

Evidence of unprecedented rise in growth synchrony from global tree ring records

Rubén Delgado Manzanedo ^{1,2} M, Janneke HilleRisLambers¹, Tim Tito Rademacher ^{3,4,5} and Neil Pederson ²

Changes in the temporal coherence between populations, which can influence their stability, resilience and persistence, remain a critical uncertainty of climate change. Recent studies have documented increasing spatial synchrony between populations at continental scales and linked it to anthropogenic climate change. However, the lack of long-term and global baseline perspectives on spatial synchrony presents a challenge to understanding the importance of these trends. Here, we show a steady rise in the spatial synchrony of annual tree growth from a global tree ring database over the past 50 years that is consistent across continents, species and environmental conditions and is unprecedented for the past millennium. Increasing growth synchrony coincided with warming trends and potentially rising synchrony in the temperature records. We discuss the potential driving mechanisms and the limitations in the interpretation of this trend, and we propose that increasing mutual dependency on external factors (also known as Moran's effect) linked to rising global temperatures is the most likely driver of more homogeneous global growth dynamics.

t is well understood that climate change will impact forests globally by shifting species' distributions and abundances¹, changing forests' species composition² and increasing forest disturbance³. Less well understood is the effect that the changing climate may have on the temporal coherence between populations, although the topic is receiving more attention recently^{4–7}. This is a pressing issue, because concurrent changes in abundance or performance over time between distinct populations (that is, spatial synchrony) is a fundamental population characteristic that influences the functioning, dynamics, persistence and stability of metapopulations^{8–10}. Indeed, changes in forest carbon dynamics are a fundamental consequence of the response of terrestrial ecosystems to global change, their stability to future changes and their ability to (at least partially) reduce the concentration of atmospheric CO₂ and the negative consequences derived from it.

Disentangling the factors influencing spatial synchrony requires long-term data from multiple taxa and at a continental-to-global scale^{4,9,11-13}. Such extensive datasets are still rare in ecological studies¹⁴, particularly those with long-term data, despite the disproportionately strong contribution of these long-term studies to advancing ecology and management policies¹⁵. Existing ecological long-term datasets, such as time series of pollen from sediment cores (see, for example, ref. 16), provide a valuable long-term view on changing forest types and shifting ecosystems at decadal-to-centennial resolutions that shows the broad patterns of ecosystem dynamics. However, their lower temporal resolution makes them less useful to explore the links between spatial synchrony and annual variations in climate, and they cannot be generally applied to explore the effects of recent climate change on high-resolution synchrony dynamics. Fortunately, the growth patterns expressed in tree rings, which combine large temporal and spatial scales with precise annual resolution, offer a unique opportunity to cover this knowledge gap. The increasing number of reports of rising spatial synchrony in multiple species and regions, some of which used tree ring records,

underscores the urgent need for a large-scale, long-term assessment of ecological synchrony to understand its importance and driving mechanisms⁴⁻⁷.

Here, we aim to investigate whether spatial synchrony in forest growth is increasing at the global scale and, if so, whether recent trends go beyond the long-term historical variability captured in these records. We also explored some of the species-, environmentand continent-specific differences in trends, and in so doing, we examined potential biotic and abiotic drivers of changes in spatial synchrony of forest populations globally. We used a global dataset comprising more than 52 million tree-growth observations stretching back 1,000+ years, the International Tree-Ring Data Bank (ITRDB). The ITRDB's extensive global database of annually resolved tree growth includes 4,042 tree populations of 226 tree taxa over many of Earth's forested ecosystems (Fig. 1). Despite its large size, this dataset is not completely free of potential taxonomical¹⁷ and changing sampling size biases¹⁸ (further discussed in subsequent sections). To retain the annual variation in growth in a comparable way across species and ecosystems, we calculated the annual growth chronologies for each tree population in the ITRDB independently, reducing the effects of local conditions, species' inherent characteristics and stem size. This results in a time series retaining annual changes in growth (white-noise time series). Previous studies have shown that white-noise time series isolate the interannual growth signal of trees through the reduction of all centennial trends and most decadal-scale variations¹⁹⁻²¹. The detrended chronologies were used to calculate how global spatial synchrony has changed during the period 1000-2016 CE using a 50-year moving window approach. We used this approach for both raw and absolute value correlations. While the comparison of raw correlation trends is the commonly used metric in synchrony studies (see, for example, ref. 5), we argue that increasing strengths of both positive and negative correlations between populations may mask each other and obscure total changes in growth synchrony. We therefore decided to examine **ARTICLES**

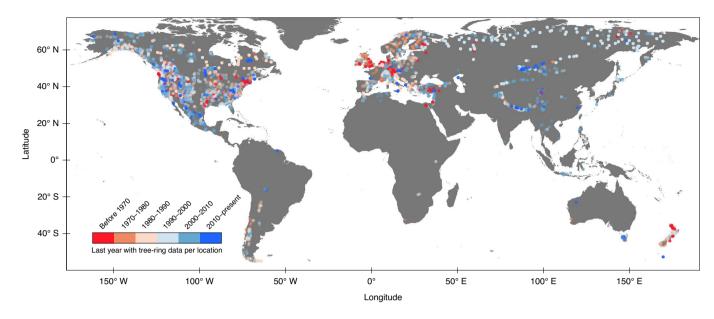


Fig. 1 | Sampling locations of the database, with the last year of data included per sampled population. Each dot represents a sampling location with time-series data of tree growth for several trees (first and third quantiles, 21–43 tree cores per location; average, 37.1 cores per location). The data were obtained from the ITRDB.

and present both metrics to extract greater insight as well as retain our ability to compare our results with those of previous studies. Since trends in positive and negative correlations may have different mechanisms and ecosystem consequences, we also tested whether the observed trends agreed among positive-only and negative-only correlations, and we found them to be highly consistent. Negative synchrony, a still scarcely studied topic, can arise through 'climate dipoles'—that is, the tendency for opposite extremes of temperature and precipitation to emerge at a continental scale or by opposed responses to the same climatic factor by multiple groups of trees (for example, higher temperatures leading to opposite responses at different altitudinal edges). However, our analysis cannot thoroughly investigate this aspect of spatial synchrony, which should be explored in future works. We include all populations and taxa in our analyses to capture the general patterns of change across ecosystems and species.

