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Abstract Tree-rings are one of the most commonly used proxies for reconstructing past climates at annual resolution. The climate information is generally deduced from tree-rings using statistical relationships, but the assumed linearity and stationarity may be inadequate. Process-based models allow for non-stationarity and non-linearity; however, many challenges are associated with their application for global scale reconstructions. In this study, we aim to test the feasibility of using the mechanistic model MAIDEN at the global scale for paleoclimate data assimilation based reconstructions by applying it to the PAGES2k tree-ring width database. We also compare its performance with the simpler model VS-Lite, often used in global applications. Both models are skillful in terms of calibration and verification correlations for a similar number of sites (63 and 64 for VS-Lite and MAIDEN, respectively). VS-Lite tends to perform better for sites where the climate signal in tree-rings is strong and clear. By contrast, MAIDEN's performance is likely mostly limited by the

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lack of data (for example, daily Gross Primary Production data or phenological timings) needed to accurately calibrate the model. However, when the calibration is robust, both models reproduce well the observed link between climate and tree-growth. In general, VS-Lite tends to overestimate the climate signal in tree-rings compared to MAIDEN, which better reproduces the magnitude of the climate signal on average. Our results show that both models are complementary and can be applied at the global scale to reconstruct past climates using an adequate protocol designed to exploit existing tree-ring data.

Keywords Ecophysiological modelling · Proxy system models · Dendroclimatology · PAGES2k tree-ring database · Paleoclimate data assimilation based reconstructions

1 Introduction

Studying past climates prior to the instrumental period requires the use of indirect records of climate variations from natural archives, commonly referred to as proxies (Jones et al., 2009). Different projects and consortia have emerged in recent years to improve global climate reconstructions using the development of global multi-proxy databases spanning last millennium (PAGES 2k Consortium, 2013; Wilson et al., 2016; Anchukaitis et al., 2017; PAGES 2k Consortium, 2017; Tardif et al., 2019; Konecky et al., 2020). Among available records, tree-rings are one of the most commonly used proxies for reconstructing past climates at high temporal (annual) resolution, due to their large spatial coverage and availability (Fritts, 1976; Jones et al., 2009; Mann et al., 2009; Wilson et al., 2016; Anchukaitis et al., 2017; Esper et al., 2018; Anderson et al., 2019; St. George and Esper, 2019).

To make the link between climate and indirect observations of paleoclimate variations from proxies, proxy system models (PSMs; i.e. models that simulate the development of measured variables, for example tree-ring width, in response to a climate forcing; Evans et al., 2013; Dee et al., 2016) must be used. Such models can be applied in the forward mode, for example to compare proxy data directly with climate model simulations when these simulations are used as inputs of the PSM. In the inverse mode, PSMs can reconstruct the climate variations that produce the measured variables (Guiot et al., 2000; Evans et al., 2013).

In the case of tree-growth proxy data (such as tree-ring width, hereafter TRW, or density), the climate information is generally deduced on the basis of a statistical relationship calibrated over the instrumental period (Fritts, 1976; Cook and Kairiukstis, 1990; Fritts, 1991; Jones et al., 1998; Mann et al., 1999, 2008). Therefore, many climate reconstructions of the period covered by dendroclimatic data have been developed with linear regressions between climate variables and proxy records (Fritts, 1991; Jones et al., 1998; Mann et al., 1999, 2008). This raises concern about the assumed linearity and stationarity of the relationship deduced from the calibration (Briffa et al., 1998; Wilson and Elling, 2004; Wilson et al., 2007; D'Arrigo et al., 2008; Guiot et al., 2014). A

complementary approach that has been expanded over the past decade is data assimilation, which combines information from the physics of the system included in climate models and indirect climate observations provided by proxy data, such as TRW (e.g. Goosse et al., 2012; Franke et al., 2017; Steiger et al., 2018; Tardif et al., 2019). So far, the studies using tree-ring proxy data with data assimilation have focused on the use of statistical PSMs (i.e., univariate or multiple linear regressions) to provide a large-scale reconstruction over the past millennia (e.g. Tardif et al., 2019).

