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A roadmap to disentangling ecogeographical patterns of spatial synchrony in dendrosciences

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Abstract

The concept of spatial synchrony in ecology refers to the presence of coordinated time fluctuations in certain characteristics that can be observed in plant and animal communities inhabiting an area. It is a well-known phenomenon common to virtually every taxon, but comparatively little attention has been given to the study of the temporal coherence of forest tree performance across biogeographical gradients. In forest ecosystems, tree growth dynamics is primarily driven by climatic variability (i.e. the Moran effect). Due to rapid climate change trees are increasingly pushed to their physiological limits up to the level that many populations are facing immediate risk of extinction. The characterization of synchrony patterns in tree growth can provide clues on the relevance of emerging climatic threats on forests, as new combinations of precipitation and temperature are entraining tree performance worldwide. In this regard, comprehensive and systematic approaches to analyse spatiotemporal dynamics of tree growth are needed. Here we present a methodology for disentangling and interpreting how the variability and common signal strength of tree growth (or other traits) are structured in tree-ring networks. It is grounded on mixed modelling principles and broadens well-known theoretical principles in dendrosciences. Based on this approach, we describe the essential properties of spatial synchrony in tree growth at multiple geographical scales. We also discuss the potential of this methodology to discern early warning signals of climate change impacts on forest ecosystems.

Keywords: biogeography; Moran effect; spatiotemporal variability; teleconnection; tree rings; tree growth

Key Message

A systematic assessment of spatial synchrony in tree growth, a fundamental feature of spatiotemporal forest dynamics, can provide valuable insights into complex tree reactions across species and environmental gradients.

Introduction

Changes of time-varying characteristics (e.g. abundance, growth rate) in geographically distant populations often exhibit correlated fluctuations, a feature known as spatial synchrony (Liebhold et al. 2004). This widespread yet highly diverse ecological phenomenon (Walter et al. 2017) can be observed in a broad range of natural systems and affects organisms such as vertebrates, insects, pathogens and terrestrial vegetation, including forest trees (Ranta et al. 1997; Koenig and Knops 1998a; Schauber et al. 2002; Defriez and Reuman 2017; Shestakova et al. 2016). It is well known that regionally correlated climatic forces engender population synchronization across vast geographical areas (i.e. the Moran effect; Moran 1953). Indeed, a climatic factor such as temperature or precipitation often varies in the same direction on large spatial scales. This variation is mainly driven by general patterns of atmospheric circulation, hence causing synchronized dynamics among disjunct populations (Hanski and Woiwod 1993; Haydon and Steen 1997; Koenig 2002). In ecology this phenomenon is often referred to as 'climatic teleconnections' – a term widely used also in dendrosciences (Fritts 1976; Feliksik 1993; Rolland 2002; Di Filippo et al. 2007; Trouet et al. 2012; St. George 2014). However, we will stick here to the generic term 'spatial synchrony' for the sake of simplicity.

According to ecological theory, populations whose dynamics are entrained by correlated environmental stochasticity face increased risk of extinction (den Boer 1981; Heino et al. 1997; Earn et al. 2000). The extent of such coordinated responses is relevant because the higher the spatial synchrony is among individuals of a metapopulation, the shorter persistence time is expected in the system (Heino et al. 1997). The reason is straightforward: if all subpopulations fluctuate in concord, then when one goes extinct, all others are expected to suffer the same fate. This behaviour

can be especially problematic in the face of emerging threats imposed by climate change such as drought and heat stress, outbreaks of pests and diseases (Sturrock et al. 2011; Allen et al. 2015). Conversely, if spatial synchrony is low, some subpopulations are likely to persist and serve to re-establish extinct subpopulations.

In forest ecosystems, coordinated fluctuations in secondary growth caused by correlated climatic anomalies have already been reported over large spatial scales (Feliksik 1993; Koenig and Knops 1998b; Shestakova et al. 2016). Indeed, the principle of limiting factors is well known in dendrochronology, in the sense that the effect of climate controlling tree performance often causes similar and synchronous responses of tree growth across vast geographical areas (Hughes et al. 1982). These similarities are important when climatic conditions become especially limiting for growth in certain years. On the contrary, when climatic conditions are favourable, local characteristics are more determinant for tree growth and the common variance between tree-ring traits due to macroclimate is lower (Fritts 1976). Framed into these considerations, the estimation of synchronous tree growth dynamics and its attribution to exogenous factors becomes highly relevant to forecast potential ecological consequences of climate change.

In recent years, considerable effort has been given to document responses of tree populations to climate variability from local to global scales (Carrer and Urbinati 2001, 2006; Case and Peterson 2005, 2007; Nakawatase et al. 2006; Littell et al. 2008; Babst et al. 2012; Kherchouche et al. 2012; Allen et al. 2015). Obviously, climate affects forest dynamics in manifold ways. On one hand, the ability of trees to cope with short-term disturbances (e.g. an extreme drought) is related to phenotypic plasticity and varies among species or functional groups (e.g. isohydric–anysohidric continuum; Klein 2014). On the other hand, their reaction to long-term changes (e.g. gradual increase in duration and severity of dry spells) relies more on the extent of selective processes

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driving population differentiation at intra- and inter-specific levels. Both mechanisms lead to changes in growth dynamics and may trigger climate-driven population synchrony at varying geographical scales. However, considering that atmospheric circulation patterns often affect neighbour biogeographical regions disparately, the ecological repercussions of climatic change (e.g. warming, increase in climate variability and frequency of extreme events) may also differ considerably among biomes (Allen et al. 2015).