Results and discussion

Recent trends in global and continental spatial synchrony. For nearly a millennium, the absolute global spatial synchrony of tree growth was very stable (1000–1970 CE, Fig. 2a). During this period, global correlation values (|r|) consistently ranged between 0.15 and 0.20 (Fig. 2a). In contrast, the past 50 years saw a sharp increase in spatial synchrony, such that by the last year of our records the global mean correlation reached a value of $|r|_{2016} = 0.26$, a value not found in any single year before 1970. Overall, the global spatial synchrony values since the 1970s were significantly higher than those of the previous 1,000 years (Fig. 2b; $D_{KS(1000-1970 \text{ versus } 1970-2016)} = 0.986$, where D_{KS} refers to the two-sample Kolmogorov–Smirnov statistic between the two described distributions (1000-1970 versus 1970-2016); P < 0.001). Although we use 1970 as the threshold after which anthropogenic warming rose consistently, it should be noted that synchrony change has been progressive, with an increasing trend starting somewhere between 1970 and 1980. The rising trend in synchrony in recent decades was consistent across continents, although lower sample sizes increased the uncertainty in regions with low replication, specifically Africa, Oceania and South America (Fig. 2c,d and Supplementary Fig. 1). Lower- and higher-elevation populations (Supplementary Fig. 2) were also consistent in their trends. Together, this suggests a major shift in the spatio-temporal dynamics of forest populations across the globe, unprecedented in the lifetime of most trees worldwide. Theoretical and observational work has linked continental synchrony to large-scale climatic variability^{5,6,22}. Our results complement previous work on the temporal trends in spatial synchrony in multiple publications that have also used tree ring approaches at multiple scales. Surprisingly, these studies have suggested increasing^{9,23}, decreasing^{24,25} or largely unchanging²⁶ spatial synchrony. The taxonomical and scale differences in these works relative to ours may partially explain the contrasting patterns, but they also emphasize the need for a mechanistic understanding of spatial synchrony in natural populations and of our expectations for its response to environmental change. We show tree-growth spatial synchrony rising consistently across the globe and reaching values significantly higher than the expected long-term natural variability.

By contrast, neither low-frequency (that is, multiannual to decadal) (Supplementary Note 3) nor raw correlation (Supplementary Note 4) synchrony had stable long-term baseline trends (Supplementary Fig. 7). Both metrics did change over time, but their interpretation may be difficult. Low-frequency chronologies may capture disturbance patterns, tree size differences, successional trajectories, multidecadal climate shifts or a combination of those factors (see, for example, refs. 19,27,28). To fully disentangle those signals would require detailed knowledge of the local forest structure, history and microhabitat for each population, including individual tree locations, currently not available for the ITRDB (ref. 17). Interestingly, although positive-only and negative-only synchrony trends were highly consistent with each other (as also shown by the small differences in raw correlation trends in Supplementary Fig. 7), we observed a slightly faster increase in positive correlations than in negative correlations (Supplementary Fig. 8). Asymmetric changes in positive versus negative synchrony would be particularly concerning because they may contribute to positive feedbacks related to carbon cycling, although this is highly speculative and would require additional work to verify. Also, raw correlation trends were not consistent across continents (Supplementary Figs. 9 and 10), and the change in raw correlations was in all cases orders of magnitude smaller than the change in absolute correlations. The potential masking of increasing synchrony due to simultaneous increases in positive and negative correlations is one of the main reasons why we also examined the absolute value of the correlations, rather than

ARTICLES

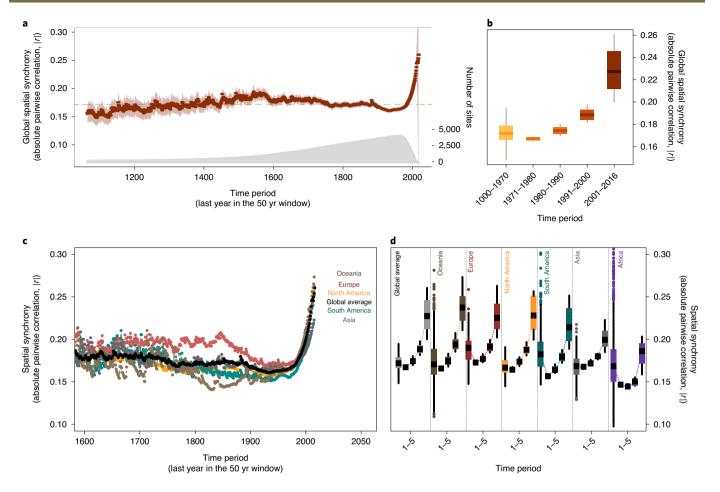


Fig. 2 | The recent increase in global synchrony in tree growth greatly exceeds the variability observed in the past 1,000 years and is consistent across all of Earth's continents. **a**, Mean absolute pairwise correlation values between tree populations for the period 1000–2016 ce. The 95% confidence interval for |r| and the sample size also displayed for each period. **b**, Decadal trend in synchrony and comparison with the historical 1000–1970 baseline. **c**, Trend in mean absolute pairwise correlation for each continent for the period 1600–2016. Values before 1600 are considered increasingly unreliable due to reduced sample sizes in some continents (see Supplementary Note 1 for the complete series). For the same reason, data from Africa are not displayed in **c**. **d**, Comparison between recent decades and the historical 1000–1970 baseline per continent. Time periods (from left to right): 1, 1000–1970; 2, 1971–1980; 3, 1980–1990; 4, 1991–2000; 5, 2001–2016. The growth time series were obtained from the ITRDB. In **b** and **d**, boxes show the interquartile range and median values while whiskers represent the nominal data range. Values outside of the nominal data range (if any) are plotted as closed circles.

limiting the analysis to the raw mean, as a proxy for spatial synchrony, but it should be noted that we would have reached different results by analysing raw correlations only. Also, since the mechanisms driving increasing negative or positive synchrony may differ, we argue that it may be interesting to study both the change in total synchrony (as absolute value) and the differences in each of the positive and negative trends. In any case, it is important to keep in mind that in the absolute correlation approach, increasing similarity (that is, increasing mean correlation) includes both positive (an increase in population A tends to coincide with an increase in population B) and negative (an increase in population A tends to coincide with a decrease in population B) relationships, and that these trends have to be interpreted while keeping the results of the raw correlation values also in mind (provided here in Supplementary Notes 1 and 2).