As a complement to statistical methods, the link between climate and tree-ring proxy data can be established from process-based PSMs. Mechanistic modelling of tree-growth dependency on climate explicitly states the processes that govern the relationship between climate and tree-growth and allows for non-stationarity and non-linearity (Guiot et al., 2014). While in regression-based PSMs, tree-growth is assumed to be only dependent on the chosen climate target variables, mechanistic modelling introduces the influence of other climate variables, for example atmospheric CO_2 concentration. Additionally, tree-ring-based reconstructions are often limited to sites where tree-growth is driven by one limiting climatic factor. Yet, process-based tree-growth models are able to extract a climate signal from tree-rings at sites where tree-growth is driven by multiple climatic factors. Accordingly, they may expand the area of dendroclimatic reconstructions to a wide range of regions away from extreme growth environments (Breitenmoser et al., 2014; Babst et al., 2018). To date, such models have only been used for local reconstructions (e.g. Boucher et al., 2014). While global scale reconstructions are theoretically possible with a data assimilation procedure including a process-based PSM, such models have only been applied in a pseudo-proxy context (Dee et al., 2016; Acevedo et al., 2017; Steiger and Smerdon, 2017). A further step would be to introduce such mechanistic models in the data assimilation procedure using actual proxy data to possibly improve the quality of the reconstruction.

However, many challenges are associated with the use of process-based tree-ring PSMs for global scale reconstructions. In particular, the inclusion of complex biological processes, for example photosynthesis and carbon allocation, usually implies a cautious initialization and calibration of the model at each particular site of interest, depending on the site environment or the tree species. This information is not readily available at global coverage with the necessary detail. Running and calibration time of such models can also be an obstacle to their utilization.

Among the many available process-based dendroclimatic models, the Vaganov-Shashkin-Lite model (VS-Lite; Tolwinski-Ward et al., 2011) has been used in several paleoclimate studies (Breitenmoser et al., 2014; Lavergne et al., 2015; Dee et al., 2016; Steiger and Smerdon, 2017; Seftigen et al., 2018; Fang and Li, 2019). The model is not considered as fully mechanistic. Indeed, VS-Lite does not include any explicit representation of tree-growth processes, but relies instead on the principle of limiting factors (soil moisture and temperature; Tolwinski-Ward et al., 2011) to mimic the response of tree-ring growth to climate conditions. The model has faced difficulties in simulating tree-growth

where the dependence on climate is not dominated by a limiting factor, such as precipitation or temperature (Breitenmoser et al., 2014).

Process-based dendroclimatic models that describe more mechanistically the response of proxy data to climate could overcome those limitations. Among the complex mechanistic models (e.g. Misson, 2004; Dufrêne et al., 2005; Vaganov et al., 2006; Drew et al., 2010), we will focus here on the model MAIDEN (Modelling and Analysis In DENdroecology; Misson, 2004) that explicitly includes biological processes and has the potential to be applied at the global scale. Unlike VS-Lite, MAIDEN also takes into account atmospheric CO_2 concentration as an input, allowing the user to consider the non-stationary dependency of tree-growth on the recent exponential increase of CO_2 (Myhre et al., 2013; Boucher et al., 2014). Another important difference between MAIDEN and VS-Lite is the theoretical basis of the models. VS-Lite is a "sink" model in the sense that it only considers the climate constraints on tree-rings (the carbon sink tissues at the tree-level; see Körner, 2015; Fatichi et al., 2014, 2019). MAIDEN is a "source-sink" mechanistic model in the sense that it first determines the carbon availability by modelling photosynthesis, and second, it allocates the available carbon to the sink tissues based on allocation and climate-dependent rules. Feedbacks between allocation and photosynthesis are also considered in MAIDEN. So far, MAIDEN has been applied to the European temperate forests (Misson, 2004; Boucher et al., 2014), to the Mediterranean forests (Gea-Izquierdo et al., 2015, 2017), to the eastern Canadian taiga (Gennaretti et al., 2017) and to Argentine forests (Lavergne et al., 2017). However, unlike VS-Lite, MAIDEN has not been applied at the global scale yet, due to its level of complexity. In particular, the need for daily climate data at high spatial resolution and for measurements of ecophysiological variables to calibrate the model parameters represents the main limitation for its systematic application in different regions. In Rezsöhazy et al. (2020), a protocol has been developed to calibrate and apply MAIDEN automatically at any site globally that contains TRW observations in the extratropical regions.

To date, the new protocol applying MAIDEN globally has not been demonstrated. To this end, this study highlights the advantages and potential limitations of using a process-based model like MAIDEN at the global scale. In the future, such mechanistic PSM could be utilized for paleoclimate data assimilation based reconstructions. Specifically, we perform a comparative analysis of the performance of the simpler VS-Lite and the more complex MAIDEN process-based models. Both models have been applied over the last century to the global TRW data network of PAGES2k (PAGES 2k Consortium, 2017), including 354 TRW records. Studies such as this which lend insight into the mechanisms controlling tree-ring width and tree-growth elevate our ability to extract meaningful climate information from tree-ring networks. This information is required to improve our understanding of natural and forced decadal climate variability, and to potentially improve reconstructions of past climate variability.