Spatial synchrony and dendrochronological data

In dendrosciences annual or intra-annual growth responses are measured at tree level through the analysis of ring-width fluctuations. Individual time series are usually combined into a site chronology which contains growth variability common to a representative number of trees (Fritts 1976). Wherever the goal is to evaluate past, current or future forest performance across large geographical areas, a burst of opportunities emerges from disentangling the information contained in tree-ring networks (Barber et al. 2000; Briffa et al. 2002, 2008; Babst et al. 2013; St. George 2014; Restaino et al. 2016; Shestakova et al. 2016). Indeed, the number of papers reporting on ecogeographical patterns of growth variability in tree-ring archives has increased exponentially over the last 30 years (Fig. 1). However, and despite a surge of interest in spatial synchrony and its underlying causes (Reuman et al. 2017; Walter et al. 2017), there is a deficit of systematic approaches to characterise geographical patterns of forest growth dynamics based on tree rings.

In early dendrochronological studies general patterns of shared temporal variability among a set of time series (site chronologies) have been roughly explored through visual assessment of temporally coincident changes in "rise and fall"

fluctuations (Fritts 1976) or by estimating "Gleichläufigkeit" coefficient of coincidence (Eckstein and Bauch 1969). Synchrony has also been assessed by informing on the temporal coincidence of peaks or *pointer* years (LaMarche and Hirschboeck 1984; Schweingruber et al. 1990; Briffa et al. 1998). An obvious numeric measure of synchrony has been the mean correlation calculated among all possible pairs of chronologies (cross-correlation) (Rolland 2002; Macias et al. 2006; Briffa et al. 2008). Multivariate approaches (e.g. Principle Component, Factor or Cluster Analyses) have also been employed to interpret complex biogeographical patterns of temporal dynamics (Peterson and Peterson 2001; Andreu et al. 2007; Babst et al. 2013). In parallel, studies on synchronous fluctuations in demographic rates have arisen from animal ecology aimed at quantifying spatial dependences in population dynamics. Techniques such as Mantel correlograms, modified correlograms and semi-variograms (Koenig and Knops 1998a; Carrer and Urbinati 2001) have been extensively applied to describe the relationship between synchrony and distance between sampling locations (reviewed in Bjørnstad et al. 1999; Koenig 1999). These methodologies investigate the underlying patterns of common growth that arise exclusively from the available data (i.e. they can be regarded as *a posteriori*, or exploratory approaches), but they do not allow for testing on hypothesized contrasting growth patterns where groups of chronologies are known or can be defined based on existing knowledge (i.e. they are less suited to evaluate specified classes *a priori*).

Tree growth synchrony is a complex phenomenon which often exhibits distinct spatial variations across different time periods (Läänelaid et al. 2012). Climate change and its spatial heterogeneity (IPCC 2013) further complicate the evaluation and future prediction of changes in population trajectories. In this context, there is an urgent need for a comprehensive evaluation and testing of synchrony patterns in forest growth over

time and across space simultaneously (Briffa et al. 2008). This is particularly relevant to dendrosciences, as tree-ring data are likely to become an essential component of global change research (Babst et al. 2017). In this work, we propose a methodology for interpreting the variability and common signal strength existing in tree-ring networks that is grounded on mixed model analysis of variance (ANOVA) principles (Wigley et al. 1984; Shestakova et al. 2014). This methodology is suited to test the presence of contrasting tree-ring patterns in pre-established classes or groups of chronologies, that is, it can be regarded as a confirmatory approach. Next, this review outlines some key insights on growth synchrony patterns at multiple spatiotemporal scales. We suggest that these patterns vary in a systematic fashion depending on (*i*) the prevailing climatic driver(s) of tree growth in an area, (*ii*) the spatial coverage of sampling sites and (*iii*) the particular impact of climate change on tree functioning. To illustrate our ideas, we compare tree-ring width records at different geographical scales (local, regional and continental) and review an array of climate effects on tree performance that may ultimately translate into enhanced spatial synchrony of growth trends as climate warms and dries.

Analytical framework

We define spatial synchrony ($\hat{a}$) in dendrosciences as the presence of a common signal in a collection of tree-ring chronologies for a time-varying characteristic (e.g. ring-width, wood density, stable isotopes). Traditionally, dendrochronologists fit standard ANOVA procedures to estimate common forcing (or "signal") among indexed tree-ring series which preserve high-frequency (i.e. inter-annual to decadal) variability (Fritts 1976; Wigley et al. 1984; Briffa and Jones 1990). In this way, the mean inter-series correlation at stand level is derived (*Rbar* statistic; Wigley et al. 1984). The

ANOVA approach, however, has severe weaknesses if applied to a set of chronologies with the purpose of estimating their common temporal signal. Particularly, (*i*) it has limited power to account for complex correlations in the data, (*ii*) it can only accommodate one error term and (*iii*) it cannot deal efficiently with unbalanced data, which is a fundamental characteristic of dendroecological archives (due to missing measurements, different time span of chronologies, etc.).