Potential mechanisms driving increasing spatial synchrony. Three main mechanisms are considered to influence the synchrony between populations: (1) Moran's effect, the mutual dependence on exogenous interconnected factors, such as climate¹²; (2) dispersal, which effectively changes population size and increases connectivity; and (3) trophic interactions with species that are themselves synchronous or mobile (that is, an external biotic driver of

synchrony). Although these mechanisms are based in the original

definition of synchrony, based in population abundances, they can also be applied to other vital rates. For example, increased connectivity through dispersal may increase genetic similarity between populations of the same species, making them less locally adapted and more responsive to general patterns, and thus increasing their synchrony (for example, see ref. ²⁹). Although all three factors could theoretically influence tree-growth performance, we believe that the strengthening of Moran's effect is the strongest candidate for recent increases in tree-growth synchrony, as it would be the most consistent with a simultaneous and steady increase in global correlations of tree growth.

While dispersal and trophic interactions can also influence population synchrony, we believe neither of these are likely to have caused the increase in growth synchrony we observed. There are multiple reasons for this. Dispersal (of seeds and/or pollen) might increase synchrony in growth via increasing genetic similarity between populations or by phase locking predator–prey cycles^{30,31}. However, both mechanisms require a consistent and simultaneous increase in dispersal across multiple taxa with different dispersal vectors and occurring within the half-life of tree longevity for most species. To our knowledge, there are no reports of recent consistent increases in dispersal that could support the role of increased dispersal in growth synchrony. Increasing trophic-mediated synchrony

ARTICLES

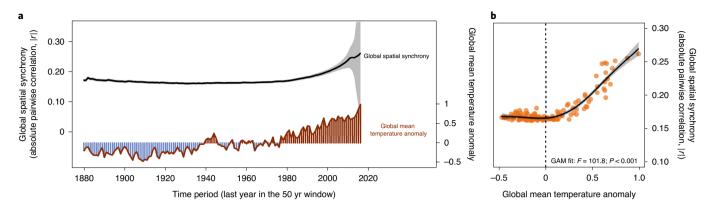


Fig. 3 | Relationship between increasing synchrony and warmer climate. a, Time series of mean absolute pairwise correlations between all populations for each period (black) and the combined land-surface air and sea-surface water temperature anomalies; positive (red) and negative (blue) temperature anomalies, as compared with the 1951–1980 mean value⁶⁰. **b**, Synchrony seems unresponsive to negative temperature anomalies but strongly correlates with positive anomalies. A fitted nonlinear GAM is displayed (black, 95% confidence intervals in grey).

is similarly unlikely to explain the observed pattern, since it would also require multiple mobile predators, herbivores, diseases or pests to increase their activity simultaneously, and for them to have had similar effects on growth on tree populations globally^{4,9}, for which there is also no supporting evidence. Finally, both dispersal- and trophic-mediated synchrony are likely to have a stronger influence at smaller scales (local to regional or continental) than climate, and are also likely to be highly stochastic, which would probably result in synchrony trends differing between continents and exhibiting high annual variability. It is, however, possible for pest pressure to be mediated by changes in temperature. Oscillations in insect populations and other pests are known to be temperature sensitive³². Rising temperatures may thus lead to higher defence demands, shifting resource allocation balance and causing reduced tree growth. It remains unclear whether the link between tree synchrony and temperature is directly mediated by tree physiology or may be affected by more complex interactions, such as those with biotic agents. In summary, our results show limited support for the dispersal or trophic hypotheses, rather pointing to the increasing mutual dependency on external factors as the most likely culprit for increasing spatial synchrony. However, singling out the concrete exogenous factors causing the observed global increase in synchrony is a more complex task.

Factors causing an increasing mutual dependency on external factors. The fact that rising global tree-growth synchrony coincides (1970-2016) and correlates (general additive model (GAM) fit, F = 101; P < 0.001) with recent large-scale increasing temperatures (Fig. 3a) supports the hypothesis that large-scale changes in climate are increasing its control over tree growth, reducing the effect of regional and local climate dynamics (which has been previously suggested for certain regions)6, and thus creating a more globally coherent response to climate³³. Indeed, recent work has shown that current climate trends are unique in their degree, extent and global coherence, even when compared with previous global climate events such as the Little Ice Age or the Medieval Warm Period34,35, consistent with our results. Furthermore, there is ample supporting evidence for the key role of temperature and water limitations in tree-growth dynamics³⁶. However, our results also suggest a complex relationship between changing climates and growth synchrony. The relationship between tree-growth synchrony and global temperature seemed nonlinear. Under normal to relatively cold conditions (temperature anomalies between approximately -0.5and 0.5), the coherence of global tree growth seemed unrelated to changes in temperature. However, further increases in average

temperature anomalies, such as the ones we are recently experiencing increasingly frequently, corresponded with higher global average correlation between forest populations (Fig. 3b).

Additional supporting evidence for increasing temperatures underlying increases in global synchrony is the concurrent increase in spatial synchrony of the temperature records themselves (Fig. 4a), a pattern not seen in precipitation records (Fig. 4b). Although both temperature and nitrogen deposition values seem to be becoming more homogeneous at a global scale for the studied populations, the timing of increasing nitrogen synchrony is not coincident with rising growth synchrony, as temperature is (Fig. 4a and Supplementary Fig. 12). Increases in geographical coherence in global surface temperatures have been previously suggested, but how to methodologically test increasing variable homogeneity is not free of controversy (see 'Spatial synchrony of environmental variables' for further information). In combination, these observations suggest that anthropogenic warming is the most likely factor influencing forest synchrony at a large scale.

While we found strong support for the hypothesis that annual global temperature variability is becoming more homogeneous and driving forest growth synchrony, we need to be cautious in these conclusions, as they are derived from observational data and correlative approaches. Regional changes in total surface irradiance, due to anthropogenic aerosol production and regulation, may also contribute to large-scale changes in tree-growth patterns. Moreover, it is possible that plant-relevant environmental factors that are correlated with temperature may also play a role in the recent increases in synchrony across populations. Positive and negative synchrony trends may also be affected by different sets of drivers or with differing relative importance. Below, we discuss other factors that may play important roles or interact with our current main driver candidate, temperature, and how likely we believe they are to influence the observed patterns.

