Received: 8 July 2019 | Revised: 9 January 2020 | Accepted: 16 February 2020
DOI: 10.1111/geb.13090

RESEARCH PAPER

Global Ecology and Biogeography A Journal of Macroecology
WILEY

A global perspective on the climate-driven growth synchrony of neighbouring trees

Ernesto Tejedor[1] | Roberto Serrano-Notivoli[2] | Martin de Luis[3,4] | Miguel Angel Saz[3,4] | Claudia Hartl[5] | Scott St. George[6] | Ulf Büntgen[7] | Andrew M. Liebhold[8,9] | Mathias Vuille[1] | Jan Esper[5]

[1]Department of Atmospheric and Environmental Sciences, University at Albany (State University of New York), Albany, NY, USA

[2]Estación Experimental de Aula Dei, Consejo Superior de Investigaciones Científicas (EEAD-CSIC), Zaragoza, Spain

[3]Departamento de Geografia y Ordenacion del Territorio, Universidad de Zaragoza, Zaragoza, Spain

[4]Instituto Universitario de Ciencias Ambientales (IUCA), Universidad de Zaragoza, Zaragoza, Spain

[5]Department of Geography, Johannes Gutenberg University, Mainz, Germany

[6]Department of Geography, Environment and Society, University of Minnesota, Minneapolis, MN, USA

[7]Department of Geography, University of Cambridge, Cambridge, UK

[8]USDA Forest Service Northern Research Station, Morgantown, WV, USA

[9]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague, Czech Republic

Correspondence
Ernesto Tejedor, Department of Atmospheric and Environmental Sciences, University at Albany (State University of New York), 1400 Washington Avenue, Albany, NY 12222, USA.
Email: etejedor@albany.edu

Funding information
U.S. Department of Agriculture Forest Service, Grant/Award Number: EVA4.0, No. CZ.02.1.01/0.0/0.0/16_019/0000803 ; National Science Foundation, Grant/Award Number: AGS-1702439 and OISE-1743738; "Juan de la Cierva" postdoctoral, Grant/Award Number: FJCI-2017-31595; Government of Aragón through the "Program of research groups", Grant/Award Number: H38

Editor: Andrew Kerkhoff

Abstract

Aim: Previous work demonstrated the global variability of synchrony in tree growth within populations, that is, the covariance of the year-to-year variability in growth of individual neighbouring trees. However, there is a lack of knowledge about the causes of this variability and its trajectories through time. Here, we examine whether climate can explain variation in within-population synchrony (WPS) across space but also through time and we develop models capable of explaining this variation. These models can be applied to the global tree cover under current and future climate change scenarios.

Location: Global.

Time period: 1901–2012.

Major taxa studied: Trees.

Methods: We estimated WPS values from a global tree-ring width database consisting of annual growth increment measurements from multiple trees at 3,579 sites. We used generalized linear mixed effects models to infer the drivers of WPS variability and temporal trends of global WPS. We then predicted WPS values across the global extent of tree cover. Finally, we applied our model to predict future WPS based on the RCP 8.5 (2045–2065 period) emission scenario.

Results: Areas with the highest WPS are characterized by a combination of environments with both high mean annual temperature (>10°C) and low precipitation (<300 mm). Average WPS across all temperate forests has decreased historically and will continue to decrease. Potential implications of these patterns include changes in forest dynamics, such as higher tree growth and productivity and an increase in carbon sequestration. In contrast, the WPS of tropical forests of Central and South America will increase in the near future owing to reduced annual precipitation.

Main conclusions: Climate explains WPS variability in space and time. We suggest that WPS might have value as an integrative ecological measure of the level of environmental stress to which forests are subjected and therefore holds potential for diagnosing effects of global climate change on tree growth.

KEYWORDS
global, synchrony, tree ring, tree stress indicator

1 | INTRODUCTION

1.1 | Importance of forests and population dynamics

Forests are important carbon pools, characterized by a continuous exchange of CO_2 with the atmosphere. Within all tropical, temperate and boreal forests, *c.* 31% of carbon is stored in biomass and 69% in soil (IPCC, 2000). What is more, in the past few decades 30% of global anthropogenic CO_2 emissions have been absorbed by the forests of the world (which is about the same amount as is taken up by the oceans; Bellassen & Luyssaert, 2014). Forests directly affect *c.* 1.6 billion people worldwide regarding economic activities such as forestry, food, agricultural policies or tourism (FAO, 2013); hence, it is essential to gain a better understanding of current and future changes in forest dynamics and evolution. However, most of our understanding of forest dynamics comes from retrospective analyses that consider how past events and stand structure led to the development of the forests that we can observe and analyse today (Waring & Running, 2007). Here, we propose an additional approach to understand forest population dynamics by analysing the within-population synchrony (WPS) of tree growth.

This method relies on the assumption that the world around us is a spatially autocorrelated system (Legendre, 1993). Derived from that concept is the spatial synchrony concept, which refers to coincident changes in the abundance or other time-varying characteristics of geographically disjunct populations (Liebhold, Koenig, & Bjørnstad, 2004). Many studies in ecology have used this concept; for instance, to investigate different ecological aspects of great significance for tree growth, such as seed production or masting (Allen, Mason, Richardson, & Platt, 2012; Kelly, 1994; Pearse, Koenig, & Kelly, 2016), host phenology (Dodd et al., 2008) or foliage-feeding herbivores as synchronizing agents in forests (Peltonen, Liebhold, Bjørstad, & Williams, 2002). In addition, the absence of spatial synchrony is generally considered key to persistence in metapopulation dynamics and might be vitally important in the conservation of species and disease eradication (Mikko, Veijo, Esa, & Jan, 1997; Noble, Machta, & Hastings, 2015). Finally, it has also been suggested that an increase in spatial correlation could be an early warning signal before a regimen shift (Dakos, van Nes, Donangelo, Fort, & Scheffer, 2010).

By studying the nature of such synchronous oscillations, we are taking steps towards a better understanding of the role of synchrony in population dynamics. Although ecologists used to be frustrated in their efforts to identify the cause of this synchrony (Liebhold, Koenig, et al., 2004), recent statistical advances have made it much easier (Gouveia, Bjørnstad, & Tkadlec, 2015; Sheppard, Bell, Harrington, & Reuman, 2016; Walter et al., 2017). The Moran effect (Moran, 1953), which describes how global random disturbances affecting populations sharing a common density-dependent structure are capable of bringing these populations into synchrony (Ranta, 1995), has frequently been used to explain the ubiquity of spatial synchrony among populations of species belonging to various taxa (Bjørnstad, Ims, & Lambin, 1999). Hence, the Moran effect is thought to be the result of universal random but synchronous weather influences acting on spatially disjunct populations (Koenig, 1999; Mikko et al., 1997).

Although the synchrony concept has been widely used in dendroclimatology as a measure of the quality of the chronology (Buras, 2017), the spatial synchrony of tree growth is an aspect that remains poorly understood (Defriez & Reuman, 2017). Nonetheless, tree-ring growth series provide long-term spatial information that can indicate, for instance, release events and allow us to detect synchronized regeneration caused by disturbance (Lorimer & Frelich, 1989; Sánchez-Salguero et al., 2012; Zielonka, Holeksa, Fleischer, & Kapusta, 2010) not only at regional scales but also at fine spatial scales (Aakala, Kuuluvainen, Wallenius, & Kauhanen, 2009; Carrer & Urbinati, 2001; Shimatani & Kubota, 2011). Following the spatial synchrony approach, it has also been suggested that the warming climate of the Earth is synchronizing forest growth across Eurasian regions and therefore providing early warning signals of climate change impacts on forest ecosystems at subcontinental scales (Shestakova et al., 2016). Furthermore, Camarero, Gazol, Sangüesa-Barreda, Oliva, and Vicente-Serrano (2015) applied the synchrony concept to study early warning signals in the growth trends of declining and non-declining trees and found a relationship between the increase in synchrony and an increase in severe droughts. Hitherto, the spatial synchrony concept in both ecology and dendrochronology has largely been applied to analyse among-population synchrony analyses rather than within-population synchrony, which we consider here.

