.00014 \text{ mm yr}^{-2}$), indicating that age-dependent declines cannot explain temporal changes in growth. Growth reduction in Mediterranean forests may be caused by increasing water limitations (6), but the lack of a positive growth response to warming in Boreal forests is puzzling. Various hypotheses have been raised to explain this phenomenon (27), but temperature-induced drought or direct heat stress are plausible constraints of forest productivity in high latitudes (16).

Increases in synchrony and absolute growth trends: taxonomic patterns

At the species level, \hat{a}_c peaks at the turn of this century in most cases (Fig. 2). Overall, species-specific changes in synchrony are in good agreement with regional trends, although *Larix gmelinii* in Siberia and *Pinus sylvestris* in Spain exhibit less obvious (but also significant) increments in \hat{a}_c over the past 120 years. Notably, the spatial synchrony between pairs of species also increases with time (Fig. 2). However, \hat{a}_c values across species pairs tend to be lower than for individual species which indicates that, while inter-specific variability in growth responses certainly exists and is important (e.g., deciduous vs. evergreen conifers in

Table 1. Multiple linear stepwise regressions explaining synchrony ($\hat{\alpha}_C$) patterns from changing growth-climate relationships (correlation coefficients, r) and climate variability (standard deviates of climate factors, SD) over the period 1930 to 2009. Codes of the variables are as in Figs. 4 and 5 (upper panels) for Siberia and Spain, respectively. Abbreviation: MSE, mean square error.

Synchrony	Initial variable	Initial r^2	Initial MSE	Final stepwise model	Final r^2	Final MSE
Siberia	correlation with climate factors ($rTmean_{APR}$, $rTmean_{JUN}$)					
	$rTmean_{APR}$	0.63**	0.020	$\hat{\alpha}_C = 0.26 - 0.29 rTmean_{APR}$	0.63**	0.020
	correlation with climate factors and variability ($rTmean_{APR}$, $rTmean_{JUN}$, $SDTmean_{APR}$, $SDTmean_{JUN}$)					
	$SDTmean_{APR}$, $SDTmean_{JUN}$	0.63**	0.020	$\hat{\alpha}_C = -0.47 + 0.28 SDTmean_{JUN}$ $+ 0.10 SDTmean_{APR}$	0.75***	0.013
Spain	correlation with climate factors ($rTmean_{FEB}$, $rPrec_{MAY}$, $rPrec_{JUN}$, $rSPEI_{MAY}$, $rSPEI_{JUN}$)					
	$rSPEI_{JUN}$	0.43*	0.003	$\hat{\alpha}_C = 0.18 + 1.03 rSPEI_{JUN} - 0.93$ $rPrec_{JUN} + 0.08 rTmean_{FEB}$	0.75***	0.002

*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

Siberia), the strength of these inter-specific differences is diminishing with time, resulting in more synchronous tree growth.

Boreal forests in Siberia, mainly limited by low temperatures (15, 16), show high synchrony irrespective of the species; instead, primarily water-limited forests in Spain (14, 19) have lower synchrony. It is likely that temperature exerts a larger influence on the spatial signal imprinted in tree rings than precipitation (10) owing to the higher spatial homogeneity of temperature in Siberia compared to the more complex rainfall pattern countrywide in Spain (*SI Appendix*, Fig. S3). In fact, *Abies alba* shows the largest $\hat{\alpha}_C$ among the three Spanish species, which could be explained by its limited spatial distribution and narrow niche amplitude at mesic sites in north-eastern Spain (mean distance between stands = 124 ± 68 km) (*SI Appendix*, Fig. S1).

To further test for spatial consistency in synchrony patterns (22), we examine how the correlations between pairs of chronologies vary with distance among forest stands. The spatial synchrony spreads over distances >900 km and >600 km for Siberia and Spain, respectively (*SI Appendix*, Fig. S3). More importantly, synchrony is higher in the second than in the first half of the twentieth century, for all species and regions at most distances (*SI Appendix*, Fig. S4). The intercept (but not the slope) of the linear relationship between r -values and distances increases for all evergreen conifers. In the case of *Larix* spp. we find significant slope changes, indicating that synchrony increases more after 1950 than before proportionally to distance. Altogether, our results suggest that external forcing factors superimpose on species-specific and local controls, hence triggering a more synchronous tree growth.