Teasing apart the relative importance and interactions between temperature-related factors of climate change (such as atmospheric CO_2 concentration, water vapour pressure deficit and changes in snow cover) is still a major challenge for observational studies, requiring further experimental and methodological developments. In the case of increasing growth synchrony among trees (as we observed), for example, it is possible that the combined effect of rising atmospheric CO_2 and temperature improved growing conditions for many forests worldwide, resulting in more homogeneous growth responses across forest populations, as they move away from being carbon and temperature limited or change their water use efficiency. This would be consistent with our results, but

NATURE ECOLOGY & EVOLUTION ARTICLES

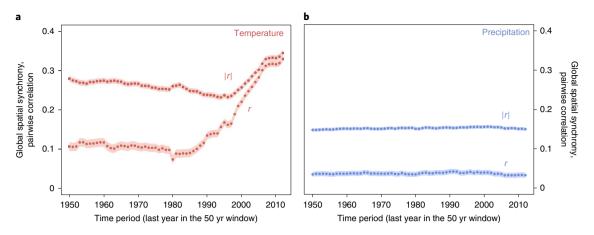


Fig. 4 | Concomitant increase in temperature synchrony between forest sampling locations supports a strengthening of Moran's effect as a main driver of rising synchrony in recent years. a,b, Temporal change in spatial synchrony in mean annual temperature (°C) (a) and total annual precipitation (mm) (b). Both the mean (r) and absolute mean (|r|) pairwise correlations are displayed. The climate data are from the version 2 of the Princeton Reanalysis project⁵⁸. The 95% confidence intervals are also shown.

there has been very limited support for an overall positive response of global forests to increased CO₂ (ref. ²⁰), and recent large-scale analysis suggests that forests are not growing faster despite increasing water use efficiency³⁷. Carefully designed experiments (see, for example, ref. ³⁸, which disentangled the roles of dispersal, environmental factors and parasite dynamics in the synchrony of *Paramecium* metapopulations) are needed to clarify which of the co-occurring drivers may best explain spatial synchrony, and it is certainly likely that interactive effects are very important in these patterns.

Rising nitrogen deposition also has the potential to systematically affect the correlation between distant populations by causing parallel growth stimulation in the time series (but see ref. ³⁸). In fact, we found an increase in the correlation between nitrogen deposition time series in the past century (Supplementary Fig. 11). However, this increase in synchrony in nitrogen deposition did not coincide with the increase in growth synchrony. Instead, it rapidly increased from 1940 to 1970 and levelled off afterwards. Given the wide range of responses to increased carbon and nitrogen availability observed across species and ecosystems^{20,37,39,40}, we consider it unlikely that increasing nutrient availability could cause a consistent and strong global rise in synchrony across taxa. However, we should be on guard for potential lagged effects or changes in limiting factors that could indicate increasing importance of nutrient availability for spatial synchrony.

Humans may also influence spatial synchrony patterns, not only indirectly through anthropogenic climate change but also directly via human disturbances and land-use change. Large-scale, spatially autocorrelated disturbances, linked to the increasing human footprint⁴¹, may result in increasing large-scale similarity between populations. However, the populations targeted in the ITRDB are strongly biased towards natural sites with little evidence of human impact (that is, logging), which substantially reduces the chances that humans exert a strong influence in our data. Furthermore, Pederson et al.42 showed that human disturbances do not mask the role of synchrony caused by climatic drivers (in their case, drought) as a driver of annual to decadal growth. Although there are currently no data that would allow us to rigorously test this (for example, the global human footprint raster dataset in ref. 41 covers the period 1993–2009, not comparable to our long-term interval approach), we consider it unlikely that humans have directly influenced synchrony in annual growth time series in remote, old-growth forests on generally rugged landscapes.

Increasing or shifting climatic teleconnections⁴³ could influence the similarity between certain distant populations. However, the fact that there has been little to no increase in the strength of the most influential global climate oscillation index, the El Niño/Southern Oscillation (ENSO), in the period 1970–2016, and no increasing linkage between the two of the most important global circulation indices, the Southern Oscillation Index (SOI) and the North Atlantic Oscillation (NAO) index (Supplementary Fig. 11), seems to offer very limited support for the role of climatic teleconnections or atmospheric circulation patterns in spatial synchrony. Overall, while teleconnections may certainly increase the connectivity between some of the populations, teleconnections are complex and temporarily varying, and they differ between continents; it is not likely that they are the main factor driving the increase in global synchrony that we observed.

Increasing frequency or intensity of extreme climate events, as has been predicted by most climate forecasts^{44–46}, could also affect growth coherence by increasing the frequency of years with extreme low (or high) ring growth in large regions or by locking large portions of the landscape in parallel successional progressions that result in higher correlations between distant, unconnected populations. A long-term database on the extent and recurrence of extreme events at the global scale could allow further tests of this hypothesis and reveal the commonalities and trends in extreme climate events⁴⁷. However, we hypothesize that increasing frequencies of highly stochastic events, such as extreme drought events, would result in a highly variable increasing trend in synchrony, which contrasts with the steady rise in spatial synchrony we observed. Alternatively, the interaction between extreme events and shifting species distributions could influence large-scale spatial synchrony by inducing a change in the baseline conditions that trees experience. Rapidly shifting climate may push tree populations beyond the bounds of their optimal climatic conditions, something supported by the reported loss in the future climatic potential distributions of species (for example, see ref. 48). These maladapted tree populations may experience more frequently suboptimal growth years, resulting in a more coherent climate response across the species range, an idea that has not been tested or reported so far in natural populations.

Limitations and caveats of large tree ring databases. It is important to keep in mind that the ITRDB represents a non-random and non-constant sample of the global forests¹⁷. Although these factors clearly affect our quantitative results, we found that the trend in

rising synchrony persisted when we controlled for sampling methodology, continental representation, temporal changes in sampling size, species diversity and changes in the average distance between populations (Supplementary Note 1). It has been discussed how the reduction in contributed series to the ITRDB since 1970 may affect the analysis of climate-change-related processes due to the co-occurrence of declining sample sizes and increasing temperatures¹⁸, and the observed increase in synchrony in the ITRDB is no exception to this. The consistency of the trend across multiple continents and hundreds of species with different sampling efforts, combined with the fact that we found no change in the average distance between populations in that period (Supplementary Fig. 6), suggests that changes in sample size or biases towards a subset of the populations are unlikely to be solely responsible for the observed increase in spatial synchrony.