1.2 | The within-population synchrony concept to study population dynamics of forests

The WPS was first described by Liebhold, Sork, et al. (2004) to study the synchronous production of large crops of seeds within a population (short distance, <10 km) rather than among separate populations (≤1,000 km). Here, we apply that approach to tree-ring width series from individual (site) populations and calculate the WPS. We believe that WPS can function as an integrative ecological measure of the level of environmental stress to which forests are subjected, such as the stresses arising from climate change.

In tree-ring research, the average correlation of all ring-width series within a given stand, indicated as RBAR (Wigley, Briffa, & Jones, 1984), is a commonly used measure of the covariance among individual series in a chronology (Fritts, 1976). It is standard in dendrochronology to use RBAR as a measure of chronology quality or signal recovery. Here, we are repurposing RBAR to determine what environmental information might be recoverable from that metric and to document the WPS of neighbouring trees. For relatively high-frequency data, RBAR is unbiased and provides an accurate measure of the signal strength inherent in a chronology (Briffa, 1999). The RBAR for a group of trees could, in theory, range from minus one to one, although in practice only positive values are meaningful (negatives values would indicate some sort of antagonistic growth interaction). The higher the value, the stronger is the underlying common signal; hence, the lower the variance within each series, the weaker the noise and the lower the number of series that must be averaged to reduce the noise remaining in the final mean chronology to an "acceptable" level (Wigley et al., 1984).

One of the strengths of the RBAR statistic is that it can be calculated for different time periods and, more importantly, it can be used for global comparisons of growth response of forests to climate change. St. George (2014) used the International Tree-Ring Data Bank (ITRDB) to study tree-ring width series of the Northern Hemisphere and indicated differences in the RBAR value among species and geographical location. In that study, consistently high values were found for most sites in the North American south-west, but also in northern Fennoscandia and the central Russian Arctic. Characteristically low values were found in tree-ring width records from European Mediterranean sites and from the Himalayas (for an example, see Supporting Information Figure S1). The highest RBAR values were found in limber pine (*Pinus flexilis* E.James), ponderosa pine (*Pinus ponderosa* P.Lawson & C.Lawson) and Douglas fir [*Pseudotsuga menziesii* (Mirbel) Franco], all growing in western North America.

In this study, we explore further how WPS varies in both space and time. There is still a lack of knowledge regarding (a) the variability and change of WPS over time, (b) the influence of the environment on WPS, and (c) the causes of geographical and temporal variation in WPS. Accordingly, in this study we quantify WPS in tree growth from tree-ring measurements using the RBAR statistic to analyse the synchrony dynamics of tree-ring width in forests at a global scale (3,579 sites) and through time (1901–2012). We then identify spatial patterns and significant changes at these sites. Finally, we develop a model that is capable of explaining the variability in synchrony and apply it initially under current climate conditions and then to forecast future conditions under a projected climate scenario.

Our hypotheses are as follows:

1. The WPS of tree growth increases as environmental conditions become more limiting (i.e., decreasing effective precipitation; Fritts, Smith, Cardis, & Budelsky, 1965). As a consequence, climate forcing will explain a large fraction of variation in synchrony within populations. Less synchronous growth would indicate a reduced importance of the general abiotic environmental factors (such as climate) and a greater influence of local abiotic and biotic factors (competition, insect outbreaks, fire, etc.).
2. Based upon the above relationships, both spatial and temporal variation in synchrony could, at least in part, be predictable globally and under different climate change scenarios. The possibility of having this predictive capability of WPS adds a new dimension to synchrony in tree growth as an ecological tool, because it represents a surrogate measure of the level of environmental stress to which the populations are subjected and thus could be of extraordinary utility for the planning of forest management with ecological, economic (e.g., productivity) and mitigation (e.g., carbon sequestration) implications.

2 | METHODOLOGY

2.1 | Data acquisition and treatment

The ITRDB (Zhao et al., 2019) is the largest archive containing digital tree-ring width measurements. As of June 2015, the ITRDB contained >4,000 ring-width records from all continents except Antarctica. These data are stored in the "Tucson Decadal Format" (Holmes, 1994) and, besides the sample identification and ring-width measurements of the individual tree-ring series, the archive contains meta-data for each series, including tree species and sampling site latitude, longitude and elevation.

In preparation for analysis, all available tree-ring records were downloaded, except for 245 records that had to be removed owing to errors detected within the data. The most frequent errors consisted of unusual formats or multiple ring-width series with the same identification codes. After removal of erroneous data, 3,936 records were used. In addition, we selected records with >10 samples per site and containing data within the 1901–2012 period in order to match the tree-ring information with available meteorological data. The final dataset considered for the study is composed of 3,579 records from both the Northern and the Southern Hemisphere. Although we are aware of the existence of additional datasets compiled by individual research groups, we believe that using these 3,579 records with global coverage should lead to robust results, allowing us to identify the main characteristics of the tree-ring covariance and to fulfil the aims of this study. We selected the 1901–2012 period because monthly meteorological data are available for it worldwide (CRU TS v.3.21.; Harris, Jones, Osborn, & Lister, 2014). Furthermore, selection of this period facilitates the analysis of the influence of the recent global warming trends on WPS variability.

In order to eliminate the tree age trend in radial growth and preserve only year-to-year variability, that is, the high-frequency signal, each of the 3,579 records was standardized using the "dplR" package (Bunn, 2008) within R (R Core Team, 2018). First, each individual tree-ring width series was detrended with a cubic spline with a 50% frequency cut-off at 30 years (Cook & Kairiukstis, 1990). Standardized series were obtained by dividing the observed values by the expected values given by the spline function. Finally, we selected the residuals from a first-order autoregressive modelling of the detrended measurement series. This method removes all but the high-frequency variation in the series.

2.2 | Measuring global within-tree growth population synchrony and its trends

To explain changes in the strength of common patterns of tree growth over the selected period, we calculated running WPS values using a 30 year moving window with a 29 year overlap (i.e., moving up by 1 year at each step). The WPS is calculated by the average Pearson correlation of all ring-width series within a given stand

(Wigley et al., 1984). Given that it is a running correlation between series, it is a good measure of the common year-to-year variability through time but is dependent upon the sample depth (Cook, Buckley, D'Arrigo, & Peterson, 2000). In this case, WPS values would range from zero, meaning a total absence of covariance within the tree-ring width series, to one, including a total agreement of the year-to-year variability within the tree-ring series.

To explore the temporal variability and change in WPS from 1901 to 2012 at each site, we evaluated variability (standard deviation) and trends using the modified Mann–Kendall test for autocorrelated data (Hamed & Ramachandra Rao, 1998) (at the 95% confidence level).

2.3 | Modelling the current and future synchrony of forest tree growth

To explore the causes of variability in WPS values through time and within each site, we used generalized linear mixed effects (GLME) models (using the R package lme4; Bates, Mächler, Bolker, & Walker, 2015). Mixed models are ideally suited to settings in which the individual trajectory of a particular outcome for a study over time is influenced both by factors that can be assumed to be the same for many sites (e.g., the effect of climate) and by characteristics that are likely to vary substantially from site to site (e.g., the identification code of each site or each population). Mixed models account explicitly for the correlations between repeated measurements within each site (Ma, Mazumdar, & Memtsoudis, 2012; Moseley et al., 2015). The WPS values observed at each site for different 30-year moving periods were considered the response variable, and climatic conditions during each period were used as fixed factors. We used mean annual temperature (T), total mean annual precipitation (P) and the interaction between these terms at the grid point closest to each tree-ring site from the CRU TS 3.21 dataset (Harris et al., 2014) during the period 1901–2012. Given that WPS values range from zero to one, the quasibinomial family was used in order to describe the error distribution. Before creating the model, we standardized the independent variables (with respect to the mean and standard deviation) to ensure a compensated weight of each variable. In addition to taking into account variations in the WPS at each individual site, we used the unique site identity code (ID) as a random effect variable (Supporting Information Equation S1). We evaluated the accuracy of the models using a likelihood ratio test by comparing the obtained models (full models) with the reduced models where explanatory variables of interest were omitted and only the intercept term was included (null models). Next, we calculated the p-values for the likelihood ratio tests that compared the full and reduced models using the χ^2 distribution.