Mixed modelling provides the very flexible framework to accomplish these tasks: when testing the effect of an explanatory variable *x* (e.g. site chronology) that is measured across years on a trait of interest *y* (e.g. ring-width), the year factor can be assumed to behave like a random sample and so is regarded as random. This decision provides inferences about the entire population of years owing to the estimation of the temporal variance for *y* that underlies the set of tree-ring chronologies. In this framework, additional random effects can be fitted if other sources of non-independence between observations are suspected. These sources may account for the presence of natural grouping in the tree-ring dataset via classification by e.g. taxonomic or biogeographical criteria. For each random effect a corresponding component of the existing variance can be estimated through different variance-covariance structures. When fitting these models, dendrochronologists will likely be more interested in the variance components associated with random coefficients than in the prediction of the random parameters themselves; indeed, variance components allow for a straightforward estimation of the signal strength shared among series or chronologies. Hence, we reckon that variance component estimation lies at the heart of mixed modelling techniques when applied to dendrosciences.

The theoretical basis for the application of mixed models in dendrosciences was established by Wigley et al. (1984). If we simply express the year factor (random) relative to the population mean, the resulting model can be written as follows:

$$y = \mu + \alpha_j + \varepsilon_{ij} \tag{1}$$

where y is the vector of measurements of the study variable (usually, a dimensionless index), μ is the intercept (the population mean), α_j is a random effect (i.e. the effect of the jth year relative to the mean) and ε_{ij} is the residual term (i.e. a random deviation of the ith chronology in the jth year). Here, we assume that covariation arises among chronologies which originates from common forcing mechanisms. In the same vein as time series of a tree-ring feature are analysed together to assess variability common to a number of trees at a site (*Rbar* statistic or cross-correlation; Wigley et al. 1984), unbiased estimates of the average correlation among pairs of site chronologies ($i = 1, N$) for a trait y, excluding the N pairs $i = i^*$, can be obtained as follows (Shestakova et al. 2014):

$$\hat{a} = \frac{\sigma_Y^2}{\sigma_Y^2 + \sigma_\varepsilon^2} \tag{2}$$

where σ_Y^2 refers to the temporal (year) variability that is common across chronologies and $\sigma_Y^2 + \sigma_\varepsilon^2$ stands for the total spatiotemporal variability. The above expression estimates the mean inter-chronology correlation over the whole set of N chronologies, which we refer to as intra-class correlation, common signal strength or spatial synchrony ($\hat{a}$) for a trait y. An intra-class correlation close to 1 indicates near-perfect synchrony of y, while a value close to 0 denotes spatial asynchrony.

We may further hypothesize about the presence of different sources of similarities–dissimilarities among tree-ring records. This may include phylogenetic (e.g.

pertinence to a species) or geographical factors (e.g. pertinence to an ecoregion), among others. If we postulate that such effects are important, then model (1) can be expanded to an alternative mixed model by adding a fixed effect β_r ($r = 1$ to n). In this case, the estimators can be defined as follows:

$$y = \mu + \beta_r + \alpha_{jr} + \varepsilon_{ijr} \tag{3}$$

where β_r is a fixed term accounting for mean differences among the n groups, α_{jr} is the random effect of the jth year in the rth group and ε_{ijr} is the residual term (i.e. a random deviation of the ith chronology in the jth year within the rth group).

According to the theory of survey sampling (Kish 1965), stratification improves accuracy of parameter estimates, provided there is heterogeneity between groups as defined by the factor(s) under evaluation. When two or more groups are defined, mixed modelling allows for correlation estimation either at the intra-group or at the inter-group level. The underlying idea is to split the mean correlation estimated between all possible pairs of chronologies drawn from the whole dataset into: (*i*) a mean correlation between pairs of chronologies for every group; and (*ii*) a mean correlation between pairs of chronologies for pairs of groups (Shestakova et al. 2014). Thus, the correlation between chronologies belonging to group r becomes:

$$\hat{a}_r = \frac{\sigma_{Y_r}^2}{\sigma_{Y_r}^2 + \sigma_{\varepsilon}^2} \tag{4}$$

Alternatively, the correlation of chronologies belonging to groups r and r^* is:

$$\hat{a}_{rr^*} = \frac{\sigma_{Y_{rr^*}}^2}{\sqrt{(\sigma_{Y_r}^2 + \sigma_{\varepsilon}^2) \times (\sigma_{Y_{r^*}}^2 + \sigma_{\varepsilon}^2)}} \tag{5}$$

Mixed models allow for flexible modelling of complex intra- and inter-group correlation patterns and heteroscedastic errors, hence providing estimates to solve

equations (4) and (5). Several examples of variance-covariance (VCOV) structures applicable to tree-ring networks are provided in Table 1. For example, under the null model (broad evaluation) the existence of groups is ignored so the year variance is constant at the within- and between-group levels. In contrast, the banded main diagonal model (narrow evaluation) constrains the covariance (and correlation) between groups to zero, thus testing for lack of common signals between chronologies belonging to different groups. While these two extreme cases may be adequate in some circumstances, a range of alternative assumptions can be covered by other VCOV structures that assign each group a particular year variance and each pair of groups a particular year covariance as outlined in Table 1 (for further details, see Shestakova et al. 2014 and Shestakova et al. 2016). For model selection, a likelihood ratio test (Jennrich and Schluchter 1986) can be used as these structures are special cases of the more general model (1) and, therefore, are nested to it (i.e. obtained by adding random terms to the simplest model [1]). The R-package 'DendroSync' implements different VCOV structures for the analysis of spatial synchrony in tree-ring networks using user-defined classification strategies and compare the fitted models through likelihood-derived goodness-of-fit statistics (https://CRAN.R-project.org/package=DendroSync).