However, it is clear that low sample sizes hinder our exploration of synchrony trends. Periods with low replication, such as 1000-1200 CE for all continents or poorly replicated African ecosystems, resulted in high year-to-year variability and large standard errors obscuring synchrony trends (Supplementary Fig. 1). This was also observed in our sensitivity analyses, where we removed 96.8% of the network, composed mostly of high-elevation conifers from North America and Europe (144 constant populations). In this extreme test, we found that the observed change in synchrony persisted, though substantially reduced in strength (Supplementary Fig. 5). It is likely that reducing the sample size exacerbates the temporal, spatial and taxonomic limitations of the database and reduces the length of the period studied¹⁷, suggesting that databases with sparse spatial coverage or reduced sample size may have problems to reliably identify long-term global dynamics of spatial synchrony. Whether this would apply to other databases depends on their signal-to-noise ratio. However, we expect the ITRDB to be fairly representative of most non-targeted aggregative large databases in ecology. In the future, the ITRDB must continue improving its coverage and representativity to become an even more reliable and powerful data source to study forests' responses to changing climate^{17,18,49}, included population synchrony.

A final issue to consider here is the sampling priorities of the ITRDB data. Dendrochronologists have traditionally targeted canopy trees and focused on populations most suited for climatic reconstructions or the study of climate-growth dependencies. As a consequence, the forests captured in the ITRDB are likely to be more sensitive to climate than randomly selected trees⁵⁰. However, the similarity in spatial synchrony between populations from markedly different environmental conditions and elevations (which the ITRDB does capture) suggests that historical sampling biases are likely to be less influential in the calculation of spatial synchrony than in the case of other ecological characteristics. For example, populations near the upper elevational tree line, which are known to be strongly climate limited⁵¹, showed very consistent trends with those at lower elevations (Supplementary Fig. 2). This hypothesis, however, should be revisited with even bigger and more complete datasets to test whether ITRDB trees may over- or underestimate the response of synchrony in global forest populations, as has been suggested for other metrics⁵⁰.

Conclusions. Overall, we found an increase in absolute synchrony of annual radial growth of tree populations around the world over the past 50 years that significantly differed from the historically constant baseline of the prior 970 years. Our analyses suggest that a warmer and more synchronous climate around the world may disrupt the millennial-length stability of large-scale tree-growth synchrony, pushing populations towards new, uncharted terrain. We also show that, despite data limitations, annual tree-growth time-series approaches can provide a long-term and large-scale baseline to understand changes in population dynamics and their

importance, and we emphasize that additional research is urgently needed to confirm and expand our results. It is important to further explore regional trends, investigate differences between positive and negative synchrony trends, and enhance the metadata associated with each of the points to tease apart the multiple mechanisms that could drive large-scale spatial synchrony. The consequences that increases in global spatial synchrony may have for the functioning and resilience of these populations are still unknown.

Methods

Tree-growth data. We used time series of annual growth available in the ITRDB (ref. ⁵²), accessible at https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring. The ITRDB is a comprehensive global database of tree growth, compiling data from 4,042 populations and 226 different taxa in 6 continents, and having a large temporal coverage (see, for example, ref. ¹⁸). The ITRDB has been used for many large-scale and long-term climate reconstructions (for example, see refs. ^{53,54}) and ecological analyses of forest growth (for example, see refs. ^{21,55}). We considered separate forest populations those entries in the ITRDB that either had unique GPS coordinates for their sampling site or had different target species. For most populations, the ITRDB provides information on tree radial growth, although a handful include data on epiphytes (woody vines) or small tree species. We used a recently cleaned and harmonized version of the dataset¹⁷, which includes all the available datasets and amounts to more than 52 million data points as of September 2017.

Calculating site chronologies. Using the dplR package⁵⁶, we calculated growth chronologies for each sampling location using a detrending method with a flexible spline of two-thirds of the total length of the growth series. The chronology for each population was calculated as the ratio between the observed and fitted values per tree and year, and the final site chronology was calculated using a bi-weight robust mean. An autocorrelation term was included in the model to remove year-to-year autocorrelation, hence creating white-noise or high-frequency time series (also known as residual chronologies) for each population. The goal of these methods is to reduce long-term trends related to age, geometrical constraints and ecological disturbances (for example, see refs. 19-21). Previous theoretical work on spatial synchrony recommends detrending the response variable to remove potentially obscuring long-term trends9 as well as pre-whitening the series to remove serial dependency (see ref. 9 and the references therein). To examine potential synchrony at low frequencies, a chronology for each population was calculated using the bi-weight robust mean of the fitted splines for each tree in each location without applying an autocorrelation term to remove year-to-year autocorrelation. These and all subsequent analyses were performed in R (ref. 57).

Spatial synchrony of growth. We calculated the trend in spatial synchrony using a 50-yr moving window for the period 1000–2016 cg. For each time interval, the mean absolute correlation is calculated from a correlation matrix that includes all complete pairwise correlations between sampling locations⁹ after removing those series that had no or only partial growth data for the time period. We studied the consistency of our results by repeating our analyses with multiple subgroups, including comparisons between continents, comparisons between high and low elevations, systematic changes in age or species diversity in the database, and randomly chosen populations to see the effects of sample size (Supplementary Note 1). We performed parallel analyses using the mean, rather than absolute correlations (Supplementary Note 2), as well as using the low-frequency spline described above (Supplementary Note 3). Tests for significant differences between synchrony metrics of different decades and with long-term values were done by two-sample Kolmogorov–Smirnov tests.

Temperature anomaly data and correlation with synchrony. To explore the role of temperature and climate change conditions in synchrony, we calculated the correlation between global synchrony and the combined land-surface air and sea-surface water temperature anomalies from meteorological records by GISTEMP Team 2018, available via the NASA repositories at https://datahub.io/core/global-temp#data-cli. Given the reported nonlinear response between synchrony and temperature*, we used a flexible GAM to estimate this relationship.