Finally, to predict future values for the temperature and precipitation parameters during the period from 2046 to 2065, we used an ensemble of multiple models for the RCP 8.5 scenario from the CMIP5 project (AR5, uploaded 15 April 2014). We applied the model across global tree cover to assess the potential effects on a global scale, including areas, such as those within the Tropics, that are poorly covered by the ITRDB network. Global tree cover was classified according to the World Wide Fund for Nature (WWF) definition of ecoregions (https://www.worldwildlife.org/biomes; Supporting Information Table S1). The predictions in each pixel are made based on a common generic "site" (same random factor throughout the space) with the objective of describing how the fixed factors (climate) differentially influence synchrony across the world.

3 | RESULTS

3.1 | Observed current synchrony values

Global forest WPS values spanning the period 1901–2012 are shown in Figure 1a. According to the WPS values of each site, we defined five categories of forest growth synchrony (Table 1), ranging from very low, meaning absence of synchrony, to very high, meaning that growth in those sites was at near to full agreement. The regions with the highest WPS values were in western North America, in central Asia and boreal forests in the Russian Arctic. In contrast, the lowest WPS values were found along the east coast of North America, along the Mediterranean fringe in Europe, in some parts of the Himalayas in Asia and in some sites in South America. Most of the sites (59%) showed a low to moderate synchrony. We also found that 17% of the sites had a very low to near-zero tree growth synchrony, whereas 24% of the sites showed a very high or almost total tree-ring growth synchrony. Lowest WPS values were located in North American boreal forests, and the highest values corresponded to sites located in the mountainous areas of Colorado, USA.

The results indicated that WPS of global forest populations had varied through time during the last 112 years (Figure 1b), meaning that it is a dynamic rather than a static indicator. In fact, among the studied sites, 77% showed a significant positive (gain) or negative (loss) trend through time (Figure 1c). These changes were mostly low (78%), although a remarkable 21% of the sites exhibited a moderate to high variability, including shifts in the category, that is, from high to moderate or from moderate to high synchrony.

Overall, the majority of sites exhibited a negative trend (decreasing WPS), as seen at sites located in eastern North America, the Himalayas, the Alps, eastern Scandinavia or southern South America. Moreover, some sites in the boreal forests of the Russian Arctic, in the mid-western USA and in western North America showed a significant positive trend (increase in WPS).

3.2 | Within-population synchrony determined by climate

By comparing our full model with a null model (Table 2), we demonstrated that the full model (including the mean annual temperature and precipitation and their interaction as fixed factors) had a better explanatory power (lower Akaike information criterion and Bayesian

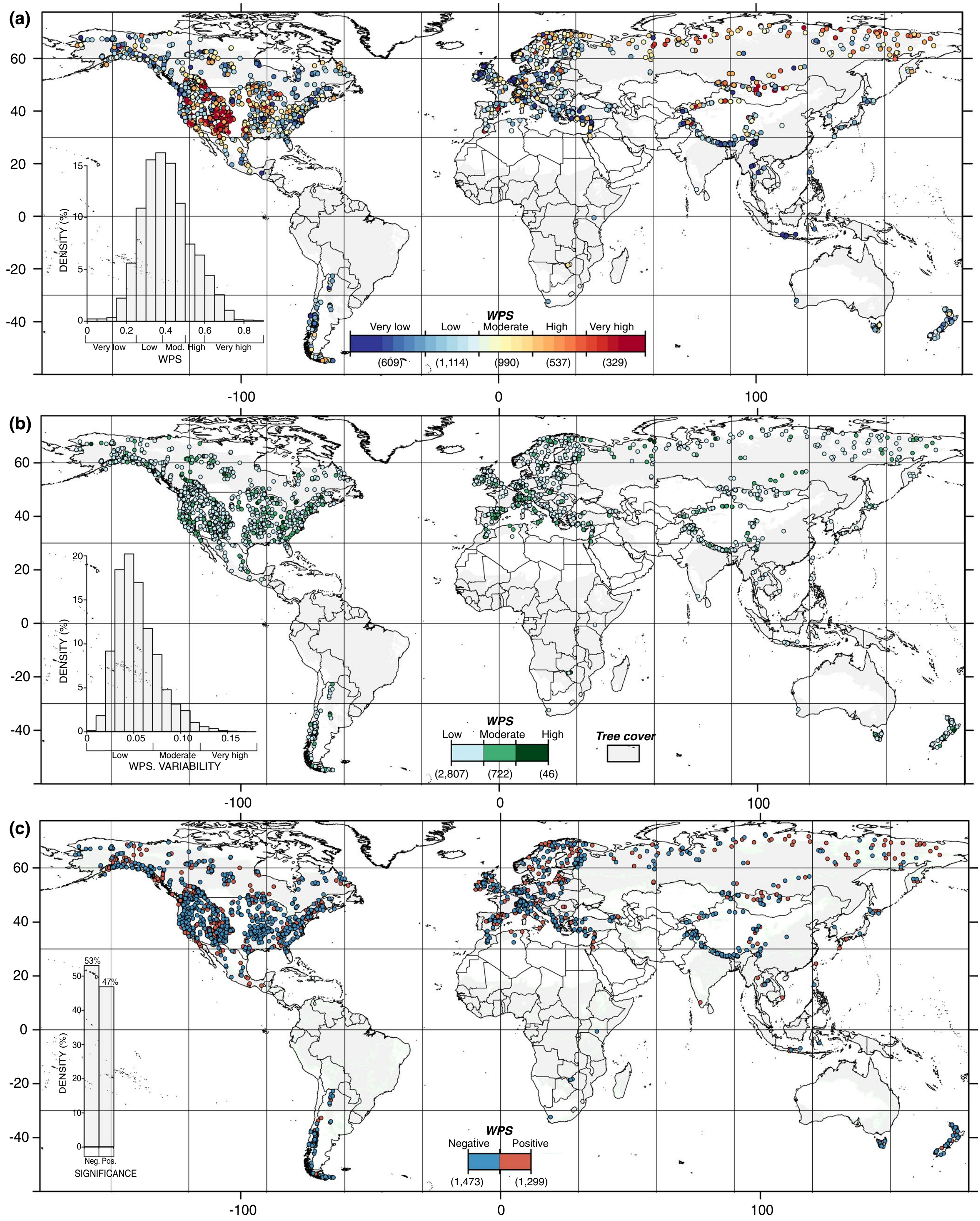

FIGURE 1 Global patterns of within-population synchrony (WPS) at International Tree Ring Databank (ITRDB) sites for the period 1901–2012. (a) Variation of WPS classified from zero (very low), meaning a total absence of synchrony, to one (very high), a perfect agreement between tree-ring growth series (see the category correspondence in Table 1). (b) WPS variability based on the standard deviation. (c) Trend and significance of such WPS changes (only significance levels of $p < .05$ are shown) [Colour figure can be viewed at wileyonlinelibrary.com]

information criterion). The WPS was positively related to the mean temperature, meaning that higher WPS occured where and when temperatures were higher, and the WPS was negatively related to the precipitation, meaning that higher WPS was found in low-precipitation environments (Table 3). The interaction between mean annual temperature and precipitation also explained a significant fraction of the variance in WPS. The WPS was higher in areas with high mean annual temperature and low total precipitation.

With these results, we gained a better understanding of the climate constraints of the observed WPS (Figure 2). The results were robust (see Supporting Information Figure S2) and highlighted the wide range of WPS levels of the observed ITRDB forest populations. Hence, higher WPS values were found in dry environments, including areas with precipitation <400 mm and mean annual temperature >0°C. Lower WPS values were found in sites with >1,000 mm of annual precipitation, although they could also be found in dry but very cold environments (−20 to −10°C). Warm (>15°C) and wet (>1,000 mm/year) environments, such as those in tropical forest areas, showed low to very low WPS. Additional findings included the climate boundaries of the distribution limits of the ITRDB studied sites, which ranged from an annual precipitation of 100 to almost 5,000 mm/year, with mean annual temperature ranging from −20 to 26°C.

