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

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Abstract

Aim

Previous work demonstrated the global variability of synchrony in tree-growth within populations, i.e. the covariance of the year-to-year variability in growth of individual neighboring trees. However, there is a lack of knowledge about the causes of such 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 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 employed 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 and 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 both high annual mean temperature (>10°C) and low precipitation (< 300 mm) environments. Average WPS across all temperate forests has historically decreased 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 due to reduced annual precipitation.

Main conclusions

Climate explains WPS variability in space and time. We suggest that WPS may 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

Synchrony, tree-ring, tree stress indicator, global

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, around 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 world's forests (which is about the same amount as is taken up by the oceans (Bellassen, 2014). Forests directly affect approximately 1.6 billion people worldwide regarding economic activities such as forestry, food, agricultural policies or tourism (FAO, 2013). Hence, it is essential to better understand 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 analyze today (Waring & Running, 2007). Here, we propose an additional approach to understand forest population dynamics by analyzing 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 employed this concept to, for instance, 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, Bjorstand, & Williams, 2002). In addition, the absence of spatial synchrony is generally considered key to persistence in metapopulation dynamics and may 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 regime shift (Dakos, van Nes, Donangelo, Fort, & Scheffer, 2010). By studying the nature of such synchronous oscillations, we are taking steps to further understand the role of synchrony in population dynamics. Though ecologists used to be frustrated in their efforts to identify the cause of such 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 synch (Ranta, 1995), has been frequently 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 quality measure of the chronology (Buras, 2017), the spatial synchrony of tree growth is an aspect that remains poorly understood (Defriez & Reuman, 2017). Yet, 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 et al., 2010) not only at regional scales but also at fine spatial scales (Aakala et al., 2009; Carrer & Urbinati, 2001; Shimatani & Kubota, 2011). Following the spatial synchrony approach, it has also been suggested that the earth's warming climate is synchronizing forest growth across Eurasian regions and hence indicating early warning signals of climate change impacts on forest ecosystems at subcontinental scales (Tatiana A. Shestakova et al., 2016). Furthermore, Camarero, Gazol, Sangüesa-Barreda, Oliva, & Vicente-Serrano, (2015) applied the synchrony concept to study early warning signals in the growth trends of declining and non-declining trees and related the increase in synchrony with a rise in severe droughts. Hitherto, the spatial synchrony concept in both ecology and dendrochronology has largely been applied to analyze *among population synchrony* analyses rather than *within population synchrony* which we consider here.

1.2. The within-population synchrony concept to study forests' population dynamics

The within-population synchrony (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 (as far as 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 those 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, 1984), is a commonly employed 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 indeed document within-population synchrony (WPS) of neighboring 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 -1.0 to 1.0, though 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 & Briffa, 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 forests' growth response to climate change. St. George (2014) used the International Tree-Ring Data Bank for studying tree-ring width series of the Northern Hemisphere and indicated differences in the RBAR value among species and geographic location. In that study consistently high values were found for most sites in the North American Southwest, but also in northern Fennoscandia and the central Russian Arctic. Characteristically low values were found in tree-ring width records from European Mediterranean and sites and from the Himalayas (see Figure S1 as an example). 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 N. America.

This study further explores how WPS varies in both space and time. There is still a lack of knowledge regarding (i) the variability and change of WPS over time, (ii) the influence of the environment on WPS and (iii) 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 analyze 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 first, under current climate conditions, and then to forecast future conditions under a projected climate scenario.

<u>Here we hypothesize that the within-population synchrony (WPS) of tree growth:</u>

a) 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.).
b) Based upon the above relationships, both spatial and temporal variation in synchrony could, at least partially, 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, since 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. <u>Data acquisition and treatment</u>

The International Tree Ring Databank (ITRDB, Zhao et al., 2019) is the largest archive containing digital tree-ring width measurements. As of June 2015, the ITRDB contained more than 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, as well as sampling site latitude, longitude and elevation.