We also investigate shifts in absolute growth trends over time at the species level (*SI Appendix*, Fig. S5). We observe a growth slowdown for all species in Spain, whereas the rate of growth changes remains steady in Siberia. Notably, growth fluctuations in Siberia become more consistent across species after the 1950s (mean correlation of growth trends between pairs of species before 1950, $r = -0.41$; after 1950, $r = 0.53$). A gradual growth decline in Spain, reflecting increasingly limiting conditions over time, and a more systematic pattern of growth changes in Siberia from 1950 onwards seem to concur with the rise in synchrony observed at different regional paces (sustained in Spain, abrupt in the last decades in Siberia) during the last 120 years.

Processes driving increases in synchrony

Increases in synchrony are usually attributed to the influence of climate on tree growth, as no other environmental driver is likely to act on the same range in time and space (8). Yet, a number of additional global drivers might also trigger the ob-

served increase in synchrony through their effect on growth. First, increasing atmospheric CO_2 concentrations can be expected to augment water-use efficiency, hence boosting forest productivity (4). Second, nitrogen deposition could further increase growth through higher rates of carbon sequestration in sites with unfertile or poorly developed soils (28). Third, a decrease in solar radiation caused by anthropogenic aerosol emissions from 1950 (global dimming; 29) may counteract the effect of CO_2 fertilisation or rising N deposition, negatively impacting on photosynthesis, especially in high latitudes (30). Fourth, changes in stand structure due to rural abandonment, limited forest management and encroachment usually increase competition for resources and could reduce tree growth (31). A detailed examination of these drivers (*SI Appendix*, section 2B) leads us to discard them as major causes of growth synchrony as opposed to climate.

We then examine whether enhanced synchrony is driven by regional climate trends. Although the Earth's surface has experienced a conspicuous warming in the last century, the pace of temperature changes differs regionally (1). Interestingly, the steady increase in synchrony among Spanish forests seems in line with the gradual warming observed over the twentieth century. In turn, temperature at high Eurasian latitudes shows a consistent upward trend since the 1970s, which coincides with the steep increase in synchrony observed in Siberia (*SI Appendix*, Fig. S6).

Analyses of climatic factors causing changes in growth and of climate drivers underlying $\hat{\alpha}_C$ fluctuations are restricted to data collected after 1930, in concert with the availability of reliable instrumental records (32). Despite species-specific ecological features, the main climate variables related to growth are regionally consistent across taxa (Fig. 3). As expected, we find strong positive associations between growth and June–July temperatures in Siberia (15, 33) (cold-limited growth) and May–July precipitation and the SPEI drought index in Spain (19) (drought-constrained growth). Besides, growth correlates with early spring (April) temperature in Siberia (negatively) and with late winter (February) temperature in Spain (positively, Fig. 3). Such contrasting regional responses to temperature in the early growing season may be a consequence of varying physiological processes underlying the mechanisms of dormancy breaking. After chilling requirements are met in winter, cambial reactivation can occur earlier in Siberia under higher April temperatures (34), hastening the onset of xylogenesis (35). However, newly formed tissues can be damaged if followed by severe frosts (33), causing hydraulic dysfunction (freeze–thaw events) (36). A warm spring may also activate the photosynthetic machinery in crowns that are func-

tionally uncoupled from roots (35), and sudden early-spring temperature drops may impair photosynthesis in Boreal evergreen conifers (37). These mechanisms may restrict radial growth in high latitudes (38). In contrast, in Mediterranean environments an early cambial reactivation triggered by warm winters usually increases carbon uptake and enhances wood formation (39).

The spatial structures of these growth-climate relationships are characterized through cross-correlation analyses. The spatial association is significant for most climate factors at sites >900 km apart in Siberia and >600 km apart in Spain (*SI Appendix*, Fig. S7), confirming the existence of consistent subcontinental forest responses to climate (11). This result means that climate is a primary mechanism of synchrony in our tree-ring network. It is therefore possible that increases in forest synchrony have been driven by concomitant increases in regional climate synchrony. However, we find that this is actually not the case (*SI Appendix*, section 2C and Fig. S8).