TABLE 1 Categories of the synchrony levels

Category	Values 1901–2012	Change 1901–2012
Very low	<.30	
Low	.30–.39	<.07
Moderate	.40–.49	.07–.12
High	.50–.59	>.12
Very high	>.59	

3.3 | Model applications to the current and future climate

The GLME model was applied to the global tree cover under the current climate (Figures 3a and 4a), emphasizing the full range of WPS levels throughout Earth's tree cover. As expected, the most limiting environments, including mean annual temperature of *c.* 30°C and mean annual precipitation between 100 and 300 mm, were characterized by a higher predicted WPS. Moreover, areas with a mean annual temperature of *c.* 25°C and mean annual precipitation between 2,000 and 5,000 mm accounted for the lower predicted WPS levels (although results for these particular areas must be treated with caution owing to the low number of observations with such climate conditions). Moderate WPS levels could be found in a wide spectrum of climates, although with a similar mean annual precipitation of 300–600 mm and mean annual temperatures that could range from −15 to 25°C.

The GLME was applied to the future emission scenario RCP 8.5 for the 2046–2065 period, yielding important projections (Figures 3b and 4b). The WPS variability was projected to decline (there are no longer any tree species living below −20°C mean annual temperature) and, considering the current tree cover, the maximum annual temperature of some sites will be pushed above 30°C. Most of the sites will have low to moderate WPS. In other words, those sites facing a rise in temperature and an increase in precipitation will be less limited and thus decrease their WPS. Moreover, those sites exposed to a significant rise in temperature but with similar or lower amounts of precipitation will be more limited and thus increase their tree growth WPS.

When considering only the effects of future climate change on WPS, larger changes in WPS (Figures 3c and 4c) will occur in those places where precipitation totals are currently high (>2,000 mm/year), but precipitation is projected to decrease, whereas smaller changes are likely within the low to moderate categories. An increase

TABLE 2 Summary statistics of the intercept-only model (null model) and the full model (including mean annual temperature and precipitation and their interaction as fixed factors)

Model	d.f.	AIC	BIC	Loglikelihood	Deviance	Chisq	d.f.	Pr(> Chisq)
Null model	2	224,219	224,239	−112107	224,215			
Full model	5	223,606	223,658	−111798	223,596	618.63	3	$<2.2 \times 10^{-16}$***

Note: We include the χ^2 test comparing both models (Chisq). The full model has a lower Akaike information criterion (AIC) and Bayesian information criterion (BIC) than the null model, indicating its better explanatory power. Signif. codes: '***' 0.001.

TABLE 3 Full model summary of the fixed effects on the WPS

Fixed effects	Estimate	*SE*	*z*-value	Pr(>|*z*|)
(Intercept)	0.03550	0.11755	0.302	0.763
TMean_Annual	0.46642	0.09761	4.778	1.77×10^{-6}***
Precip_Annual	−0.14758	0.01797	−0.8214	$<2 \times 10^{-16}$***
TMean:Precip	−0.07180	0.01552	−4.626	3.73×10^{-6}***

Note: Abbreviations: Precip_Annual, Mean Annual Precipitation; TMean_Annual, Mean Annual Temperature; Tmean:Precip, Interaction between Mean Annual Temperature and Mean Annual Precipitation. Number of observations is 186,750. Within-population synchrony (WPS) will be higher where temperature is higher and where precipitation is lower. Signif. codes: '***' 0.001.

in tree-ring growth WPS will occur mainly in the Mediterranean basin, in the tropical forest of India and in the Amazon Basin rainforest. Moreover, Northern Hemisphere forests, and particularly the boreal forests, will experience no change or a slight decrease in their WPS, owing to an increase in precipitation.

4 | DISCUSSION

4.1 | The potential of the internal synchrony of populations as an indicator of the level of climatic stress

The WPS (or RBAR in the field of dendrochronology) in tree-ring research has been used traditionally to define reconstruction periods (Buras, 2017) as a parameter in the expressed population signal (EPS) formula (Wigley et al., 1984).

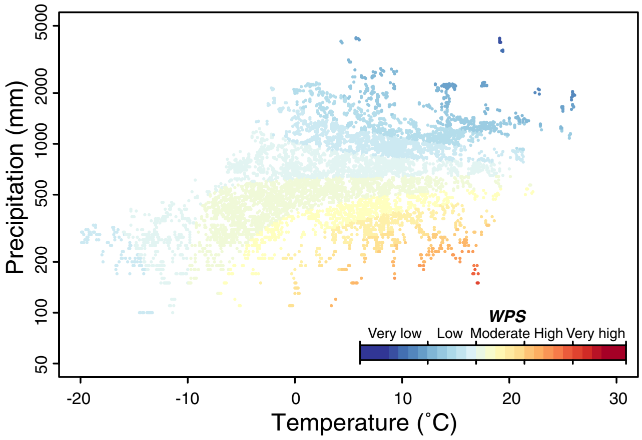

FIGURE 2 Modelled distribution of the within-population synchrony (WPS) applied to the current climate (annual means) of each observed site; that is, the climate envelope covered by the tree-ring network [Colour figure can be viewed at wileyonlinelibrary.com]

In the present study, however, we used the WPS to calculate the synchrony between trees within populations to study the impact of climate change in time and space on forest growth dynamics. The analysis was focused on the high-frequency domain through a robust detrending. Consequently, the results were not biased or affected by trend distortions that might potentially have occurred if low-frequency detrending methods had been applied (Melvin & Briffa, 2008). We demonstrated that the WPS has a great potential to assess associated levels of climatic stress. We thus encourage the use of the unbiased (retaining only the high-frequency variability) WPS (or synchrony, when applied to dendroecological aspects) as a useful indicator for describing environmental stress of forests. In the near future, as the climate warms, it is likely that additional non-synchronous endogenous disturbances, such as nutrient availability, fire, permafrost melting, insect outbreaks or species-specific imprints would become increasingly dominant as factors influencing tree growth, including a reduction in the effect of cold limitation (Fajardo & McIntire, 2012; Ponocná et al., 2018). Consequently, it is crucial to understand the current factors limiting productivity of forests to enable better prediction of changes in future forest population distributions.

4.2 | Within-population synchrony tested on a global tree-ring dataset; opportunities and limitations

The WPS concept was tested with global tree-ring data from the ITRDB (3,579 single sites), which is a robust and diverse dataset useful not only for dendroclimatic studies but also to assess global dendroecological questions (Babst et al., 2019; St. George, 2014). The ITRDB does not contain metadata on the distance between sampled trees or within forests (information that could potentially alter our analysis; Supporting Information Figure S3). However, it is very unlikely that there is a systematic trend or bias in the distance between trees in the ITRDB. Since the ITRDB was created, its main purpose has been to develop climatic reconstructions (Zhao et al.,

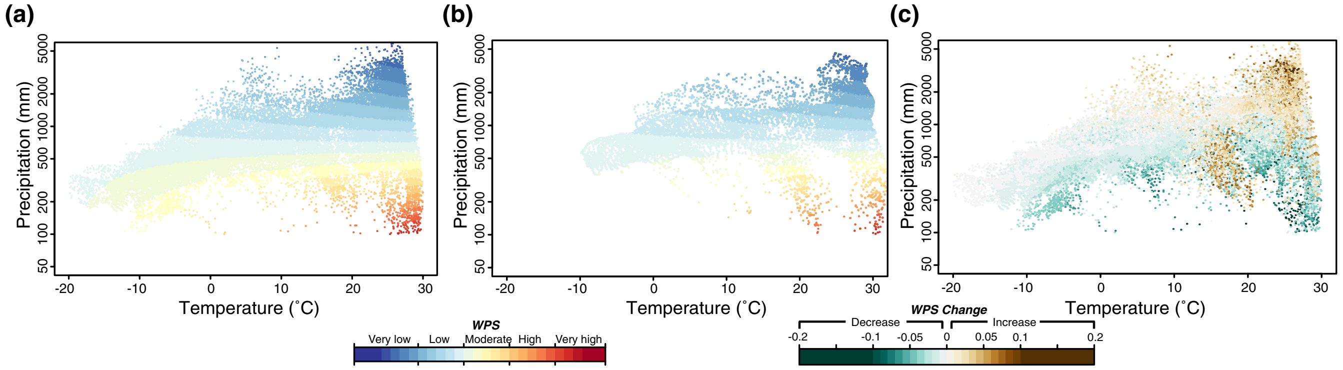

FIGURE 3 Forecasted within-population synchrony (WPS) values. (a) Modelled distribution of the WPS using the current climate and applied to the global tree cover extension. (b) Modelled distribution of the WPS using the RCP 8.5 scenario (2045–2065) and applied to the global tree cover extension. (c) Differences in the WPS between current and future climate scenario [Colour figure can be viewed at wileyonlinelibrary.com]