Unscrambling the complexities of tree-ring signals

At the core of dendrochronology lies the fundamental principle of a common signal shared by tree rings across time and space (Fritts 1976). Climate is generally accepted as the major driver of tree performance (Hughes et al. 1982), prompting common variability in tree-ring traits that often spreads over vast extensions of land (Briffa et al. 2002; Wettstein et al. 2011; Babst et al. 2013). However, different physiological responses among species or across environmental gradients challenge

inferences on existing or emergent biogeographical properties and processes recorded in dendroecological networks (Galván et al. 2014). Unscrambling the complexities of tree-ring signals offers tremendous opportunities for improving our understanding of the external drivers of tree performance across multiple spatiotemporal scales and of how tree responses are modified under current climate change.

Tree-ring width measurements usually integrate the prevailing environmental conditions during the growing season and, thus, reflect variability in local and global factors controlling tree performance (Fritts 1976). Therefore, the spatial patterns of forest growth are expected to be strongly driven by the geographical consistency of these factors. Particularly, the geographical variation in the climate driver(s) of tree performance is fundamental to explain regional differences in tree growth (Babst et al. 2013). Such coherence is high in the case of temperature at cold high latitudes and low in the case of precipitation in drought-prone environments from mid-latitudes, hence providing theoretical thresholds for synchronous growth (Wettstein et al. 2011; St. George 2014) (Fig. 2). In this regard, Boreal forests from Siberia or Fennoscandia show high $\hat{a}$ values that are strikingly similar to the mean correlation between co-occurring trees within a stand (*Rbar* statistic), while $\hat{a}$ drops significantly in Mediterranean mountain forests (Shestakova et al. 2016).

Another potentially important cause of synchronous–asynchronous growth patterns is the extent of adaptive divergence among populations arising through localized selection in allogamous species such as most forest trees (Loveless and Hamrick 1984). Spatially-structured genetic variation is a common feature of most plant species, and genecological studies indicate that genetic clines in growth rate are usually more strongly associated with temperature regimes than with precipitation for temperate species (Aitken and Bemmels 2016). This feature links bioclimatic envelope and

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adaptive structure along a geographical continuum in cold-limited forests, with both factors together likely eliciting highly synchronous growth responses at the intra-specific level, but also at the inter-specific level. Conversely, the adaptive spatial structure of forest populations thriving in drought-prone environments is far more complex and dependent on post-glacial colonisation routes and local factors, including edaphic characteristics, competition, topography and biotic stressors (Mátyás 1997; Robledo-Arnuncio et al. 2005). These characteristics often result in divergent growth patterns among neighbouring regions (Alía et al. 1997).

A relevant issue for interpreting patterns of common growth variability concerns the density of the tree-ring network used to evaluate synchrony. Indeed, $\hat{a}$ values calculated on dense networks are expected to be higher than those calculated on sparse ones for a particular area (Fig. 2a). This is the result of a greater spatial saturation of sampling sites and, thus, a lower mean distance among pairs of chronologies in the former case. Ideally, site coverage should be kept approximately constant across the study area to ensure meaningful inferences on spatial synchrony patterns. This is, however, often impossible, especially when dealing with tree-ring networks made up of species having different distribution ranges. Factors such as uneven spatial distribution, distinct niche amplitude or habitat heterogeneity may influence spatial synchrony at the within- and between-group levels and should be taken into account to avoid misleading interpretations (e.g. *Abies alba* limited to mesic, high-altitude areas of South Europe compared with the more widespread *Pinus sylvestris*; Shestakova et al. 2016). Naturally, spatial synchrony also varies across geographical scales, decreasing as the land extension covered by the sampled sites increases. Thus, $\hat{a}$ declines roughly inversely with the log of the average distance among stands (Fig. 2b). These dependencies are largely expected and indicate that the strength of common climate

forcing diminishes with distance (Koenig 2002). Several studies have also shown that tree-ring growth variability from different zones within the same biome can be opposite (out of phase) if synoptic weather conditions are determined by opposite phase effects of the mode of atmospheric circulation patterns under the influence of different climate teleconnections (Trouet et al. 2012; Dorado-Liñán et al. 2017). However, a sizeable common signal can even be detected at continental scales (Fig. 2b). This reinforces climate as main cause of the shared variability among chronologies as no other external factor can vary synchronously to such extent in the high frequency domain.

In summary, the temporal similarities among tree-ring chronologies depend largely on network density but are ultimately entrained by the prevailing patterns of climatic variability, as shown by the climatic envelopes represented in Figure 2a. Indeed, a proper spatial coverage aids at identifying local to continental climate drivers of tree growth, and previous works suggest that significant common signals in ring-width records can be observed in stands separated up to 1000 km (Shestakova et al. 2016). Through mixed modelling it is possible to disentangle how the regional synchrony in tree growth is structured considering, for instance, biogeographical criteria such as belt position along an altitudinal gradient or ecoregion membership. An application of VCOV modelling to infer synchrony patterns at local, regional and continental scales in Europe is presented in Figure 3. This example compares the output provided by a widely-used multivariate approach such as Principal Component Analysis (PCA) with the information derived from VCOV modelling. At small geographic scales and with a low number of chronologies PCA gives similar insights into how growth patterns are structured in the dataset, although the extent of spatial synchrony can be directly quantified by means of VCOV modelling. At progressively larger geographical scales, the variance accounted for by the first two PCA dimensions usually becomes

small or very small, so the extent of common temporal signals shared within and between groups is less obvious to determine, either visually or through a more detailed interpretation of component scores. Such qualitative assessment is further complicated if the number of available chronologies is large or the chronologies partially overlap. In comparison, VCOV modelling tests for the adequate structure of the data based on the predefinition of groups and provides maximum likelihood estimates of synchrony regardless of the number and, eventually, incomplete temporal coverage of chronologies. In this particular example, there is statistical support for a varying magnitude of synchronous growth within and between groups at local, regional and continental scales in Europe. If required, best linear unbiased predictors of year effects can be easily obtained at the group level based on the selected VCOV structure for input into further analyses (e.g., climate-growth relationships) (Shestakova et al. 2016, 2017).