Alternatively, we evaluate whether enhanced synchrony is related to climate trends and variability. For this purpose we first assess regional changes in growth-climate relationships through moving correlations. Most relevant changes span from the onset of the growing season through early summer, hence matching the period of earlywood formation. For Siberia, the negative dependence of growth on warmer April temperature increases over time (Fig. 4A); for Spain, high February temperatures and high May–June precipitation and SPEI become more important for growth (Fig. 5). In this regard, we observe that $\hat{\alpha}_C$ values are significantly associated to the correlation coefficients of the varying relationship between growth and early growing-season temperature. Notably, this association is negative for April in Siberia (Fig. 4A) and positive for February in Spain (Fig. 5), hence indicating divergent regional growth dynamics. In both cases, we interpret this result as a sign of earlier cambial reactivation promoting more synchronous growth over time. Rising temperatures may induce an earlier cambial reactivation (40) resulting in both a higher rate of xylem cell production and a longer duration of cambial growth which, in principle, should increase ring-width (41). However, this is not the case for Siberia, where an earlier onset of cambial activity might be associated with increasing risk of frost damage to the cambium (40). In this region tree growth remains limited by low summer temperatures (Fig. 4A and *SI Appendix*, S9) but this constraint has decreased after the 1970s because of the positive warming trend (*SI Appendix*, Fig. S6), exerting a growth desynchronization in June (Fig. 4A). This effect is counterbalanced by a reinforcement of the negative impact of high April temperatures on growth as a driver of synchrony (Fig. 4A). In Spain we also observe a diminishing growth dependence on July precipitation and SPEI (*SI Appendix*, Fig. S10) (19), which suggests a reduction of cambial activity in summer (36) in response to warming-induced drought (*SI Appendix*, Fig. S11) and a growth shift towards spring (May–June) (Fig. 5), hence enhancing synchrony.

Synchrony patterns may not be exclusively linked to long-term climate trends but also to changes in climate extremes over time (26), as suggested by the reported independence of spatial correlations of record-breaking monthly temperatures time series from those of the temperatures themselves (42). In general, significant linear trends in climate variability (i.e. standard deviates of monthly climate factors; *SI Appendix*, Fig. S11) are observed for relevant growth periods (*cf.* Fig. 3). We find that a more synchronous growth in Siberia is related to a larger temperature variability in April and June (Fig. 4B), but not in peak summer (July; *SI Appendix*, Fig. S9). Instead, the variability of climate is unrelated to changes in synchrony in Spain (*SI Appendix*, Fig. S10).

Finally, we explore the complementarity of climate trends and variability in explaining regional synchrony through stepwise

linear regressions (Table 1). Initially, the impact of climate trends on synchrony is considered using the subset of monthly climate factors whose temporal relationships with growth exhibit a significant association with $\hat{\alpha}_C$ values (Figs. 4 and 5). These models provide a good explanation of synchrony changes (especially for Spain), indicating that recent warming is a significant driver of synchrony across the studied Eurasian forests. However, if climate variability is also considered the model fitting is further improved in Siberia up to r^2 -values similar to those for Spain. In fact, climate variability for April and June in Siberia and climate trends for February temperature and June water availability (precipitation and SPEI) in Spain explain 75% of the observed regional synchrony patterns. Unravelling the exact effects of climate warming and extremes on forest synchrony would require both a higher spatial saturation of site chronologies and more detailed instrumental records covering large geographic areas.

This study illustrates how early signals of climate change impacting on forests can be traced back through the interpretation of synchrony patterns stored in tree rings. Here we demonstrate that climate change is modulating spatial synchrony in tree growth over disparate Eurasian regions, increasing the strength of the common signal shared by trees under warmer conditions to levels comparable to the mean synchrony between co-occurring trees within a stand. Even reporting on different *Pinaceae*, including evergreen and deciduous conifers, our results are consistent across species. The mechanisms behind this pattern require further examination, but they seem to be dependent on the increasing importance of regional-scale climate signals in tree rings overriding local growth drivers. The observed enhanced synchrony may anticipate declines in tree vigor and growth that are critical for the functioning and maintenance of forest ecosystem services under a warmer future climate.

Materials and methods

Tree-ring indices and absolute growth trends. Site chronologies of tree-ring indices (*SI Appendix*, section 1B) were obtained by cross-dating the tree-ring width (TRW) series and posterior detrending and autocorrelation removal with the Friedman supersmoother spline and autoregressive modeling (43). This procedure eliminates the juvenile growth trend and generates stationary (mean = 1) and residual TRW chronologies of dimensionless indices that preserve common variance encompassing inter-annual timescales (high-frequency variability potentially related to climate). Adequacy of sample size for capturing the hypothetical population signal was assessed by the Expressed Population Signal (EPS), with a threshold value of 0.85 used to identify the ‘critical year’ at which the site chronology becomes reliable (44). The study period was 1890 to 2009, i.e. period when the impact of climate change on tree performance becomes noticeable (45). The common time span across chronologies was 1924 to 1990 (central Siberia) and 1950 to 1988 (Spain).