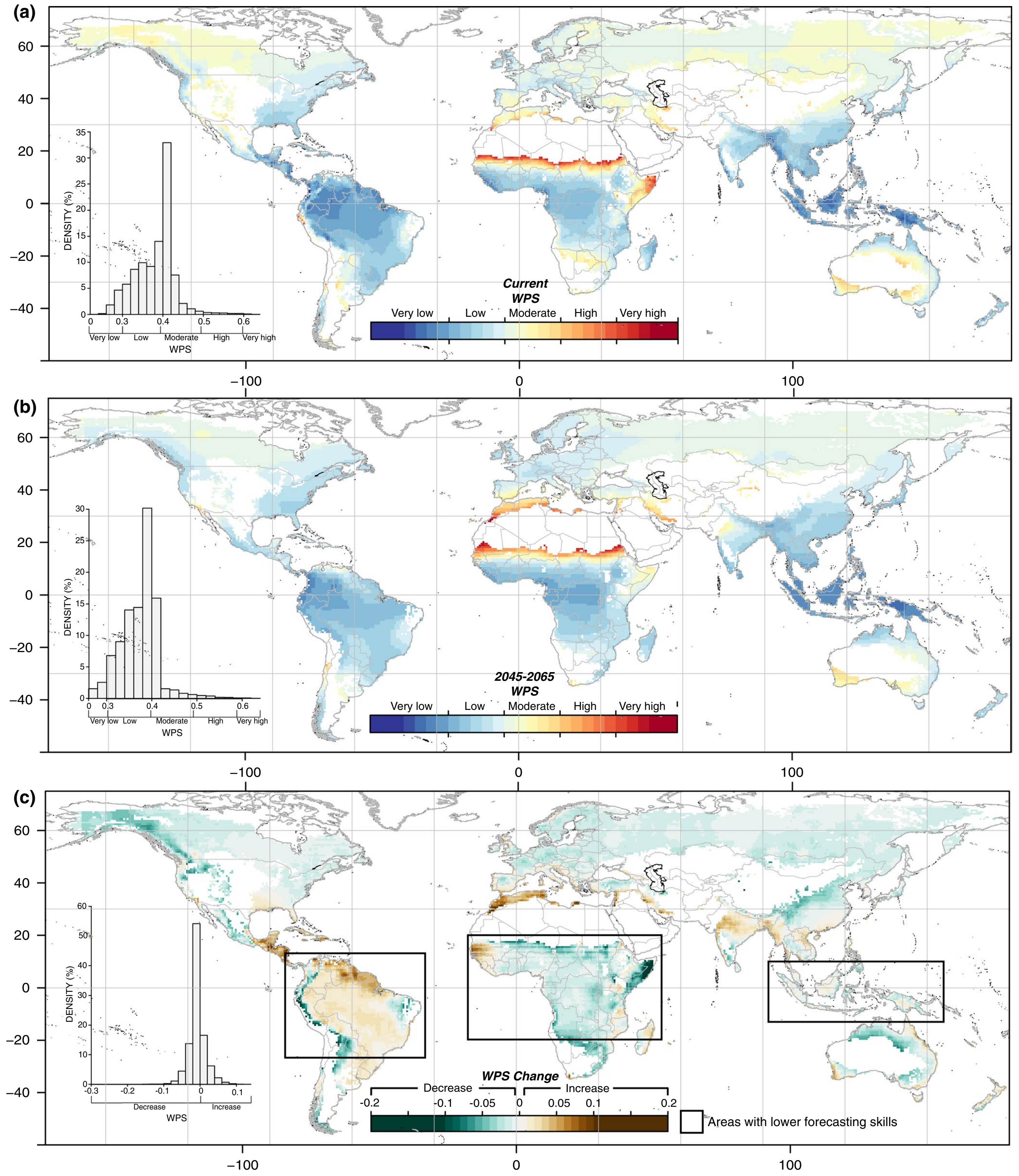

FIGURE 4 (a) Spatial distribution of the within-population synchrony (WPS) model using the current climate and applied to the global tree cover. (b) Spatial distribution of the WPS model using the RCP 8.5 scenario (2045–2065) and applied to the global tree cover. (c) Spatial distribution of the differences in the WPS between current and future climate scenario [Colour figure can be viewed at wileyonlinelibrary.com]

2019). This implies that the selection of the trees to be sampled is based on maximizing the climatic signal and not on other factors (such as competition). The distance between sampled trees is not explicit, precisely because it is considered to be a variable that has no effect on growth (it is large enough). Nonetheless, Zhao et al. (2019) concluded that the extensive data and coverage of the ITRDB show great promise for addressing macroecological questions. The majority of the sites included in the ITRDB are found in the Northern Hemisphere, whose species, distributions and ecoregions are well represented. Moreover, large areas of Africa and tropical South America are clearly underrepresented, especially the tropical and subtropical moist broadleaf forests, and thus the results in those regions must be treated with caution. However, in the present study we attempted to demonstrate a global pattern of synchrony change and trend throughout the 20th century and towards the mid- to late 21st century, being aware that the predictive skills for large areas over the tropics are lower than for the temperate regions.

The mixed model for explaining synchrony, using data on temperature and precipitation from each site, provides reliability to extend results to areas where chronologies are largely absent but that potentially play key roles in the global carbon cycle or forest biomass productivity (among other functions). Under the current climate, drivers of tree-ring growth have already changed and will continue changing in a projected future warmer climate (Babst et al., 2019). In the 20th century, the main drivers have transitioned from energy limitation towards water limitation drivers, especially in the boreal and temperate zones (Babst et al., 2019), and in the near future these drivers will affect growth rates of forest ecosystems (Charney et al., 2016; Tei et al., 2017) and thus their internal synchrony (WPS).

4.3 | Forest growth limitations associated with different factors

Our results show that a large proportion of the spatial and temporal variation in WPS is attributable to the influence of climate, suggesting that the Moran effect might cause synchrony in tree-ring width series also at local scales. It is well known that weather is generally the only environmental driver likely to act in the same range in space and time (Fritts, 1976). Thus, the primary factors limiting tree-ring growth in forest populations are generally climatic. If climate is found to be the main driver, hence the most limiting factor, it will manifest itself through synchronous growth in the population. In addition, there are other global drivers, aside from climate, that are capable of altering the synchrony, such as an increase of the atmospheric CO_2 concentration (McMahon, Parker, & Miller, 2010) or a decrease in solar radiation caused by anthropogenic aerosol emissions after 1950 (global dimming; Liepert, 2002). Moreover, when climatic conditions are more favourable, local characteristics become more determinant for tree growth, and the common variance between tree-ring traits attributable to macroclimate is reduced (Fritts, 1976).

Our results not only support such a theory but also confirm our first hypothesis and initial objective; spatial patterns of WPS are closely related to climate distribution patterns. Higher WPS is found in warm and dry areas (mean annual temperature >10°C and annual precipitation <300 mm), whereas a lower WPS is found in warm (mean annual temperature >15°C) and wet environments (precipitation >1,000 mm/year) and in extremely cold and dry environments (mean annual temperature <−10°C). Thus, the drivers that are associated with WPS are also likely to be drivers determining the extent of forest cover. These patterns are similar to those described by Babst et al. (2019). Although their results are based on growth patterns, our higher WPS zones coincide with their lower growth zones and vice versa. Hence, these results also confirm our second hypothesis and second goal; WPS spatio-temporal distribution patterns are closely related to climate and therefore predictable (from the ITRDB database, unbiased and representative; Babst et al., 2019) at the level of global forest extent. We show that WPS is not static over time, but its variation is associated with climate variability and change. This finding represents an important milestone because it allows us to predict the future behaviour and climatic stress levels in environments where no information is available, but which might be able to sustain forest cover in the future. We are thus able to detect hotspots, highlighting populations or locations that are particularly sensitive to climate change, which might require focus for conservation and management efforts. (Post et al., 2009). In addition, we now have the possibility of predicting spatially explicit climate stress levels (WPS) in future climate scenarios that allow us to determine potential adaptation/mitigation measures for specific regions.