Climate change drivers of spatial synchrony

Tree rings provide a direct estimate of stem growth, which represents the principal above-ground carbon pool of forests. Because tree growth is sensitive to changes in the physical environment, tree-ring proxies are valuable tools to track species responses to moving climate optima in time and space (Pease et al. 1989; Polechová et al. 2009). These responses play a crucial role in determining present and future carbon budgets of forests, but many uncertainties still remain in our understanding of climate change impacts on forest ecosystems (Millar et al. 2007; Sitch et al. 2015). Meanwhile, the importance of tree responses to climate in modulating spatiotemporal growth variability has been reported worldwide (Ciais et al. 2005; Williams et al. 2013; Allen et al. 2015), including regions that are not typically

considered as drought-limited (Barber et al. 2000; Wilmking et al. 2005; Silva et al. 2010).

A systematic examination of spatial synchrony across varying geographical scales offers an alternative way to assess subtle changes in growth patterns of forest trees as affected by climate change. For example, warming-induced enhanced synchrony has been reported in Mediterranean forests along the twentieth century: $â ≈$ 0.44–0.58 before and after 1965, respectively, for *Pinus pinea* in central-south Iberian Peninsula (Natalini et al. 2015), $â = 0.33$–0.49 before and after 1962, respectively, for five pine species along an altitudinal gradient in eastern Spain (Shestakova et al. 2017), and $â = 0.19$–0.24 before and after 1950, respectively, for three conifer species in Spain (Shestakova et al. 2016). These results can be interpreted as early warning signals of reduced forest resilience in the face of rapid climate change. Indeed, an enhanced synchrony among trees at stand level preceding massive tree mortality triggered by extreme drought events has been reported for *Cedrus atlantica* forests in the Atlas range (Algeria) (Kherchouche et al. 2012). This suggests that forests are approaching an unprecedented state during the Anthropocene in some parts of the world such as the Mediterranean basin. The comparison of long-term trends for healthy and die-back affected forests, along with a larger spatial coverage, would be required to project synchrony-based local, regional and global tipping points responsible for strong and sudden changes in these ecosystems (Reyer et al. 2015).

Two major responses of forest trees to climate warming are commonly reported, namely an advancement of early season responsiveness and a modulation of physiological processes during the growing season (Menzel et al. 2006; Anderegg et al. 2012). Both may trigger more synchronous growth from local to continental scales (Parmesan and Yohe 2003) (Fig. 4). Late winter to early spring temperatures affect the

physiological processes that are involved in the initiation of cambial cell division and xylem differentiation in trees from different biomes, including Boreal and Mediterranean (Badeck et al. 2004; Aerts et al. 2006; Gordo and Sanz 2009). Nevertheless, advances in early season phenology may lead to opposing growth responses in contrasting biomes. Particularly, warmer springs have been found to be negatively related to radial growth in Siberia (Knorre et al. 2006; Shestakova et al. 2016), which may be associated with increasing risk of frost damage to the cambium (Begum et al. 2013). In contrast, early cambial reactivation triggered by warm winters essentially enhances wood formation in Mediterranean environments (Bigelow et al. 2014; Shestakova et al. 2016).

Counteracting these effects, a relaxation of cold limitation on growth during summer months are observed at high latitudes and along altitudinal gradients in mountain systems (Briffa et al. 2002; Tardif et al. 2003), while increasing drought stress negatively impacts on growth in the Mediterranean owing to reduced cambial activity in peak summer (Bernal et al. 2011; Gutiérrez et al. 2011). Altogether, climate warming is producing coordinated changes in tree performance, in turn triggering more synchronous growth at varying geographical scales. This effect can be attributed to an amplified climatic control of tree growth over large extensions (Ciais et al. 2005; Williams et al. 2013; Allen et al. 2015). In fact, enhanced synchrony is observed among co-occurring species growing under common climate influences (Shestakova et al. 2016, 2017), which further implies increasing vulnerability of forests across broad environmental gradients. Threshold limits for spatial synchrony in a particular area are naturally defined by the extent of synchronous growth observed between trees within a stand (*Rbar* statistic *sensu* Wigley et al. [1984]). The observation that small-scale synchrony (i.e. within several tens of kilometres) may be eventually approaching its

theoretical maximum in water-limited environments is a matter of concern (Fig. 4). If warming continues, we may expect a gradual extension of this phenomenon at increasingly large geographical scales, anticipating a progressive exposure of forest populations to increased stress and mortality risk across terrestrial biomes.

Outlook for future research

In dendrosciences significant progress has been made over the last few decades to improve our knowledge about tree growth responses to external drivers at different spatial scales, ranging from local (Tardif et al. 2003; Carrer and Urbinati 2001, 2006; Planells et al. 2009) and regional (Peterson and Peterson 2001; Frank and Esper 2005; Andreu et al. 2007; Restaino et al. 2016) to continental (Babst et al. 2012). The analysis and interpretation of spatial synchrony must contribute further to our understanding of complex patterns of tree-ring signals across such multiple scales and how these patterns are modified by recent climate change. Yet, some challenges remain that deserve special attention before the analysis of synchrony patterns in tree-ring records may reach its full potential.