In preparation for analysis, all available tree-ring records were downloaded, except for 245 records, which had to be removed due to errors detected within the data. Most frequent errors consisted of unusual formats or multiple ring-width series with the same identification codes. After removing erroneous data, 3,936 records were used. In addition, we selected records with more than 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 southern hemisphere. Even though 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 hence fulfil the aims of this study. We selected the 1901-2012 period since monthly meteorological data are available worldwide (CRU TS v.3.21.; Harris, Jones, Osborn, & Lister, 2014). Furthermore, selection of this particular 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, i.e. the high-frequency signal, each of the 3,579 records were standardized using the 'dplR' package (Bunn, 2008) within R (R Development Team, 2018). First, each individual tree-ring width series was detrended with a cubic spline with a 50 % frequency cutoff at 30 years (Cook et al., 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 modeling 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 (WPS) 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 one year at each step). WPS is calculated by the average Pearson correlation of all ring-width series within a given stand (Wigley & Briffa, 1984). Because 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 0, meaning a total absence of covariance within the tree-ring width series to 1, 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 95% confidence level).

2.3. Modeling 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 employed generalized linear mixed effects models (GLME; 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-

ID- of each site or each population). Mixed models explicitly account 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, while 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 0 to 1, the quasibinomial family was used in order to describe the error distribution. Prior to 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 (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 Chi square distribution.

Finally, to predict future values for the temperature and precipitation parameters during the 2046-2065 period, we used an ensemble of multiple models for the RCP 8.5 scenario from the CMIP5 project (AR5, uploaded 15th 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, which are poorly covered by the ITRDB network. Global tree cover was classified according to the World Wildlife Fund (WWF) definition of ecoregions (https://www.worldwildlife.org/biomes)(Table S1). The predictions in each pixel are made based on a common generic 'site' (same random factor all across 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 spanning the period 1901-2012 is shown in Figure 1a. According to the WPS values of each site, we define five categories of forest growth synchrony (Table 1), ranging from very low, absence of synchrony, to very high, meaning that growth in those sites is at near to full agreement. The regions with the highest WPS values are western North America, in central Asia and boreal forests in the Russian Arctic. In contrast, the lowest WPS values are found along the east coast of North America, along the Mediterranean fringe in Europe in some parts of the Himalayas in Asia and some sites in South America. Most of the sites (59%) show a low to moderate synchrony. We also found that 17% of the sites have a very low to near-zero tree-growth synchrony, whereas 24% of the sites show a very high or almost total tree-ring growth synchrony. Lowest WPS values are located in North American boreal forests, while the highest values correspond to sites located in the mountainous areas of Colorado, USA.

Results indicate that WPS of global forest populations has varied through time during the last 112 years (Figure 1b) i.e., it is a dynamic rather than a static indicator. In fact, among the studied sites, 77% show a significant positive (gain) or negative (loss) trend through time (Figure 1c). These changes are mostly low (78%) although a remarkable 21% of the sites are showing a

moderate to high variability, including shifts in the category, i.e. from high to moderate or from moderate to high synchrony.

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

3.2. WPS determined by climate

By comparing our full model with a null model (Table 2) we demonstrate that the full model (including the mean annual temperature and precipitation and its interaction as fixed factors) has a better explanatory power (lower AIC and BIC). The WPS is positively related with mean temperature, i.e. higher WPS occurs where and when temperatures are higher, and the WPS is negatively related with precipitation, i.e. higher WPS is found in low precipitation environments (Table 3). The interaction between annual mean temperature and precipitation also explains a significant fraction of the WPS variance. WPS is higher in areas with high annual mean temperature and low precipitation totals.

With these results, we now better understand the climate constraints of the observed WPS (Figure 2). The results are robust (see Figure S3) and highlight the wide range of WPS levels of the observed ITRDB forest populations. Hence, higher WPS values are found in dry environments, including areas with precipitation below 400 mm, and mean annual temperature above 0°C. Lower WPS values are found in sites with more than 1,000 mm of annual precipitation, although they can 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 show low to very low WPS. Additional findings include the climate boundaries of the distribution limits of the ITRDB studied sites, which range from 100 to almost 5,000 mm/year, and from -20°C to 26°C annual mean temperature.

3.3. Model applications to the current and future climate

The GLME model is 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 around 30°C and mean annual precipitation between 100 and 300 mm, are characterized by a higher predicted WPS. On the other hand, areas with ~25°C mean annual temperature, and between 2,000 and 5,000 mm of mean annual precipitation account for the lower predicted WPS levels (although results for these particular areas must be treated with caution due to the reduced number of observations with such climate conditions). Moderate WPS levels can be found in a wide spectrum of climates, although with a similar mean annual precipitation of 300-600 mm and annual mean temperatures that can range from -15°C 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, 4b). First, WPS variability is 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. On the other hand, those sites exposed to a significant rise in temperature, but with similar or lower precipitation amounts will be more limited and thus increase their tree-growth WPS.