4.4 | Implications of our findings

Our most significant results of the spatial distribution of future WPS changes (Figure 4c) are based on the most extreme projected future scenario (RCP 8.5; Riahi, Grübler, & Nakicenovic, 2007). This RCP is characterized by a sustained increase in greenhouse gas emissions over time, leading to high atmospheric greenhouse gas concentrations (Riahi et al., 2007, 2011), including an increase in global temperature of 4.9°C by 2100. Although the projected increase in temperature exhibits relative spatial homogeneity, the projected change in precipitation varies greatly in space. Temperate forests and the tropical forests of Africa and Asia are projected to experience an increase in precipitation, whereas Mediterranean forests and the Amazon tropical forest will be exposed to a decrease ranging from 500 to 1,000 mm/year (International Monetary Fund, 2017). Larger changes in WPS are in agreement with projected changes in precipitation (although the results for the tropical areas must be treated with caution). A pronounced decrease in synchrony is projected for the north-west coast of Alaska, the Colombian, Ecuadorian and Peruvian Andes and the “Gran Chaco” region between Paraguay and Argentina. These regions are projected to experience a reduction of the thermal limitations owing to rising temperature and increasing precipitation, which can be interpreted as reduced climatic stress. Such a decrease of the WPS would be reflected as an increase in tree-ring growth, as suggested already from some regions of the globe for certain specific species [e.g., high-elevation bristlecone pines, western North America, (Salzer, Hughes, Bunn, & Kipfmueller, 2009), boreal Eurasian forests (Shestakova, Gutiérrez, Valeriano, Lapshina, & Voltas, 2019)]. Moreover, the Mesoamerican region and the Amazon Basin will be areas with a potential increase of limiting factors, attributable to a reduction in precipitation and an increase in temperature, leading to an enhanced climatic stress. It must be mentioned that here we do not account specifically for extreme weather events, such as a higher frequency of droughts or floods, nor are we considering other disturbance factors, such as insect outbreaks, tree disease epidemics or fires, whose regimens might be altered with climate change. In any case, based on our results, it is very likely that an increase in the WPS and therefore the climatic stress in the Amazon forest will occur.

Whether tree-ring growth is positively related to carbon sequestration has been a recent recurring topic (see Körner, 2006 and references therein), and the discussion is still on-going. Here, we assume that CO_2 sequestration tracks tree-ring growth variability (as demonstrated, among others, by Dawes, Zweifel, Dawes, Rixen, and Hagedorn [2014]). However, the vast majority of species dominating the current biosphere evolved under CO_2 concentrations of *c*. 240 ppm according to ice core data considering the last 650,000 years (Körner, 2006). Thus, the anthropogenic rate of atmospheric CO_2 enrichment is likely to create an unprecedented environment for modern plant life, because as of December 2019, the CO_2 concentration has already exceeded 410 ppm (GLOBALVIEW-CO2, 2013). On top of the increase in atmospheric CO_2, plants are dealing with a rapidly changing climate, which is causing, for instance, a reduction in carbon sequestration over the Amazon Basin (Brienen et al., 2015). Given that the WPS is calculated from the tree-ring growth and explained by climate, we believe that it is an additional and essential ecological and integrative tool to be used when facing forest dynamics and evolution under future climate change scenarios (climatic stress). This might allow us to identify potential patterns that indicate changes in forest dynamics and the carbon balance of global ecosystems. In addition, understanding long-term synchrony patterns of tree growth becomes highly pertinent to identifying broad-scale emerging threats to forests and threshold tree responses to climate change (Shestakova, Gutiérrez, & Voltas, 2018).

4.5 | Population dynamics, evolution and distribution

Finally, one of the major uncertainties associated with climate-change projections is the extent to which tree species will be able to disperse into their newly suitable habitats under future climate change scenarios. Here, we provide evidence of the dependence of tree growth synchrony on climate, which is crucial to a better understanding of current population dynamics and evolution. However, future distributions will be determined not only by climate but also by a hierarchy of factors such as dispersal ability, biotic interactions (i.e., competition and predation), genetic adaptation and abiotic factors (e.g., soil conditions). Also influencing future outcomes is the role of humans. It is crucial to define what path greenhouse gas emissions will take over the next 10–50 years. Will we redistribute species purposefully or accidentally as habitats change?

5 | CONCLUSIONS

We demonstrate that climate determines variations in WPS across space and through time. We use the most extreme climate scenario to address future synchrony of global tree growth in forests. As a result of the new climate state, some of the most important tropical forests on Earth will increase their WPS and therefore undergo enhanced climatic stress, resulting in a reduced potential to act as carbon sinks. Moreover, temperate forest might benefit from a warmer and more humid planet. Nonetheless, some level of uncertainty surrounding this topic will remain, given the complex and stochastic nature of both plant migration and climate change. All exercises of this type are predicated on general circulation models (GCMs). Thus, improvements in global climate modelling will clearly have downstream effects on spatial projections of biological responses to climate change. We therefore endorse the pursuit of multiple modelling strategies to increase confidence in climate change projections. Ultimately, we suggest that WPS might have value as an integrative ecological measure of the level of environmental stress to which forests are subjected, and therefore holds potential for diagnosing effects of climate change on tree growth.

ACKNOWLEDGMENTS

E.T. and M.V. were partially supported by National Science Foundation - Partnership in International Research and Education (OISE-1743738) and National Science Foundation - Paleo Perspectives on Climate Change (AGS-1702439). R.S.-N. is funded by a “Juan de la Cierva” postdoctoral grant FJCI-2017-31595. E.T., M.S., R.S.-N. and M.D.L. are supported by the Government of Aragón through the “Program of research groups” (group H38, “Clima, Agua, Cambio Global y Sistemas Naturales”). A.L. was supported by grant EVA4.0, No. CZ.02.1.01/0.0/0.0/16_019/0000803, financed by OP RDE and by the U.S. Department of Agriculture Forest Service.

DATA AVAILABILITY STATEMENT

The ITRDB dataset is available via the NOAA Web repository: https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring. The global tree cover is available from the World Wide Fund for Nature (WWF) via: https://www.worldwildlife.org/biomes

Climate scenario RCP 8.5 was obtained from the Program for Climate Model Diagnosis & Intercomparison via Web repository: https://pcmdi.llnl.gov/mips/cmip5/data-portal.html

ORCID

Ernesto Tejedor https://orcid.org/0000-0001-6825-3870
Roberto Serrano-Notivoli https://orcid.org/0000-0001-7663-1202
Martin de Luis https://orcid.org/0000-0002-7585-3636
Claudia Hartl https://orcid.org/0000-0001-9492-4674
Scott St. George https://orcid.org/0000-0002-0945-4944
Ulf Büntgen https://orcid.org/0000-0002-3821-0818
Andrew M. Liebhold https://orcid.org/0000-0001-7427-6534
Mathias Vuille https://orcid.org/0000-0002-9736-4518

REFERENCES

Aakala, T., Kuuluvainen, T., Wallenius, T., & Kauhanen, H. (2009). Contrasting patterns of tree mortality in late-successional *Picea abies* stands in two areas in northern Fennoscandia. *Journal of Vegetation Science*, *20*, 1016–1026. https://doi.org/10.1111/j.1654-1103.2009.01100.x

Allen, R. B., Mason, N. W. H., Richardson, S. J., & Platt, K. H. (2012). Synchronicity, periodicity and bimodality in inter-annual tree seed production along an elevation gradient. *Oikos*, *121*, 367–376. https://doi.org/10.1111/j.1600-0706.2011.19306.x

Babst, F., Bouriaud, O., Poulter, B., Trouet, V., Girardin, M. P., & Frank, D. C. (2019). Twentieth century redistribution in climatic drivers of global tree growth. *Science Advances*, *5*, eaat4313. https://doi.org/10.1126/sciadv.aat4313

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bellassen, V., & Luyssaert, S. (2014). Carbon sequestration: Managing forests in uncertain times. *Nature*, *506*, 153–155. https://doi.org/10.1038/506153a

Bjørnstad, O. N., Ims, R. A., & Lambin, X. (1999). Spatial population dynamics: Analyzing patterns and processes of population synchrony. *Trends in Ecology and Evolution*, *14*, 427–432. https://doi.org/10.1016/S0169-5347(99)01677-8

Brienen, R. J. W., Phillips, O. L., Feldpausch, T. R., Gloor, E., Baker, T. R., Lloyd, J., … Zagt, R. J. (2015). Long-term decline of the Amazon carbon sink. *Nature*, *519*, 344–348. https://doi.org/10.1038/nature14283

Briffa, K. R. (1999). Analysis of dendrochronological variability and associated natural climates – the last 10000 years (ADVANCE-10K). *PAGES Newsletter*, *7*, 6–8.