Although dendrochronologists generally aim to obtain a good representation of the population variability, field sampling is often biased towards dominant, large and healthy trees (Bowman et al. 2013). Thus, the appropriateness of such sampling schemes to accurately represent population responses to environmental variation is increasingly questioned (Cherubini et al. 1998; Brienen et al. 2012). This may introduce considerable bias in upscaling local observations to broad geographical trends in coordinated tree responses. Stratified sampling schemes, including trees of different age, size and social status, would allow for a straightforward separation of class-specific variability in the analysis of population-wide synchronous responses. This would

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improve our ability for detecting a number of climatic and ecological processes that are recorded in tree rings (Voelker 2011).

As a rule, dendrochronologists also seek individuals that demonstrate sensitive growth responses, as these trees maximize the amount of climatic information that can be recovered and are more likely to cross-date (Fritts 1976). The choice of sampling sites, guided by this distinction, often leads to another important caveat in most tree-ring datasets, which are increasingly used to assess tree population dynamics and growth responses to environmental fluctuations. Being particularly susceptible to climate, trees growing in marginal conditions such as altitudinal or latitudinal limits may largely mislead our conclusions on forest vulnerability to climate change effects (Cernusak and English 2015). Moreover, the most extensively sampled regions in the world consist of coniferous species due to their high tolerance to harsh environmental conditions, long life span and accurate cross-dating. Indeed, enhanced warming-induced growth synchrony has mainly been reported for conifers growing in the Mediterranean basin (Tardif et al. 2003; Macias et al. 2006; Andreu et al. 2007; Natalini et al. 2015). However, this reaction is unlikely to be tied to a certain species or region (Wettstein et al. 2011; Latte et al. 2015; Zhou et al. 2016). Additional sampling efforts, including temperate, alpine and boreal biomes and broadleaf species, will allow evaluating broad patterns of growth synchrony and their drivers more faithfully. In summary, there is a need for more exhaustive studies across species and regions, especially in areas located at the interior of the climatic space over which forests are distributed.

Regional- to continental-scale syntheses of climate change impacts on forest populations are essential for understanding long-term spatiotemporal variability in tree growth and for properly assessing ecosystem risks on short- and long-term timescales. However, comprehensive dendroecological investigations based on annual stem growth

could be challenged by miscellaneous environmental signals recorded in ring-width chronologies. This is especially true for temperate forests thriving under near-optimal conditions where local factors (e.g. competition, soil properties, nutrient availability) buffer regional climatic signals (Esper et al. 2012). Meanwhile, alternative tree-ring proxies such as stable isotopes have been shown to be less dependent on site conditions compared with growth and, therefore, the study of isotope variations can provide additional information on the physiological responses of trees to climate (McCarroll and Loader 2004; Gessler et al. 2014). Thus, the simultaneous analysis of both ring-width and isotope signals (in addition to other tree-ring features such as wood density) may broaden our understanding of biogeographical interactions underlying spatial patterns of tree growth dynamics, especially in the context of climate change. Although multi-proxy datasets are relatively new in dendrosciences, multi-trait information can easily be embedded in a mixed modelling framework (Shestakova et al. 2017). Undoubtedly, multi-proxy tree-ring archives should be widely targeted in future research to expand our knowledge on the physiological processes responsible for climate-induced growth changes of forest trees and their capability to cope with increased climate stress.

Author contribution statement

T.A.S. and J.V. conceived the ideas, carried out the analysis and led the writing, with substantial contributions from E.G. All the authors read and approved the final draft of the manuscript.

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Table 1. Description of some variance-covariance (VCOV) structures applicable for modelling synchrony patterns in tree-ring networks according to the assignment of chronologies to pre-defined groups. For further details, see Shestakova et al. (2014).

VCOV structures	Interpretation	Variances	Covariances	Correlations
None	Null model. Broad evaluation ignoring groups	Single	–	–
Banded main diagonal	Narrow evaluation. Lack of common signal between groups	Heterogeneous	Zero	Zero
Compound symmetry	Homogeneity of year variances and covariances across groups	Homogeneous	Homogeneous	Homogeneous[a]
Toeplitz	Same covariances and correlations between group pairs separated by a common distance, but values change with distance	Homogeneous	Heterogeneous	Heterogeneous
Heterogeneous compound symmetry	Different variances but equal year correlation between all group pairs[b]	Heterogeneous	Heterogeneous	Homogeneous
Unstructured	Full model (different variances and correlations). All causes of year × group interaction allowed	Heterogeneous	Heterogeneous	Heterogeneous