First, we describe MAIDEN and VS-Lite in Sect. 2.1, as well as the TRW data network (Sect. 2.2) and climate data (Sect. 2.3) used in this study.

The calibration (Sect. 2.4) and verification (2.5) procedure of both models is then presented. The models are calibrated and applied to the PAGES2k TRW database in Sect. 3.1. We provide explanations on the performance of the models in Sect. 3.2. The ability of MAIDEN and VS-Lite to reproduce the climate signal in tree-rings is then evaluated in Sect. 3.3 and, finally, the implications of including atmospheric CO_2 concentration as an input of MAIDEN are assessed in Sect. 3.4.

2 Material and Methods

2.1 Tree-growth models

2.1.1 MAIDEN

MAIDEN (Misson, 2004; Gea-Izquierdo et al., 2015; Gennaretti et al., 2017) is a complex tree-growth model that explicitly includes biological processes (photosynthesis and carbon allocation to different tree compartments) to simulate, among other outputs, the annual quantity of carbon allocated to the stem. This key variable is hereafter referred to as Dstem, in grams of carbon per square meter of stand per year. In this study, Dstem is assumed to be proportional to tree-ring growth so as to compare it with TRW observations. The model runs on a daily basis with maximum and minimum air temperature, cumulative precipitation and atmospheric CO_2 concentration as inputs.

In this study, we use a combined version of the model from Gea-Izquierdo et al. (2015) (initially developed for Mediterranean forests; hereafter GI2015) and Gennaretti et al. (2017) (initially developed for boreal tree species; hereafter Ge2017) developed by Fabio Gennaretti (unpublished) that gives the possibility to switch between those two versions. The versions from GI2015 and Ge2017 only differ in some mechanistic rules used in the photosynthetic and allocation modules, but they are identical otherwise. The structure of the MAIDEN model is provided online (`https://figshare.com/articles/MAIDEN_ecophysiological_forest_model/5446435/1`, last access: 16 May 2020) and its modules are available upon request.

The model includes constants to describe the conditions at the tree-ring observations site and the climate station (Table S1). As in Rezsöhazy et al. (2020), the constants are derived from observations. However, slope and aspect constants are set to zero, as we do not have the field knowledge needed to extract the information from a Digital Elevation Model. MAIDEN includes a four-layer soil module (1-15cm; 15-30cm; 30-65cm; 65-100cm) for which we have to provide the main characteristics (clay and sand fractions; Table S1). The soil characteristics are obtained from the Harmonized World Soil Database (hereafter HWSD) v1.2 at a 30 arc-second spatial resolution (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012), as in Rezsöhazy et al. (2020).

2.1.2 VS-Lite

The Vaganov-Shashkin Lite model (Tolwinski-Ward et al., 2011) is a simple tree-growth model that simulates a unitless annual tree-growth increment based on latitude, monthly cumulative precipitation and average temperature of the study site as inputs. It is based on the limiting factors principle (temperature and soil moisture) and on the use of threshold growth response functions. VS-Lite is derived from the full process-based Vaganov-Shashkin model (Vaganov et al., 2006) that has been developed to explicitly quantify the influence of climate and environmental variables on tree-ring formation. While the full model is a two-block model, i.e. a block with cell growth, division and multiplication in the cambium and a growth block based on the limiting factor principle, the Lite version just uses the second block.

2.2 PAGES2k tree-ring width data

The PAGES2k working group aims to reconstruct the climate of the last two millennia based on proxy records (PAGES 2k Consortium, 2017). Their community database contains 692 temperature-sensitive proxy records from different archives (trees, ice, sediment, coral, speleothems, documentary evidence, and other archives), among which 354 TRW time series are of interest for our work (PAGES 2k Consortium, 2017). We were able to retrieve the species information needed to run MAIDEN at 307 sites. Time series ending before 1979 were excluded to allow for a long enough calibration period (at least 30 years starting from 1950, Sect. 2.4), leaving 302 TRW time series for our analysis (Fig. 1). The resulting TRW network covers a large range of environmental conditions and tree species (evergreen and deciduous), but is mostly located in the Northern Hemisphere, specifically in North America and Asia. As a consequence, the TRW network is dominated by cold and dry sites (Fig. S1). The tree-ring proxy records in the PAGES2k database have been specifically selected for their local sensitivity to temperature (PAGES 2k Consortium, 2017). However, correlations with other environmental variables can be significant as well, for example with precipitation, and a gradient of environmental sensitivity is thus obtained (water limited sites, temperature limited sites or unclear limiting factor). This can be illustrated by the comparison of the correlations of TRW observations with annual cumulative precipitation against the correlations with mean annual temperature over 1901-2000 (Fig. S2). A wide range of values in the correlations is observed with both variables, with the mean being slightly higher for temperature (0.07 mean correlation, compared to 0.05 for precipitation). TRW data are available online (PAGES 2k Consortium, 2017).