Bunn, A. G. (2008). A dendrochronology program library in R (dplR). *Dendrochronologia*, *26*, 115–124. https://doi.org/10.1016/j.dendro.2008.01.002

Buras, A. (2017). A comment on the expressed population signal. *Dendrochronologia*, *44*, 130–132. https://doi.org/10.1016/j.dendro.2017.03.005

Camarero, J. J., Gazol, A., Sangüesa-Barreda, G., Oliva, J., & Vicente-Serrano, S. M. (2015). To die or not to die: Early warnings of tree dieback in response to a severe drought. *Journal of Ecology*, *103*, 44–57. https://doi.org/10.1111/1365-2745.12295

Carrer, M., & Urbinati, C. (2001). Assessing climate-growth relationships: A comparative study between linear and non-linear methods. *Dendrochronologia*, *19*, 57–65.

Charney, N. D., Babst, F., Poulter, B., Record, S., Trouet, V. M., Frank, D., … Evans, M. E. K. (2016). Observed forest sensitivity to climate implies large changes in 21st century North American forest growth. *Ecology Letters*, *19*, 1119–1128. https://doi.org/10.1111/ele.12650

Cook, E. R., Buckley, B. M., D'Arrigo, R. D., & Peterson, M. J. (2000). Warm-season temperatures since 1600 BC reconstructed from Tasmanian tree rings and their relationship to large-scale sea surface temperature anomalies. *Climate Dynamics*, *16*, 79–91. https://doi.org/10.1007/s003820050006

Cook, E. R., & Kairiukstis, L. A. (1990). Tree-ring standardization and growth trend estimation. In E. R. Cook & L. A. Kairiukstis (Eds.), *Methods of dendrochronology: applications in the environmental sciences* (pp. 104–162). Dordrecht: Kluwer Academic Publishers.

Dakos, V., van Nes, E. H., Donangelo, R., Fort, H., & Scheffer, M. (2010). Spatial correlation as leading indicator of catastrophic shifts. *Theoretical Ecology*, *3*, 163–174. https://doi.org/10.1007/s12080-009-0060-6

Dawes, M. A., Zweifel, R., Dawes, N., Rixen, C., & Hagedorn, F. (2014). CO_2 enrichment alters diurnal stem radius fluctuations of 36-yr-old *Larix decidua* growing at the alpine tree line. *New Phytologist*, *202*, 1237–1248. https://doi.org/10.1111/nph.12742

Defriez, E. J., & Reuman, D. C. (2017). A global geography of synchrony for terrestrial vegetation. *Global Ecology and Biogeography*, *26*, 878–888. https://doi.org/10.1111/geb.12595

Dodd, R. S., Hüberli, D., Mayer, W., Harnik, T. Y., Afzal-Rafii, Z., & Garbelotto, M. (2008). Evidence for the role of synchronicity between host phenology and pathogen activity in the distribution of sudden oak death canker disease. *New Phytologist*, *179*, 505–514. https://doi.org/10.1111/j.1469-8137.2008.02450.x

Fajardo, A., & McIntire, E. J. B. (2012). Reversal of multicentury tree growth improvements and loss of synchrony at mountain tree lines point to changes in key drivers. *Journal of Ecology*, *100*, 782–794. https://doi.org/10.1111/j.1365-2745.2012.01955.x

FAO. (2013). Climate change guidelines for forest managers. In *FAO Forestry Paper No. 172*. Rome: Food and Agriculture Organization of the United Nations.

Fritts, H. C. (1976). *Tree rings and climate* (pp. 567). London: Academic Press.

Fritts, H. C., Smith, D. G., Cardis, J. W., & Budelsky, C. A. (1965). Tree-ring characteristics along a vegetation gradient in northern Arizona. *Ecology*, *46*, 394–401. https://doi.org/10.2307/1934872

Gouveia, A. R., Bjørnstad, O. N., & Tkadlec, E. (2015). Dissecting geographic variation in population synchrony using the common vole in central Europe as a test bed. *Ecology and Evolution*, *6*, 212–218. https://doi.org/10.1002/ece3.1863

Hamed, K. H., & Ramachandra Rao, A. (1998). A modified Mann-Kendall trend test for autocorrelated data. *Journal of Hydrology*, *204*, 182–196. https://doi.org/10.1016/S0022-1694(97)00125-X

Harris, I., Jones, P. D., Osborn, T. J., & Lister, D. H. (2014). Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. *International Journal of Climatology*, *34*, 623–642. https://doi.org/10.1002/joc.3711

Holmes, R. L. (1994). *Dendrochronology program library user's manual*. Tucson, AZ: Laboratory of Tree-Ring Research; University of Arizona.

International Monetary Fund. (2017). *World Economic outlook, October 2017: Seeking sustainable growth: Short-term recovery, long-term challenges (world economic and financial surveys)*. Washington, DC: International Monetary Fund.

IPCC. (2000). In R. T. Watson, I. R. Noble, B. Bolin, N. H. Ravindranath, D. J. Verardo & D. J. Dokken (Eds.),*A special report of the IPCC. Land use, land-use change, and forestry*. Cambridge: Cambridge University Press.

Kelly, D. (1994). The evolutionary ecology of mast seeding. *Trends in Ecology and Evolution*, *9*, 465–470. https://doi.org/10.1016/0169-5347(94)90310-7

Koenig, W. D. (1999). Spatial autocorrelation of ecological phenomena. *Trends in Ecology and Evolution*, *14*, 22–26. https://doi.org/10.1016/S0169-5347(98)01533-X

Körner, C. (2006). Plant CO_2 responses: An issue of definition, time and resource supply. *New Phytologist*, *172*, 393–411. https://doi.org/10.1111/j.1469-8137.2006.01886.x

Legendre, P. (1993). Spatial autocorrelation: Trouble or new paradigm? *Ecology*, *74*, 1659–1673. https://doi.org/10.2307/1939924

Liebhold, A., Koenig, W. D., & Bjørnstad, O. N. (2004). Spatial synchrony in population dynamics. *Annual Review of Ecology, Evolution, and Systematics*, *35*, 467–490. https://doi.org/10.1146/annurev.ecolsys.34.011802.132516

Liebhold, A., Sork, V., Peltonen, M., Koenig, W., Bjørnstad, O. N., Westfall, R., … Knops, J. M. H. (2004). Within-population spatial synchrony in mast seeding of North American oaks. *Oikos*, *104*, 156–164. https://doi.org/10.1111/j.0030-1299.2004.12722.x

Liepert, B. G. (2002). Observed reductions of surface solar radiation at sites in the United States and worldwide from 1961 to 1990. *Geophysical Research Letters*, *29*, 61–64. https://doi.org/10.1029/2002GL014910

Lorimer, C. G., & Frelich, L. (1989). A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research*, *19*, 651–663. https://doi.org/10.1139/x89-102

Ma, Y., Mazumdar, M., & Memtsoudis, S. G. (2012). Beyond repeated-measures analysis of variance: Advanced statistical methods for the analysis of longitudinal data in anesthesia research. *Regional Anesthesia and Pain Medicine*, *37*, 99–105. https://doi.org/10.1097/AAP.0b013e31823ebc74