[a]if homoscedastic residual variance; [b]if null residual variance

Figure captions

Fig. 1 Scholarly output of the subject area published since 1985 (first record found in the database) as derived from a search for ("tree-ring" OR "dendrochronology") AND ("synchrony" OR "teleconnection" OR "spatiotemporal patterns") in the title, abstract or keywords of scientific literature. Source: Scopus.
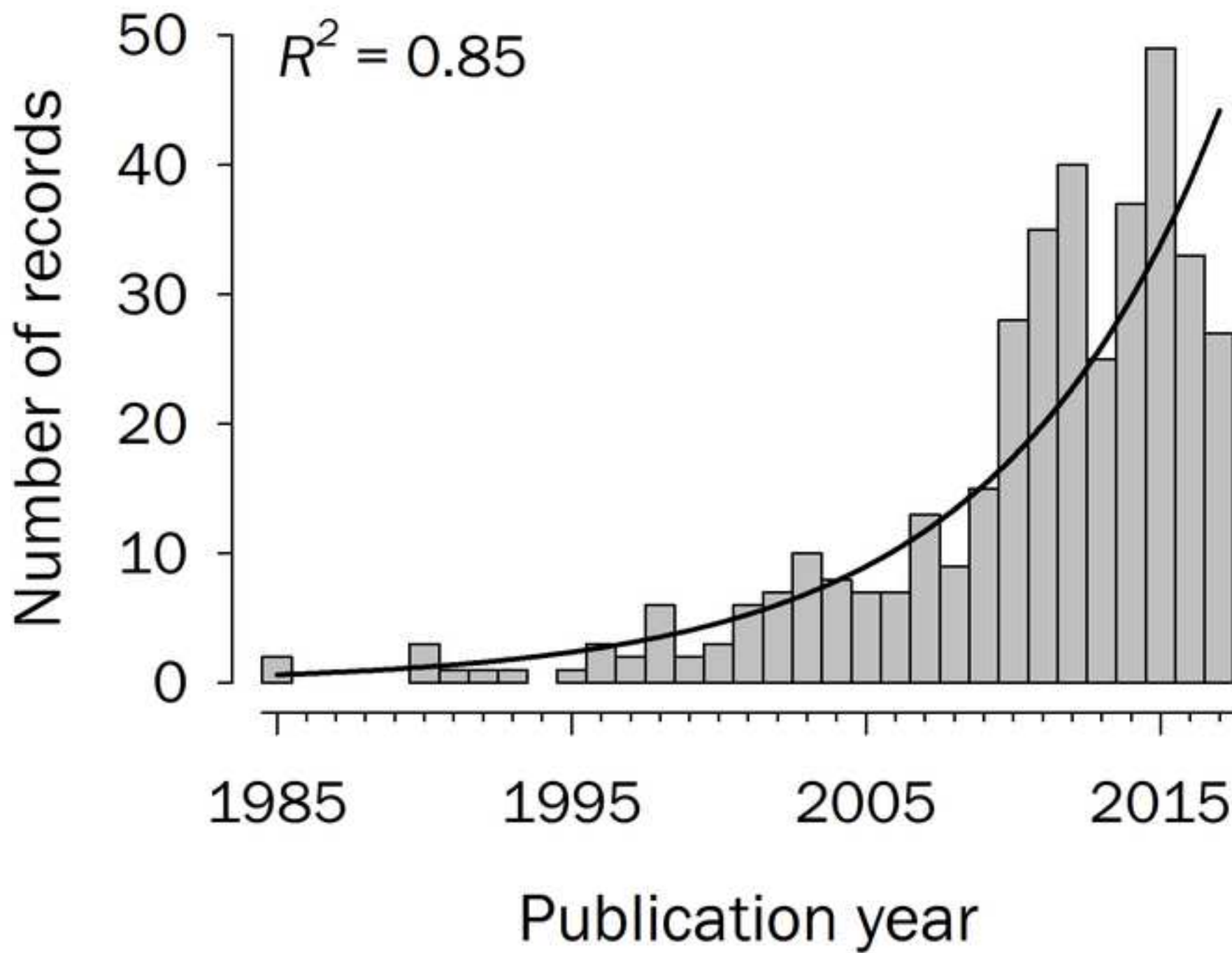
Fig. 2 Spatial synchrony ($\hat{a}$) of tree growth according to (a) sample replication and (b) geographical scale covered by the sampling sites. **(a)** Synchrony patterns based on dense (n $\geq$ 45 chronologies) or sparse (n = 4 chronologies) tree-ring width networks for the Iberian Peninsula (water-limited growth; black bars) and central Siberia (dense) or Fennoscandia (sparse) (temperature-limited growth; grey bars). White bars represent the spatial synchrony of primary limiting climate factors (annual total precipitation, blue; annual mean temperature, red) calculated following Eq. 4 in main text and corresponding to the sampling sites used in ring-width networks. Local climate series were obtained from the nearest to each sampling site grid (0.5° × 0.5°) point of CRU TS 3.10 dataset (Harris et al. 2014). They were standardized by fitting a straight line and keeping the residuals of these linear fits. **(b)** Synchrony patterns (bars) at local (Gúdar range, eastern Spain, n = 7; Shestakova et al. 2017), regional (Iberian Peninsula, n = 48; Shestakova et al. 2016) and continental (Europe, n = 80; the International Tree-Ring Data Bank (ITRDB), Grissino-Mayer and Fritts 1997) scales. Dots denote mean geographical distance among chronologies (on a log scale) at each spatial level. All calculations were based on indexed ring-width chronologies for the common period 1900–2003 in which only high-frequency (i.e. inter-annual) variability was preserved. To this end, tree-ring width records were transformed into site chronologies of
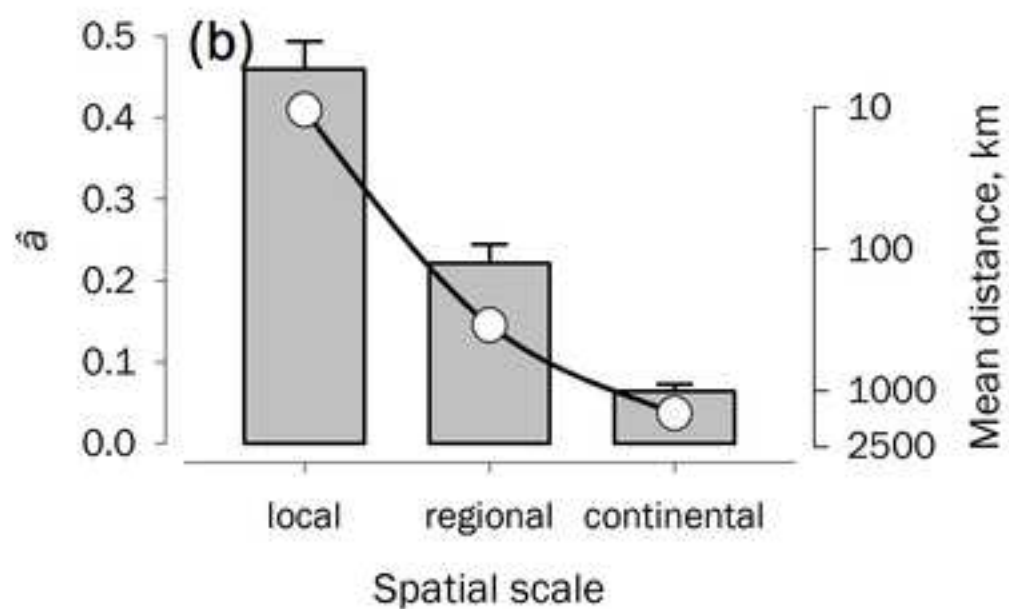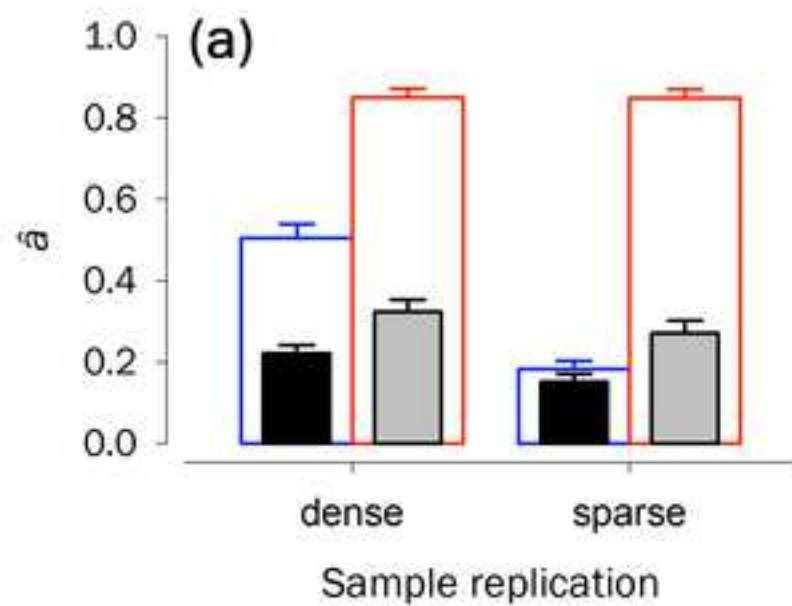
dimensionless indices with the Friedman supersmoother spline (Friedman 1984) and posterior autoregressive modelling. Error bars denote standard errors.