When considering only the effects of future climate change on WIPS, larger changes in WPS (Figures 3c, 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 in tree-ring growth WPS will occur mainly in the Mediterranean basin, in the tropical forest of India, and in the Amazon Basin rainforest. Northern Hemisphere forests, on the other hand, and particularly the boreal forests, will experience no change or a slight decrease in their WPS, due 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 traditionally used to define reconstruction periods (Buras, 2017) as a parameter in the Expressed Population Signal (EPS) formula (Wigley & Briffa, 1984).

In this 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 may potentially occur if low-frequency detrending methods would have 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 forests environmental stress. 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 of 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 better predict changes in future forests population distributions.

4.2. WPS tested on a global tree-ring dataset; opportunities and limitations

The WPS concept is 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, Figure S2). However, it is very unlikely that there is a systematic trend or bias in the inter-distance between trees in the ITRDB. Since the ITRDB was created, its main purpose was to develop climatic reconstructions (Zhao et al., 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, etc.). The distance between sampled trees is not explicit, precisely because it is considered 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 to address macroecological questions. The majority of the sites included in the ITRDB correspond to the Northern Hemisphere, whose species, distributions and ecoregions are well represented. On the other hand, 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 this study we attempted to demonstrate a global pattern of synchrony change and trend throughout the twentieth century and towards the mid-late twenty-first 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 toward areas where chronologies are largely absent but 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 twentieth century the main drivers have transitioned from energy limitation toward 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 due 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, 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). On the other hand, when climatic conditions are more favorable, local characteristics become more determinant for tree growth and the common variance between tree-ring traits due 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 (>10°C annual mean temperature and <300 mm annual precipitation) whereas a lower WPS is found in warm (mean annual temperature >15°C) and wet environments (precipitation >1,000 mm/year), and in extreme cold and dry environments (mean annual temperature <-10°C). Thus, the drivers that are associated with WPS are also likely 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 since it allows us to predict the future behavior and climatic stress levels in environments where no information is available, but which may be able to sustain forest cover in the future. We are thus able to detect hot spots, 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 which 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 (Fig.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 greenhouse gas concentration levels (Riahi et al., 2007, 2011), including a rise in global temperature of 4.9°C by 2100. While the projected temperature increase is relatively spatially homogenous, the projected precipitation change varies strongly in space. Temperate forests and the tropical forests of Africa and Asia are projected to experience an increase in precipitation, while Mediterranean Forests and the Amazon tropical forest will be exposed to a decrease ranging from 500 to 1000 mm per year (International Monetary Fund, 2017). Larger changes in WPS are in agreement with projected precipitation changes (although the results for the tropical areas must be treated with caution). A pronounced decrease in synchrony is projected for the Northwest 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 due to rising temperature and increasing precipitation, that 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 N. America, (Salzer, Hughes, Bunn, & Kipfmueller, 2009), boreal Eurasian forests (Shestakova, Gutiérrez, Valeriano, Lapshina, & Voltas, 2019). The Mesoamerican region and the Amazon basin on the other hand, will be areas with a potential increase of limiting factors, due 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 specifically account 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 regimes may 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 with 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 by (Dawes, Zweifel, Dawes, Rixen, & Hagedorn, 2014, among others). 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, as by December 2019, the CO_2 concentration has already exceeded 410 ppm (NOAA, 2019). 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). Since the WPS is calculated from the tree-ring growth and explained by climate, we believe it is an additional and essential ecological and integrative tool to be used when facing forests 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 on forests and threshold tree responses to climate change (Tatiana A 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, crucial to better understand 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 to 50 years. Will we purposely or accidentally redistribute species as habitats change?

5. Conclusions

We demonstrate that climate determines WPS variations across space and also 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. On the other hand, temperate forest may 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 may 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.