Spatial synchrony of environmental variables. We calculated the spatial synchrony in temperature and precipitation using a similar method to that used for the growth time series. Annual precipitation and mean temperature data were obtained from the Princeton Reanalysis data version 2 (ref. ⁵⁸), available at http://hydrology.princeton.edu/data.pgf.php. Mean annual temperature and total annual precipitation time series were computed from daily data for each $0.5^{\circ} \times 0.5^{\circ}$ grid cell containing an ITRDB sampling location. The change in nitrogen synchrony was calculated using annually resolved time series of nitrogen deposition from the ISIMIP2b input data, available at https://www.isimip.org/gettingstarted/details/24/ as NHX and NOY time series ⁵⁹. We combined NHX and NOY to create a time series of total nitrogen deposition for each ITRDB coordinate that was used to explore changes in nitrogen's spatial synchrony (Supplementary Fig. 12).

NATURE ECOLOGY & EVOLUTION ARTICLES

Analysing NHX and NOY separately showed consistent results (these data are not shown). We finally detrended the time series of precipitation, temperature and nitrogen to test whether the long- or short-term changes in those variables may be linked to increasing synchrony (Supplementary Fig. 12b,d,f). Whether increasing homogeneity of environmental values should be inferred from the detrended or undetrended time series remains unclear. Unlike tree growth, where inherent differences between ecosystems, species and tree age make standardization a necessity to obtain a comparable metric, temperatures do not have such local or taxon-specific differences. We therefore consider synchrony analyses of the undetrended time series to be the most informative metric, as they retain the large-scale temperature patterns. However, since the correlation analysis of the detrended time series showed no increase across sites similar to that of the raw values, we prefer to show both for clarity and to aid the reader's interpretation (Supplementary Fig. 12b,d,f).

We also tested the trends in the most important global circulation index, ENSO, using data from NOAA, available at ftp://ftp.ncdc.noaa.gov/pub/data/paleo/treering/reconstructions/enso-li2013.txt. The changes in the relationship between these patterns were explored by calculating the change in correlation between the SOI and the NAO index, using a 50-yr moving correlation window (Supplementary Fig. 11). However, this analysis should be interpreted with caution, as both indices may have partially overlapping data sources. The SOI and NAO data are available at https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/.

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

Data availability

All the data used in this study are publicly available. The tree-growth data are available via the NOAA web repository at https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring. The combined land-surface air and sea-surface water temperature anomaly data from GISTEMP Team 2018 are available via the NASA repositories at https://datahub.io/core/global-temp#data-cli. The annual precipitation and mean temperature data from the Princeton Reanalysis data version 2 are available at http://hydrology.princeton.edu/data.pgf.php. The nitrogen deposition data from the ISIMIP2b input data are available at https://www.isimip.org/gettingstarted/details/24/. The ENSO, SOI and NAO time series from NOAA are available at ftp://ftp.ncdc.noaa.gov/pub/data/paleo/treering/reconstructions/enso-li2013.txt and https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/. The version of the data used in this manuscript is available at https://figshare.com/articles/dataset/Data_for_Evidence_of_unprecedented_rise_in_growth_synchrony_from_global_tree_ring_records_/12623501.

Code availability

The R script used to analyse the data and generate the graphs is available at https://figshare.com/articles/dataset/Annex_5_script/12623492. The graphs were generated in R and then imported to Inkscape for final formatting.

Received: 9 September 2019; Accepted: 21 August 2020; Published online: 26 October 2020

References

- 1. Thomas, C. D. et al. Extinction risk from climate change. Nature 427, 145-148 (2004).
- Alexander, J. M., Diez, J. M. & Levine, J. M. Novel competitors shape species' responses to climate change. *Nature* 525, 515–518 (2015).
- Seidl, R., Schelhaas, M.-J., Rammer, W. & Verkerk, P. J. Increasing forest disturbances in Europe and their impact on carbon storage. *Nat. Clim. Change* 4, 806–810 (2014).
- 4. Post, E. & Forchhammer, M. C. Synchronization of animal population dynamics by large-scale climate. *Nature* **420**, 168–171 (2002).
- Koenig, W. D. & Liebhold, A. M. Temporally increasing spatial synchrony of North American temperature and bird populations. *Nat. Clim. Change* 6, 614–617 (2016).
- Shestakova, T. et al. Forests synchronize their growth in contrasting Eurasian regions in response to climate warming. *Proc. Natl Acad. Sci. USA* 113, 662–667 (2016).
- Black, B. A. et al. Rising synchrony controls western North American ecosystems. Glob. Change Biol. 24, 2305–2314 (2018).
- Heino, M. Noise colour, synchrony and extinctions in spatially structured populations. Oikos 83, 368–375 (1998).
- Liebhold, A., Koenig, W. D. & Bjørnstad, O. N. Spatial synchrony in population dynamics. *Annu. Rev. Ecol. Evol. Syst.* 35, 467–490 (2004).
- Gouhier, T. C., Guichard, F. & González, A. Synchrony and stability of food webs in metacommunities. Am. Nat. 175, E16–E34 (2010).
- 11. Elton, C. S. Periodic fluctuations in the numbers of animals: their causes and effects. *Br. J. Exp. Bot.* **2**, 119–163 (1924).
- 12. Moran, P. A. P. The statistical analysis of the Canadian lynx cycle. *Aust. J. Zool.* 1, 291–298 (1953).