Fig. 3 (a) Principal components analysis (PCA) of tree growth performed on the residual chronology covariance matrix at different geographical scales (local = Gúdar range, eastern Spain; regional = Iberian Peninsula; continental = Europe) as detailed in the caption for Figure 2b. The periods analysed having fully overlapping chronologies were as follows: 1915–2003 (local), 1950–1988 (regional) and 1909–1975 (continental). The proportion of total variance captured by the first two PCs is also shown. Symbol colours correspond to pre-defined groups of chronologies as explained later in this caption. Circles indicate perfect representation of chronologies in the two-dimensional spaces. **(b)** Spatial synchrony ($\hat{a}$) of tree growth within and between pre-defined groups at different geographical scales (local, regional and continental) over the twentieth century. At each spatial scale tree-ring width records were divided into three groups: at local level, high-, mid- and low-elevation belts in Gúdar range; at regional level, northern, central and southern Iberian Peninsula; at continental level, eastern, western and southern Europe. Synchrony estimates ($\hat{a}$) within groups (G_1, G_2 and G_3; Equation 4 in main text) and between groups (G_1/G_2, G_1/G_3, G_2/G_3; Equation 5 in main text) were obtained based on indexed ring-width chronologies for the common period 1900–2003 (i.e. partially overlapping chronologies) as detailed in the caption for Figure 2b. The selected variance-covariance (VCOV) structures were Compound Symmetry Heterogeneous (CSH) at local scale and Compound Symmetry (CS) at regional and continental scales (Table 1). For model selection, the Bayesian information criterion (BIC) was used as measure of goodness-of-fit. In all cases, heterogeneous error

variances provided better model fit. Error bars denote standard errors. Tree-ring data are described in the caption for Figure 2b.

Fig. 4 Changes in spatial synchrony ($\hat{a}$) of tree growth over the twentieth century at multiple geographical scales. Synchrony estimates ($\hat{a}$) were calculated for two consecutive non-overlapping periods (1900–1950 and 1951–2003) at local, regional and continental scales using indexed tree-ring width chronologies (see Figure 2b for details). Shaded area indicates mean synchrony between co-occurring trees within a stand (*Rbar* statistic) over the period 1900–2003. Error bars denote standard errors.

Figure 1

Figure 1

Figure 2   Click here to download Figure Fig. 2.jpg

Figure 3

Figure 3

Figure 4

Figure 4