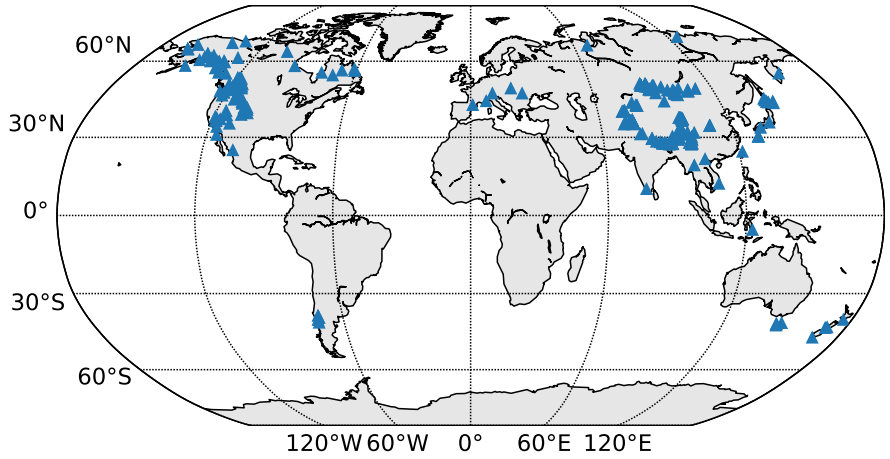

Fig. 1 PAGES2k (PAGES 2k Consortium, 2017) tree-ring width sites used in this study (302 sites). Background map from Hunter (2007).

2.3 Climate data

Daily climatic inputs are needed to run MAIDEN (Sect. 2.1.1) while VS-Lite needs monthly climate inputs (Sect. 2.1.2). In this study, we use the *Global Meteorological Forcing Dataset for land surface modelling* (v2) (`http://hydrology.princeton.edu/data.php`, last access: 13 March 2020; Sheffield et al., 2006) at 0.5° resolution over the 1901-1949 and 1950-2000 time periods. Daily maximum and minimum temperature and daily cumulative precipitation were extracted for MAIDEN from the grid cell closest to each individual site. Daily mean temperature and cumulative precipitation were averaged and summed, respectively, for VS-Lite at a monthly time step. Annual atmospheric CO_2 concentration data are from Sato and Schmidt (`https://data.giss.nasa.gov/modelforce/ghgases/`, last access: 6 January 2020) and were linearly interpolated at a daily time step. Note that for the Southern Hemisphere climate data start in July instead of January to match the seasonality of tree-growth.

2.4 Calibration

2.4.1 MAIDEN

A protocol has been developed in Rezsöhazy et al. (2020) to calibrate MAIDEN in a systematic and automatic way following a Bayesian procedure with Markov Chain Monte Carlo sampling using the DREAMzs algorithm (Hartig et al., 2019). Because we are working with the two versions of MAIDEN here (Gea-Izquierdo et al., 2015; Gennaretti et al., 2017), the procedure has been adapted

to the version from Gea-Izquierdo et al. (2015), that was not used in Rezsöhazy et al. (2020). The Bayesian procedure allows for calibration of the most sensitive parameters of the model. This includes parameters influencing the simulated stand growth primary production or GPP (6 parameters in the Ge2017 version and 5 parameters in the GI2015 version) and parameters influencing the simulated daily quantity of carbon allocated to different tree compartments (12 parameters in the Ge2017 version and 13 parameters in the GI2015 version). Those parameters are referenced hereafter as photosynthesis and carbon allocation parameters, respectively. The calibration starts from prior distributions, assumed to be uniform over an acceptable range, to produce posteriors for each of the 18 calibrated parameters. It is based on the comparison between the normalized (i.e. with a null mean and a standard deviation of 1) simulated annual quantity of carbon allocated to the stem or Dstem and normalized observed TRW time series. Tables S2 and S3 give the definition of each calibrated parameter for both versions. The ranges of the parameters are available for both versions in Tables S4 and S5.