- Loreau, M. & de Mazancourt, C. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. Am. Nat. 172, E48–E66 (2008).
- Buma, B. et al. The value of linking paleoecological and neoecological perspectives to understand spatially-explicit ecosystem resilience. *Landsc. Ecol.* 34, 17–33 (2018).
- Hughes, B. B. et al. Long-term studies contribute disproportionately to ecology and policy. BioScience 67, 271–281 (2017).
- Gajewski, K., Viau, A. E., Sawada, M., Atkinson, D. E. & Fines, P. Synchronicity in climate and vegetation transitions between Europe and North America during the Holocene. Clim. Change 78, 341–361 (2006).
- Zhao, S. et al. The International Tree-Ring Data Bank (ITRDB) revisited: data availability and global ecological representativity. *J. Biogeogr.* https://doi. org/10.1111/jbi.13488 (2018).
- Babst, F., Poulter, B., Bodesheim, P., Mahecha, M. D. & Frank, D. C. Improved tree-ring archives will support earth-system science. *Nat. Ecol. Evol.* 1, 0008 (2017).
- Cook, E. R. & Peters, K. Calculating unbiased tree-ring indices for the study of climatic and environmental change. *Holocene* 7, 361–370 (1997).
- Gedalof, Z. E. & Berg, A. A. Tree ring evidence for limited direct CO₂ fertilization of forests over the 20th century. Glob. Biogeochem. Cycles 24, GB3027 (2010).
- Gazol, A., Camarero, J. J., Anderegg, W. R. L. & Vicente-Serrano, S. M. Impacts of droughts on the growth resilience of Northern Hemisphere forests. *Glob. Ecol. Biogeogr.* 26, 166–176 (2016).
- Pomara, L. Y. & Zuckerberg, B. Climate variability drives population cycling and synchrony. *Divers. Distrib.* 23, 421–434 (2017).
- Briffa, M. et al. Trends in recent temperature and radial tree growth spanning 2000 years across northwest Eurasia. *Phil. Trans. R. Soc. B* 363, 2271–2284 (2008).
- Ponocná, T. et al. Deviations of treeline Norway spruce radial growth from summer temperatures in East-Central Europe. Agric. Meteorol. 253, 62–70 (2018).
- Shestakova, T. A., Gutiérrez, E., Valeriano, C., Lapshina, E. & Voltas, J. Recent loss of sensitivity to summer temperature constrains tree growth synchrony among boreal Eurasian forests. *Agric. Meteorol.* 268, 318–330 (2019).
- Schurman, J. S. et al. Large-scale disturbance legacies and the climate sensitivity of primary *Picea abies* forests. *Glob. Change Biol.* 24, 2169–2181 (2018).
- Schweingruber, F. H. Tree Rings: Basics and Applications of Dendrochronology (Springer Science & Business Media, 1996).
- 28. Speer, J. H. Fundamentals of Tree-Ring Research (Univ. of Arizona Press, 2010).
- Savolainen, O., Pyhäjärvi, T. & Knürr, T. Gene flow and local adaptation in trees. Annu. Rev. Ecol. Evol. Syst. 38, 595–619 (2007).
- Ripa, J. Analysing the Moran effect and dispersal: their significance and interaction in synchronous population dynamics. Oikos 89, 175–187 (2000).
- Hopson, J. & Fox, J. W. Occasional long distance dispersal increases spatial synchrony of population cycles. *J. Anim. Ecol.* 88, 154–163 (2019).
- Johnson, C. A. et al. Effects of temperature and resource variation on insect population dynamics: the bordered plant bug as a case study. *Funct. Ecol.* 30, 1122–1131 (2016).
- Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42 (2003).
- 34. St. George, S. The aberrant global synchrony of present-day warming. *Nature* 571, 483–484 (2019).
- 35. Neukom, R. et al. Consistent multidecadal variability in global temperature reconstructions and simulations over the common era. *Nat. Geosci.* **12**, 643–649 (2019).
- 36. Babst, F. et al. Twentieth century redistribution in climatic drivers of global tree growth. Sci. Adv. 5, eaat4313 (2019).
- Giguère-Croteau, C. et al. North America's oldest boreal trees are more
 efficient water users due to increased [CO₂], but do not grow faster. *Proc. Natl Acad. Sci. USA* 116, 2749–2754 (2019).
- Duncan, A. B., Gonzalez, A. & Kaltz, O. Dispersal, environmental forcing, and parasites combine to affect metapopulation synchrony and stability. *Ecology* 96, 284–290 (2015).
- Girardin, M. P. et al. No growth stimulation of Canada's boreal forest under half-century of combined warming and CO₂ fertilization. *Proc. Natl Acad. Sci.* USA 113, E8406–E8414 (2016).
- Manzanedo, R. D. et al. Increase in CO₂ concentration could alter the response of Hedera helix to climate change. Ecol. Evol. 8, 8598–8606 (2018).
- 41. Venter, O. et al. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat. Commun.* 7, 12558 (2016).
- Pederson, N. et al. Long-term drought sensitivity of trees in second-growth forests in a humid region. Can. J. Res. 42, 1837–1850 (2012).
- Kug, J. S., An, S. I., Ham, Y. G. & Kang, I. S. Changes in El Niño and La Niña teleconnections over North Pacific–America in the global warming simulations. *Theor. Appl. Clim.* 100, 275–282 (2010).
- Rahmstorf, S. & Coumou, D. Increase of extreme events in a warming world. *Proc. Natl Acad. Sci. USA* 108, 17905–17909 (2011).

ARTICLES NATURE ECOLOGY & EVOLUTION

- 45. Cai, W. et al. Increasing frequency of extreme El Niño events due to greenhouse warming. *Nat. Clim. Change* 4, 111–116 (2014).
- Fischer, E. M., Beyerle, U. & Knutti, R. Robust spatially aggregated projections of climate extremes. Nat. Clim. Change 3, 1033–1038 (2013).
- Trenberth, K. E., Fasullo, J. T. & Shepherd, T. G. Attribution of climate extreme events. *Nat. Clim. Change* 5, 725–730 (2015).
- 48. Thurm, E. A. et al. Alternative tree species under climate warming in managed European forests. *Ecol. Manage.* 430, 485–497 (2018).
- Manzanedo, R. D. & Pederson, N. Towards a more ecological dendroecology. Tree Ring Res. 75, 152–159 (2019).
- Klesse, S. et al. Sampling bias overestimates climate change impacts on forest growth in the southwestern United States. *Nat. Commun.* 9, 5336 (2018).
- Ettinger, A. K., Kevin, R. F. & HilleRisLambers, J. Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology* 92, 1323–1331 (2011).
- Grissino-Mayer, H. D. & Fritts, H. C. The International Tree-Ring Data Bank: an enhanced global database serving the global scientific community. *Holocene* 7, 235–238 (1997).
- 53. Wilson, R. et al. Last millennium Northern Hemisphere summer temperatures from tree rings. Part I: the long term context. *Quat. Sci. Rev.* 134, 1–18 (2016).
- Cook, B. I., Anchukaitis, K. J., Touchan, R., Meko, D. M. & Cook, E. R. Spatiotemporal drought variability in the Mediterranean over the last 900 years. J. Geophys. Res. Atmos. 121, 2060–2074 (2016).
- Charney, N. D. et al. Observed forest sensitivity to climate implies large changes in 21st century North American forest growth. *Ecol. Lett.* 19, 1119–1128 (2016).
- Bunn, A. G. A dendrochronology program library in R (dplR). Dendrochronologia 26, 115–124 (2008).
- R: A Language and Environment for Statistical Computing Version 3.5.0 (R Core Team, 2017).
- Sheffield, J., Goteti, G. & Wood, E. F. Development of a 50-yr high-resolution global dataset of meteorological forcings for land surface modelling. *J. Clim.* 19, 3088–3111 (2006).