Temporal trends in tree growth were characterized by the estimation of growth rate changes using raw TRW records. To this end, the slope of the linear regression of TRW on time was calculated for each chronology for successive 30-year periods lagged by five years. The slopes were then averaged for a particular region and for each period, and a simple linear function was fitted after visual inspection. The slope of this function was interpreted as rate of regional (or species) growth change. Comparison of growth rates between regions (species) was performed through ANOVA heterogeneity of slopes.

Mixed modelling. To investigate spatial synchrony patterns in indexed chronologies we made extensive use of variance-covariance (VCOV) mixed modelling (20) (*SI Appendix*, section 1C). To this end, chronologies were grouped into potentially homogeneous subsets (20). First, two groups were formed corresponding to each region. Next, chronologies were classified at the regional level into three groups according to membership to a particular species. A number of VCOV models accommodating between- and within-group variability were tested (*SI Appendix*, section 1C) and compared by Akaike and Bayesian information criteria, which favour parsimonious models (46). We then derived estimates of spatial synchrony (or mean inter-chronology correlation, $\hat{\alpha}_C$) for chronologies belonging to either the same region (species) or different regions (pairs of species) through the best VCOV model (*SI Appendix*, section 1D, Tables S2 and S3). The parameter $\hat{\alpha}_C$ is related to the mean inter-series correlation defined at the intra-site level in dendrosciences (44). In both cases, VCOV structures were tested for successive 30-year segments lagged by five years. The length of 30 years was established by plotting the standard error of $\hat{\alpha}_C$ against segments of varying length (from 10 to 50 years) for each region. The segment length corresponding to the

inflection point of the curves was selected as a balance between number of years and precision achieved (SI Appendix, Fig. S12).

Development of regional and species master chronologies. TRW indices at the regional and species levels were estimated by best linear unbiased prediction (BLUP), thus obtaining regional and species master chronologies underlying the network of site chronologies (SI Appendix, section 1E). We derived BLUP estimates from the best VCOV model fitted to the whole study period using either a regional or a species classification as grouping criterion. BLUPs were used as input for climate analysis.

Spatial patterns in synchrony. To assess how far the spatial patterns in forest synchrony extend, we calculated the geographical distance between pairs of chronologies, which were used (i) to obtain correlograms (47) testing for significant correlations between chronologies located within ranges of 300 km apart (SI Appendix, section 1F) and (ii) to regress correlations between pairs of chronologies on distances. The linear regressions were calculated at the species level for the periods 1890–1949 and 1950–2009 and their slopes tested through ANOVA heterogeneity of slopes. Regression slopes were interpreted as indicators of spatial synchrony.

Relationships with climate. The effect of temperature, precipitation and SPEI (48) on the inter-annual variability of TRW indices was quantified through bootstrapping correlations and response function analyses (8) relating regional and species master chronologies to monthly climatic data (SI Appendix, section 1G). Growth-climate relationships were analyzed from the previous October to current September, i.e. the year of tree-ring formation. In addition, we obtained correlograms for temperature and precipitation testing for significant correlations between sites located within ranges of 300 km apart (47). We also performed cross-correlation analyses to test for causality of synchrony patterns in relevant climate factors as drivers of forest synchrony over progressively larger distances (SI Appendix, section 1F) (47).

The influence of climate change on regional synchrony was assessed through a two-step procedure. First, a moving correlation analysis involving regional chronologies and monthly climate factors was performed for successive 30-year periods lagged by five years; subsequently, changes in temporal dependence of growth on climate (i.e. r -values of the moving correlation analysis) were related to variation in $\hat{\alpha}_c$ over time through simple correlations. Second, we examined a possible role of climate variability in explaining changes in synchrony. To this end, we calculated the standard deviation (SD) for monthly climate factors of successive 30-year periods lagged by five years. The relationships between SD of climate variables and $\hat{\alpha}_c$ were also investigated through simple correlations. The analyses of both climate trends and variability determining synchrony was restricted to the subset of climate factors showing a significant impact on growth for the entire period, 1930 to 2009, as a prerequisite for identifying climate drivers of $\hat{\alpha}_c$ fluctuations. To determine the predictive ability of climate factors and their variability on the explanation of synchrony patterns, linear stepwise models were built at the regional level using as independent variables the r -values of the moving correlation analysis (step 1) and the SD changes over time (step 2), with a threshold value of $p = 0.15$ as the criterion for variables to be either included or removed.

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