Ideally, photosynthesis parameters should be calibrated by comparing simulated against observed GPP instead of simulated Dstem against observed TRW and prior ranges would have been more informative for each species or biome (Misson, 2004; Danis et al., 2012; Gea-Izquierdo et al., 2015, 2017; Gennaretti et al., 2017; Lavergne et al., 2017). However, this is not possible here as the information is lacking for the majority of sites. Furthermore, the tree-growth index simulated by MAIDEN, which is derived from the annual quantity of carbon allocated to the stem, is not directly comparable to TRW without standardization. We are thus unable to both calibrate the variance and evaluate the error variance of tree-growth (Rezsöhazy et al., 2020). Information is thus missing to guide the Bayesian calibration towards a biologically plausible set of parameters. For example, we miss information to properly constrain phenology. Consequently, the selection of parameters for our simulations has been slightly updated compared to Rezsöhazy et al. (2020). The set of photosynthesis parameters with the highest posterior (Maximum *a posteriori* value or MAP; Hartig et al., 2019) is selected as in Rezsöhazy et al. (2020). The carbon allocation parameters are then calibrated as in Rezsöhazy et al. (2020). In addition, after the calibration procedure, the model is iteratively run over the top 10% carbon allocation parameters. The photosynthesis parameters are fixed at their calibrated values. To avoid unrealistic growth period lengths, a parameter set which simulates a growth period of less than 20 days for each year of the calibration period (hereafter, phenological criterion) is excluded. At the end of the iterations, we keep the set of parameters with the highest likelihood. Note that if none of the parameter sets meet the phenological criterion, the MAIDEN calibration is considered as non-valid for this site with the forcing used.

MAIDEN was calibrated at the TRW sites with at least 30 TRW observations available over the 1950-2000 period, using the climate data described in Sect. 2.3. For simplicity, the calibration period will be referred to as 1950-2000.

2.4.2 VS-Lite

The Bayesian approach proposed in Tolwinski-Ward et al. (2013) was used to calibrate the four VS-Lite parameters linked to the growth response (lower and upper temperature and soil moisture thresholds of the model; T_1 and T_2, and M_1 and M_2, respectively, in Tolwinski-Ward et al., 2011). This Bayesian approach is based on a standard Markov Chain Monte Carlo method to sample the posterior distribution, i.e., a Metropolis-Hastings algorithm embedded within a Gibbs sampler. Default values were given to the other parameters (six soil moisture parameters and two integration window parameters) as provided in the standard version of the model code (`https://www.ncei.noaa.gov/pub/data/paleo/softlib/vs-lite/`, last access: 16 March 2021).

VS-Lite was optimized at the 302 TRW sites over the same time period as MAIDEN and using the climate dataset described in Sect. 2.3.

2.5 Verification

Both models were tested over the 1901-1949 time period, with the same climate data as described in Sect. 2.3. Models were run over the verification period using the parameters calibrated over the 1950-2000 time period as in Sect. 2.4. Pearson correlation coefficients and their corresponding confidence levels were calculated at each site between simulated tree-ring indexes from MAIDEN or VS-Lite and observed TRW on both the calibration and the verification time periods.

3 Results

Section 3.1 assesses and compares the general performance of both VS-Lite and MAIDEN models with respect to calibration (Sect. 2.4) and independent verification (Sect. 2.5), in order to determine the sites with the best performance. Section 3.2 explains the performance of both models, by focusing on its relationship with different environmental characteristics, such as climate and tree leaf traits. Section 3.3 evaluates the ability of both PSMs to reproduce the climate signal recorded in tree-rings, and then their potential for paleoclimate data assimilation based reconstructions. Finally, Section 3.4 assesses the effect of CO_2 concentration in the MAIDEN model with a sensitivity analysis.