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Figures

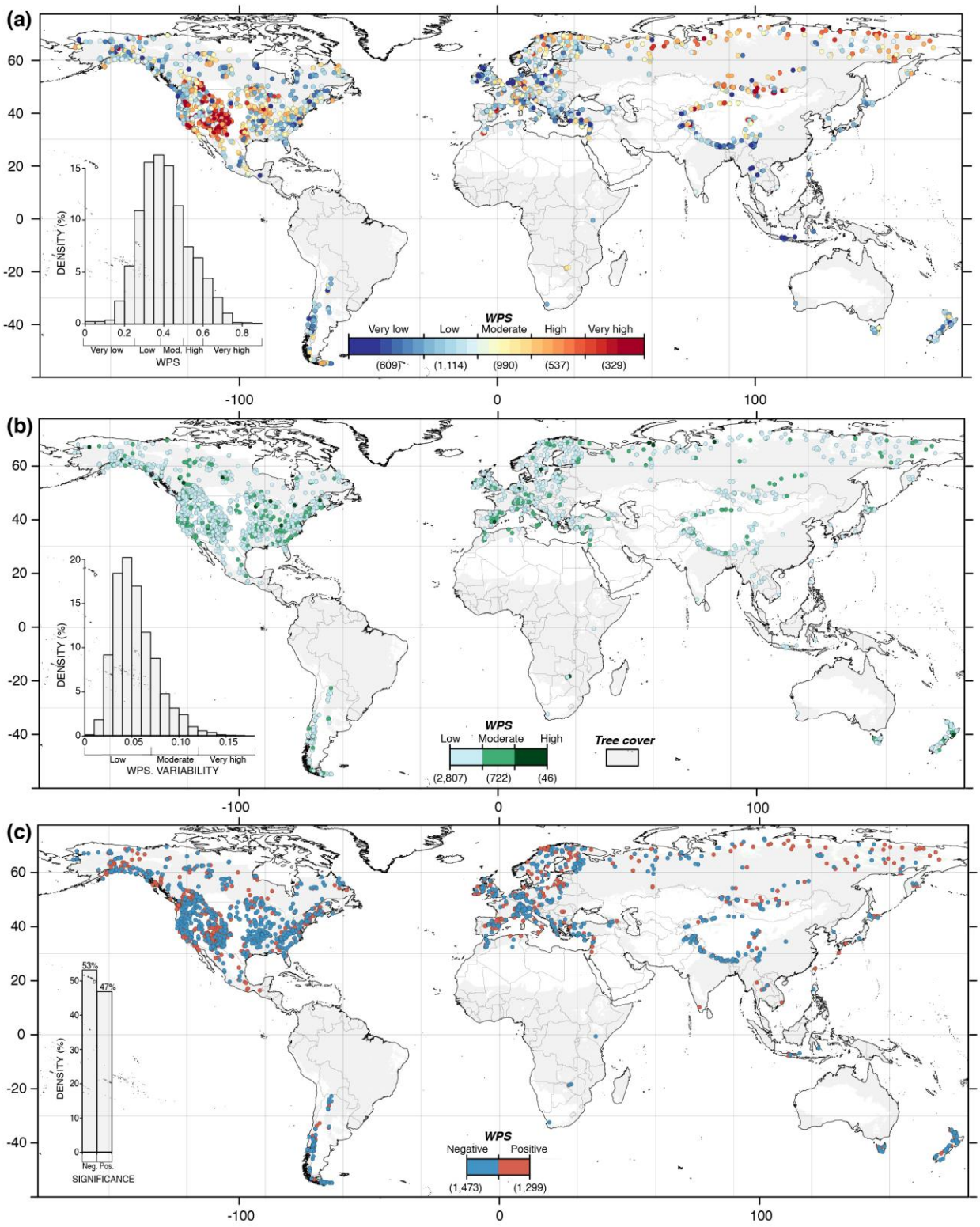

Figure 1. Global patterns of within-population synchrony (WPS) at ITRDB sites for the 1901-2012 period) a) Variation of WPS classified from 0 (Very Low), meaning a total absence of synchrony, to 1 (Very High), a perfect agreement between tree-ring growth series (see the categories