- Lamarque, J.-F. et al. The Atmospheric Chemistry and Climate Model Intercomparison Project (ACCMIP): overview and description of models, simulations and climate diagnostics. Geosci. Model Dev. 6, 179–206 (2013).
- GISTEMP Team GISS Surface Temperature Analysis (GISTEMP) Version 4 (NASA Goddard Institute for Space Studies, accessed 2 July 2018); https://data.giss.nasa.gov/gistemp/

Acknowledgements

We thank all the generous contributors of the ITRDB; without them this work would not be possible. We thank T. Mandra and J. Maxwell for providing insightful comments in earlier versions of this manuscript. This work was supported by the Swiss National Science Foundation (SNF) through the Early Postdoc.Mobility scheme, and the Harvard Forest.

Author contributions

R.D.M., J.H. and N.P. conceived and designed the main research questions and methodology. R.D.M. and T.T.R. analysed the data. R.D.M. created the figures and the first draft of the manuscript. All authors contributed to the interpretation and writing in successive versions of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-020-01306-x.

Correspondence and requests for materials should be addressed to R.D.M.

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

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

© The Author(s), under exclusive licence to Springer Nature Limited 2020

nature research

Corresponding author(s):	Rubén Delgado Manzanedo		
Last updated by author(s):	Jul 6, 2020		

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see our Editorial Policies and the Editorial Policy Checklist.

_		-		
Ci	- ~ :	₽ï.	\sim +	ics
^	_		SI.	10°

For	For all statistical analyses, confirm that the fo	lowing items are present in the figure legend, table legend, main text, or Methods section.						
n/a	Confirmed							
	\square The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement							
\boxtimes	A statement on whether measureme	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly						
	The statistical test(s) used AND whet Only common tests should be described s	The statistical test(s) used AND whether they are one- or two-sided Only common tests should be described solely by name; describe more complex techniques in the Methods section.						
	A description of all covariates tested							
\boxtimes	A description of any assumptions or	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons						
	A full description of the statistical pa AND variation (e.g. standard deviation	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)						
	For null hypothesis testing, the test s Give P values as exact values whenever su	For null hypothesis testing, the test statistic (e.g. <i>F</i> , <i>t</i> , <i>r</i>) with confidence intervals, effect sizes, degrees of freedom and <i>P</i> value noted Give <i>P</i> values as exact values whenever suitable.						
\boxtimes	For Bayesian analysis, information or	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings						
\boxtimes	For hierarchical and complex designs	, identification of the appropriate level for tests and full reporting of outcomes						
\boxtimes	Estimates of effect sizes (e.g. Cohen's <i>d</i> , Pearson's <i>r</i>), indicating how they were calculated							
	Our web collection on <u>statistics for biologists</u> contains articles on many of the points above.							
Software and code								
Poli	Policy information about <u>availability of compu</u>	<u>ter code</u>						
Da	Data collection The data was collected from	available sources, listed and available						
Da	Data analysis The data was analysed in R s	oftware, code in R syntax is provided.						
		nat are central to the research but not yet described in published literature, software must be made available to editors and mmunity repository (e.g. GitHub). See the Nature Research <u>guidelines for submitting code & software</u> for further information.						

Data

Policy information about <u>availability of data</u>

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data $% \left(1\right) =\left(1\right) \left(1\right) \left($
- A description of any restrictions on data availability

In the method section each data source is listed. All data sources for this manuscript are openly available. The main data source (global tree ring data) has the following data availability statement:

"We used time series of annual growth available in the International Tree Ring Data Bank (ITRDB, (46)), accessible via: https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring."

For reproducibility, the version of the data used in our code has been uploaded to the repository, together with the code.

_	•		1			C:				•
┖.	-			\sim		t 10	ro	no	rt	\mathbf{n}
		I U	-5	いて	: U. I	TIU.	re	IJU.	/I L I	שווו
•	. –	. –	_	~ ~	٠.	•	. •	P -		· · · O

	· · · ·					
Please select the one below	v that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.					
Life sciences	Behavioural & social sciences					
For a reference copy of the docum	ent with all sections, see <u>nature.com/documents/nr-reporting-summary-flat.pdf</u>					
Ecological, e	volutionary & environmental sciences study design					
All studies must disclose or	these points even when the disclosure is negative.					
Study description	We carried out a moving correlation analysis using time series of annual tree growth globally. The tested potential mechanisms influencing trends in global spatial synchrony via correlative approaches and the change in synchrony in the environmental variables themselves using a consistent approach.					
Research sample	Tee ring series in the International Tree Ring Data Bank (ITRDB), which collects data from multiple tree species across the globe. The ITRDB is the largest growth data collection available, with wide taxonomic, temporal, and spatial coverage; although it also has certain limitations in terms of the scope of the data collected (tencency towards conifer species in higher elevation places and climate-limited). These are important to consider when interpreting the data and we made sure to clearly highlight them and how they may affect our results in the main manuscript.					
Sampling strategy	Multiple sampling strategies, as the ITRDB is composed of a collection of samples from a diverse set of studies and researchers.					
Data collection	Each data accession in the ITRDB includes species names, tree indicators, growth per year and tree individual, contributor, mean sampling area coordinates, and, in many cases, main sampling area elevation.					
Timing and spatial scale	Annual growth measurements. Duration of each time series depends on species and location. Maximum timespan used in our analyses is 1000-2016					
Data exclusions	Only samples with no growth data for the range 1000-2016 were excluded					
Reproducibility	The R code is provided for reproducibility					
Randomization	Our study does not include control/treatment differences. All locations and species were considered					
Blinding	Our study does not include control/treatment sample assignment. We had no control over which species / locations were included in each time period					
Did the study involve field	d work? Yes No					
Reporting fo	r specific materials, systems and methods					
We require information from a	authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, evant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.					
Materials & experime						
n/a Involved in the study	n/a Involved in the study					
Antibodies	ChIP-seq					
Eukaryotic cell lines	Flow cytometry					
Palaeontology and a	archaeology MRI-based neuroimaging					
Animals and other of	organisms					
Human research pa	rticipants					
Clinical data						
Dual use research o	f concern					