3.1 Applying MAIDEN and VS-Lite to the PAGES2k TRW sites

Substantial challenges arose in the calibration of MAIDEN. In particular, at some sites, we were unable to properly set phenology due to the lack of information available for calibration (Sect. 2.4.1). From all 302 calibration experiments (Sect. 2.4.1), 113 sites for Ge2017 and 142 sites for GI2015 were excluded based on the phenological criterion (Sect. 2.4.1). The remaining sites (189 sites for

Ge2017 and 160 sites for GI2015) will be referred to as MAIDEN selected sites. All the analyses for MAIDEN are performed on these selected sites. From all calibration (Sect. 2.4.1) and verification (Sect. 2.5) experiments for both versions (Gea-Izquierdo et al., 2015; Gennaretti et al., 2017) of MAIDEN (Figs. S3 – S6), we consider a site as well-fitted only if the following conditions are fulfilled, whatever the model version used: (i) a significant (at the 95% confidence level) calibration (1950-2000) and verification (1901-1949) correlation ≥ 0.3; (ii) a growth period length of at least 20 days for each year of the calibration (Sect. 2.4.1) and verification period. If conditions are fulfilled for both versions, the version leading to the highest verification correlation at the site is kept. Based on these criteria, we retained 64 well-fitted sites (Fig. 2a).

For VS-Lite (Sect. 2.4.2 and 2.5; Figs. S7 and S8), the condition for retaining a site is also to have a significant (at the 95% confidence level) calibration (1950-2000) and verification (1901-1949) correlation ≥ 0.3. As for MAIDEN, VS-Lite simulated time series were checked for consistency as correlation is not able to account for all artefacts in simulated chronologies. Two sites were considered as invalid since estimated tree-growth indexes were found constant (no growth) for more than 10 successive years. Based on these criteria, we retained 63 well-fitted sites (Fig. 2b).

Considering the loss of correlation from calibration to verification, VS-Lite appears more stable than MAIDEN (Fig. 3, see Fig. S9 for by-site correlations). Calibrating MAIDEN at the global scale without overfitting is indeed a challenge. The mean calibration and mean verification correlations for MAIDEN are 0.68 (with a standard deviation of 0.10) and 0.43 (0.10) respectively, and 0.49 (0.14) and 0.43 (0.11) for VS-Lite. 18 well-fitted sites are in common between VS-Lite and MAIDEN (Fig. 4). On average, verification correlations are 0.47 for MAIDEN and 0.48 for VS-Lite with a standard deviation of 0.10 and 0.14 respectively. MAIDEN and VS-Lite are skillful at a similar number of mostly different sites, spread all over the globe. The reasons behind their performance are consequently also different and will be addressed in the next section. However, at the common sites, their respective performances are equivalent.

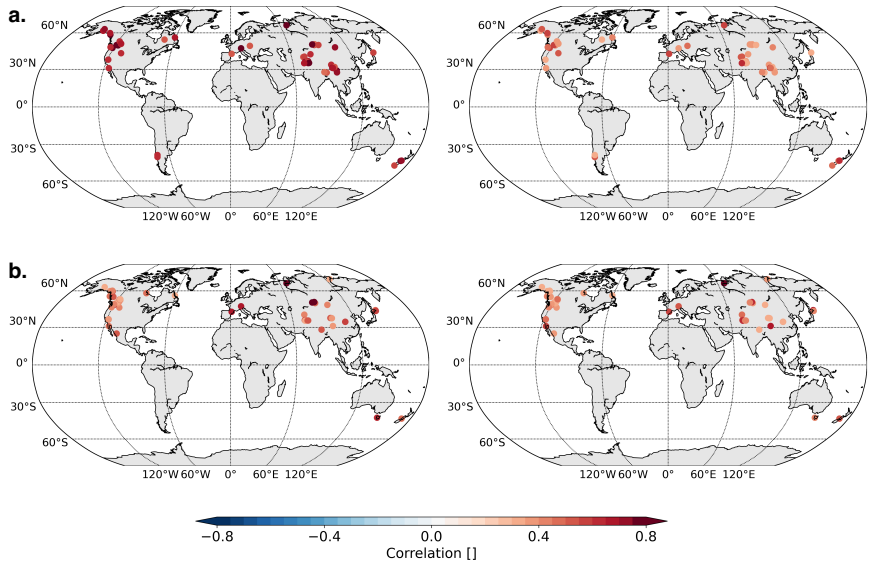

Fig. 2 (a) MAIDEN (64 sites) and (b) VS-Lite (63 sites) calibration (left) and verification (right) correlations for well-fitted sites (Sect. 3.1). All correlations are significant at the 95% confidence level. Background maps from Hunter (2007).