665 correspondence in Table 1) . b) WPS variability based on the standard deviation. c) Trend and
666 significance of such WPS changes (only significance levels at p<0.05 are shown).
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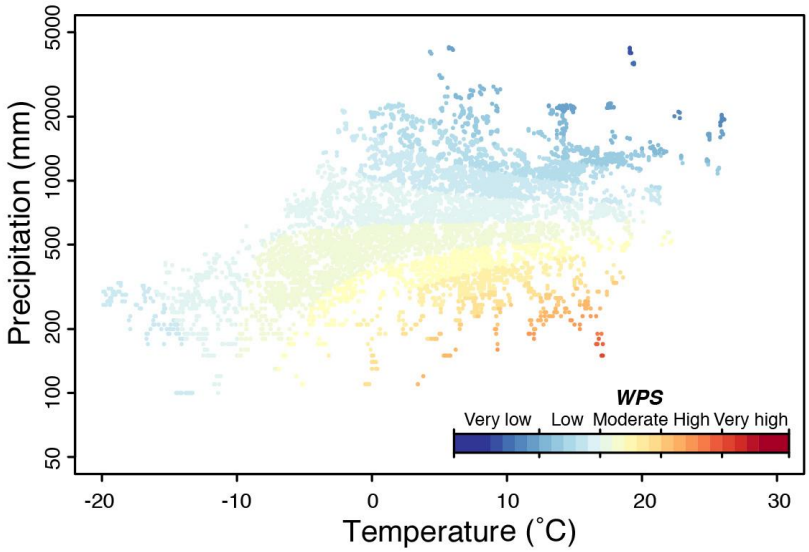

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670 **Figure 2**. Modeled distribution of the WPS applied to the current climate (annual means) of each
671 observed site i.e., the climate envelope covered by the tree-ring network.
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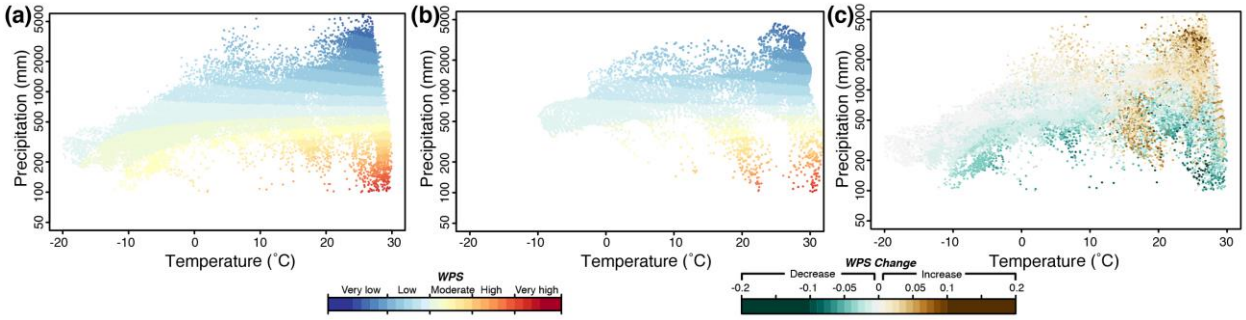