McMahon, S. M., Parker, G. G., & Miller, D. R. (2010). Evidence for a recent increase in forest growth. *Proceedings of the National Academy of Sciences USA*, *107*, 3611–3615. https://doi.org/10.1073/pnas.0912376107

Melvin, T. M., & Briffa, K. R. (2008). A "signal-free" approach to dendroclimatic standardisation. *Dendrochronologia*, *26*, 71–86. https://doi.org/10.1016/j.dendro.2007.12.001

Mikko, H., Veijo, K., Esa, R., & Jan, L. (1997). Synchronous dynamics and rates of extinction in spatially structured populations. *Proceedings of the Royal Society B: Biological Sciences*, *264*(1381), 481–486. https://doi.org/10.1098/rspb.1997.0069

Moran, P. A. P. (1953). The statistical analysis of the Canadian Lynx cycle. *Australian Journal of Zoology*, *1*, 291–298. https://doi.org/10.1071/ZO9530291

Moseley, A. M., Beckenkamp, P. R., Haas, M., Herbert, R. D., Lin, C.-W.-C., & EXACT Team. (2015). Rehabilitation after immobilization for ankle fracture: The EXACT randomized clinical trial. *JAMA*, *314*, 1376–1385. https://doi.org/10.1001/jama.2015.12180

Cooperative Global Atmospheric Data Integration Project. (2013). *Multi-laboratory compilation of synchronized and gap-filled atmospheric carbon dioxide records for the period 1979-2012*. Colorado, USA: NOAA Global Monitoring Division.

Noble, A. E., Machta, J., & Hastings, A. (2015). Emergent long-range synchronization of oscillating ecological populations without external forcing described by Ising universality. *Nature Communications*, *6*, 6664. https://doi.org/10.1038/ncomms7664

Pearse, I. S., Koenig, W. D., & Kelly, D. (2016). Mechanisms of mast seeding: Resources, weather, cues, and selection. *New Phytologist*, *212*, 546–562. https://doi.org/10.1111/nph.14114

Peltonen, M., Liebhold, A. M., Bjørstad, O. N., & Williams, D. W. (2002). Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. *Ecology*, *83*, 3120–3129. https://doi.org/10.1890/0012-9658(2002)083[3120:SSIFIO]2.0.CO;2

Ponocná, T., Chuman, T., Rydval, M., Urban, G., Migała, K., & Treml, V. (2018). Deviations of treeline Norway spruce radial growth from summer temperatures in East-Central Europe. *Agricultural and Forest Meteorology*, *253–254*, 62–70. https://doi.org/10.1016/j.agrformet.2018.02.001

Post, E., Brodie, J., Hebblewhite, M., Anders, A. D., Maier, J. A. K., & Wilmers, C. C. (2009). Global population dynamics and hot spots of response to climate change. *BioScience*, *59*, 489–497. https://doi.org/10.1525/bio.2009.59.6.7

Ranta, E. (1995). Synchrony in population dynamics. *Proceedings of the Royal Society B: Biological Sciences*, *262*(1364), 113–118. https://doi.org/10.1098/rspb.1995.0184

Riahi, K., Grübler, A., & Nakicenovic, N. (2007). Scenarios of long-term socio-economic and environmental development under climate stabilization. *Technological Forecasting and Social Change*, *74*, 887–935. https://doi.org/10.1016/j.techfore.2006.05.026

Riahi, K., Rao, S., Krey, V., Cho, C., Chirkov, V., Fischer, G., … Rafaj, P. (2011). RCP 8.5—A scenario of comparatively high greenhouse gas emissions. *Climatic Change*, *109*, 33. https://doi.org/10.1007/s10584-011-0149-y

Salzer, M. W., Hughes, M. K., Bunn, A. G., & Kipfmueller, K. F. (2009). Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *Proceedings of the National Academy of Sciences USA*, *106*, 20348–20353. https://doi.org/10.1073/pnas.0903029106

Sánchez-Salguero, R., Navarro-Cerrillo, R. M, Camarero, J. J., Fernández-Cancio, A., Swetnam, T. W., & Zavala, M. A. (2012). Vulnerabilidad frente a la sequía de repoblaciones de dos especies de pinos en su límite meridional en Europa. *Ecosistemas*, *21*, 31–40. https://doi.org/10.1175/2008MWR2773.1

Sheppard, L. W., Bell, J. R., Harrington, R., & Reuman, D. C. (2016). Changes in large-scale climate alter spatial synchrony of aphid pests. *Nature Climate Change*, *6*, 610–613. https://doi.org/10.1038/nclimate2881

Shestakova, T. A., Gutiérrez, E., Kirdyanov, A. V., Camarero, J. J., Génova, M., Knorre, A. A., … Voltas, J. (2016). Forests synchronize their growth in contrasting Eurasian regions in response to climate warming. *Proceedings of the National Academy of Sciences USA*, *113*, 662–667. https://doi.org/10.1073/pnas.1514717113

Shestakova, T. A., Gutiérrez, E., Valeriano, C., Lapshina, E., & Voltas, J. (2019). Recent loss of sensitivity to summer temperature constrains tree growth synchrony among boreal Eurasian forests. *Agricultural and Forest Meteorology*, *268*, 318–330. https://doi.org/10.1016/j.agrformet.2019.01.039

Shestakova, T. A., Gutiérrez, E., & Voltas, J. (2018). A roadmap to disentangling ecogeographical patterns of spatial synchrony in dendrosciences. *Trees*, *32*, 359–370. https://doi.org/10.1007/s00468-017-1653-0

Shimatani, I. K., & Kubota, Y. (2011). The spatio-temporal forest patch dynamics inferred from the fine-scale synchronicity in growth chronology. *Journal of Vegetation Science*, *22*, 334–345. https://doi.org/10.1111/j.1654-1103.2010.01255.x

St. George, S. (2014). An overview of tree-ring width records across the Northern Hemisphere. *Quaternary Science Reviews*, *95*, 132–150. https://doi.org/10.1016/j.quascirev.2014.04.029

R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org

Tei, S., Sugimoto, A., Yonenobu, H., Matsuura, Y., Osawa, A., Sato, H., … Maximov, T. (2017). Tree-ring analysis and modeling approaches yield contrary response of circumboreal forest productivity to climate change. *Global Change Biology*, *23*, 5179–5188. https://doi.org/10.1111/gcb.13780

Walter, J. A., Sheppard, L. W., Anderson, T. L., Kastens, J. H., Bjørnstad, O. N., Liebhold, A. M., & Reuman, D. C. (2017). The geography of spatial synchrony. *Ecology Letters*, *20*, 801–814. https://doi.org/10.1111/ele.12782

Waring, R. H., & Running, S. W. (2007). Forest Ecosystems. *Analysis at Multiple Time and Space Scales* (3rd ed.). San Diego, CA: Academic Press. https://doi.org/10.1016/B978-012370605-8.50005-0

Wigley, T. M. L., Briffa, K. R., & Jones, P. D. (1984). On the average of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology*, *23*, 201–203.

Zhao, S., Pederson, N., D'Orangeville, L., HilleRisLambers, J., Boose, E., Penone, C., … Manzanedo, R. D. (2019). The International Tree-Ring Data Bank (ITRDB) revisited: Data availability and global ecological representativity. *Journal of Biogeography*, *46*, 355–368. https://doi.org/10.1111/jbi.13488

Zielonka, T., Holeksa, J., Fleischer, P., & Kapusta, P. (2010). A tree-ring reconstruction of wind disturbances in a forest of the Slovakian Tatra Mountains, Western Carpathians. *Journal of Vegetation Science*, *21*, 31–42. https://doi.org/10.1111/j.1654-1103.2009.01121.x

BIOSKETCH

The research interests of all authors focus on the intersection between dendrochronology, ecology, biogeography and climatology.

Ernesto Tejedor focuses on the understanding of climate processes, the effects of human-caused climate change on these processes, and how these changes affect ecological systems and humanity through time.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

How to cite this article: Tejedor E, Serrano-Notivoli R, de Luis M, et al. A global perspective on the climate-driven growth synchrony of neighbouring trees. *Global Ecol Biogeogr*. 2020;29:1114–1125. https://doi.org/10.1111/geb.13090