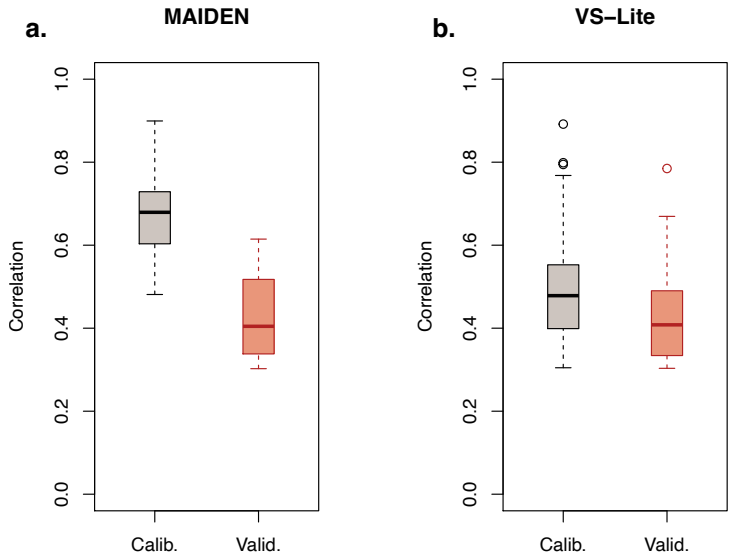

Fig. 3 (a) MAIDEN (64 sites) and (b) VS-Lite (63 sites) calibration (1950-2000) and verification (1901-1949) correlations (all significant at the 95% confidence level) boxplots for well-fitted sites (Sect. 3.1).

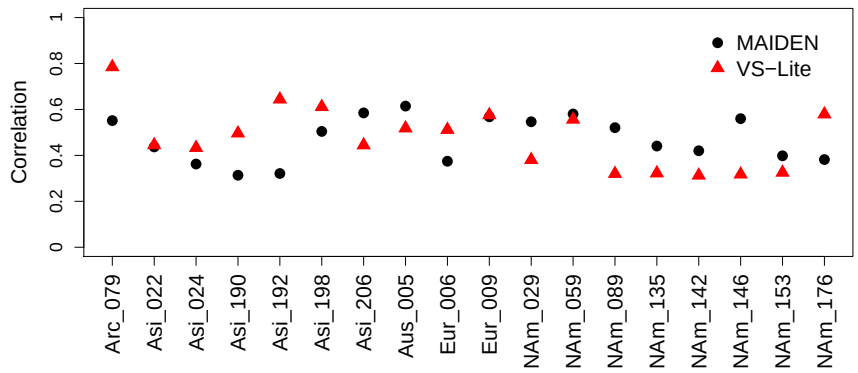

Fig. 4 MAIDEN and VS-Lite verification (1901-1949) correlations (all significant at the 95% confidence level) for common well-fitted sites (Sect. 3.1) (18 sites, with names from the PAGES2k database: *NAm* for North American sites; *Asi* for Asian sites; *Eur* for European sites; *Arc* for Arctic sites; *Aus* for Australian, Tasmanian or New Zealand sites; *SAm* for South American sites).

3.2 Explaining the performance of VS-Lite and MAIDEN

In this section, we want to understand the underlying factors driving the performance of both models. We focus on two site characteristics: tree leaf traits and climate. The relationship between models performance and altitude, latitude or calibration period length (ranging from 30 to 51 years) was also checked but none of these variables were found to be a significant driver of models skill. We are here considering all calibrated sites (Sect. 2.4), irrespective of whether they were identified as well-fitted in the previous section or not.

Verification correlations as a function of tree leaf traits (deciduous or evergreen) are shown on Fig. 5 for both versions of MAIDEN and for VS-Lite. VS-Lite performance (Fig. 5c) does not seem to be influenced by leaf trait, with an average correlation of 0.184 and 0.221 for deciduous and evergreen trees respectively. 13 sites out of 63 well-fitted sites are deciduous which is comparable to the proportion of deciduous sites in the PAGES2k TRW database (64 deciduous out of 302 sites, i.e. around 20%). For MAIDEN (Fig. 5a and b), verification correlations are also very close on average for deciduous (0.073 for GI2015 and 0.101 for Ge2017) and evergreen trees (0.087 for GI2015 and 0.113 for Ge2017). However, there is a low proportion of deciduous trees for Ge2017 (Fig. 5b) that passes the phenological criterion for the calibration described in Sect. 2.4.1 (9 out of 64 sites) compared to evergreen trees (180 out of 238 sites). Conversely, this proportion is far higher for GI2015 (36 sites out of 64; Fig. 5a) and comparable to evergreen trees (124 sites out of 238). Besides, seven sites out of 64 well-fitted sites are deciduous which is less than the proportion of deciduous sites in the PAGES2k TRW database (64 out of 302