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677 **Figure 3**. Forecasted within-population synchrony (WPS) values. a) Modeled distribution of the
678 WPS using the current climate and applied to the global tree cover extension. b) Modeled
679 distribution of the WPS using the RCP 8.5 scenario (2045-2065) and applied to the global tree
680 cover extension. c) Differences in the WPS between current and future climate scenario.
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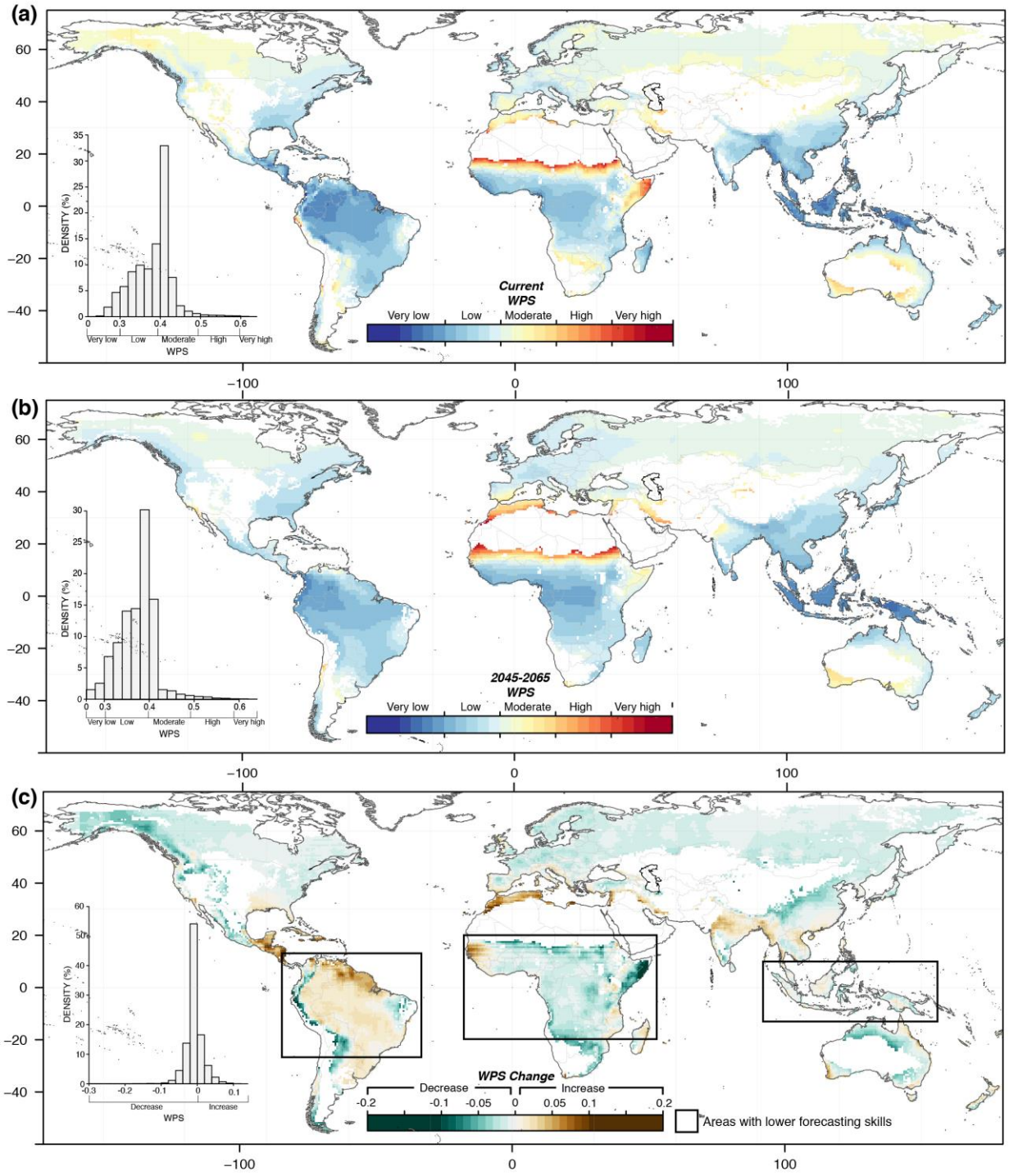

Figure 4. a) Spatial distribution of the within-population synchrony (WPS) model using the current climate and applied to the global tree cover. b) Spatial distribution of the WPS model using the RCP 8.5 scenario (2045-2065) and applied to the global tree cover. c) Spatial distribution of the differences in the WPS between current and future climate scenario.

Category	***Values 1901-2012***	***Change 1901-2012***
Very low	< 0.30	
Low	0.30– 0.39	<0.07
Moderate	0.40 – 0.49	0.07-0.12
High	0.50 – 0.59	>0.12
Very high	> 0.59	

Table 1. Categories of the synchrony levels.

Model	***Df***	***AIC***	***BIC***	***logLik***	***Deviance***	***Chisq***	***Df***	***Pr(>Chisq)***
Null model	2	224219	224239	-112107	224215			
Full model	5	223606	223658	-111798	223596	618.63	3	< 2.2e-16***

Table 2. Summary statistics of the Intercept-only model (Null model) and the full model (including mean annual temperature and precipitation and its interaction as fixed factors). We include the Chi-squared test (Chisq) comparing both models. The full model has a lower AIC (Akaike information criterion) and BIC (Bayesian information criterion) than the null model indicating its better explanatory power.

	Estimate	**Std. Error**	**Z value**	**Pr(>|z|)**
(Intercept)	0.03550	0.11755	0.302	0.763
TMean_Annual	0.46642	0.09761	4.778	1.77e-06 ***
Precip_Annual	-0.14758	0.01797	-0.8214	< 2e-16 ***
TMean:Precip	-0.07180	0.01552	-4.626	3.73e-06 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*'

Table 3. Full model summary of the fixed effects on the WPS. Number of observations is 186,750. WPS will be higher where temperature is higher and where precipitation is lower.

Supplementary Material

Figure S1. Example of the WPS at contrasting sites.
Figure S2. Spatial correlogram of the mean of WPS.
Figure S3. Spatial distribution of the residuals.
Table S1. Types of forests included in the tree cover.
Equation S1. Mixed model equation.