sites). Only one deciduous well-fitted site is simulated by Ge2017, and six by GI2015. A possible reason is that only the version from Gea-Izquierdo et al. (2015) has already been applied to deciduous trees sites (*Quercus Pyrenaica*; Gea-Izquierdo et al., 2017). Consequently, we were able to use the initialization parameters already applied to deciduous trees in this version solely. The version from Gennaretti et al. (2017) has never been specifically calibrated for deciduous trees and some initialization parameters are likely not adapted in that case. This exemplifies the fact that the calibration and initialization of MAIDEN are probably the main obstacles for a better performance of the model at the global scale.

To study the influence of climate on the performance of both models, we focus on different climate indicators: cumulative October to September precipitation, annual mean temperature and mean July-August-September temperature. In general, correlations of climate indicators with verification scores at all sites are low and not significant for both VS-Lite and MAIDEN (Table S6). This means that the performance of both models does not depend primarily on the mean climate at a site. Another hypothesis to test is whether the models perform better for sites where tree-ring growth is strongly controlled by climate. To this end, we compare the correlations between climate variables and observed TRW to the verification correlations (Table 1). Since none of the correlations in Table 1 are significant (p-value < 0.05) for MAIDEN, its performance does not rely significantly on tree-growth correlation with climate. On the contrary, VS-Lite performance shows a higher dependency on tree-growth correlation with climate, especially temperature (Table 1). Indeed, all correlations between the tree-growth relationship with climate and verification scores for VS-Lite are significant and particularly high for annual (0.467) and July-August-September (0.506) temperature. We obtain the same result for VS-Lite when the analysis is restricted to the MAIDEN selected sites (Sect. 2.4.1) (Table S7). This dependence of VS-Lite performance to the presence of a strong climate driver of tree-growth is consistent with what has been highlighted in Breitenmoser et al. (2014). It is likely due to the structure of VS-Lite on itself (Sect. 2.1.2), as tree-growth directly depends on the identified limiting climatic factor (temperature or soil moisture) at the site in the model. VS-Lite tends to be better where tree-growth is predominantly driven by climate, which can be limiting for its application in many regions of the world away from the treeline environments (for example high-altitude or high-latitude environments), often not considered for paleoclimate reconstruction (Breitenmoser et al., 2014; Babst et al., 2018). Conversely, in MAIDEN, multiple biological processes shape the links that exist between climate and tree-growth. This potentially brings a better suitability of MAIDEN to work in a larger range of environments than VS-Lite, where the relationship between climate and tree-growth is more complex.

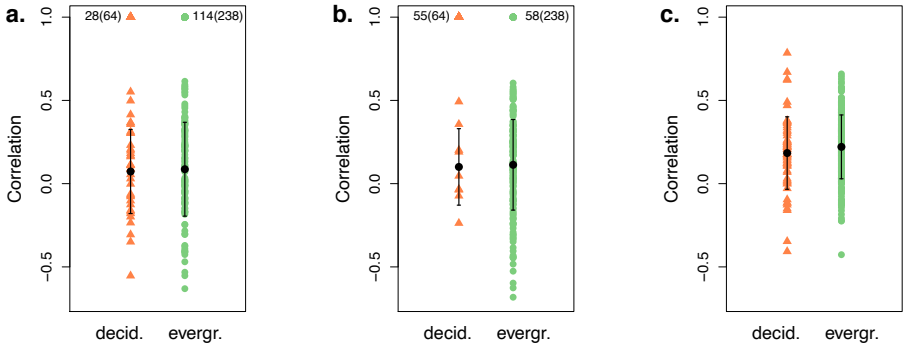

Fig. 5 Verification correlations, mean and standard deviation by tree types (deciduous or evergreen) for the MAIDEN version of GI2015 (a) and Ge2017 (b), for selected sites (160 sites for GI2015 and 189 for Ge2017, Sect. 2.4.1; others have been put to 1; the number of sites that have been put to 1 is indicated by category with the total number of sites in each category in brackets) and VS-Lite, for all 302 sites (c).

Table 1 Pearson correlations between correlations of observed TRW with different climate indicators and MAIDEN or VS-Lite verification correlations (1901-1949). O-S stands for the year starting from October (previous year) to September (current year); P for precipitation; JAS for July-August-September; T for temperature. Asterisks stand for significant correlations (p-value < 0.05). The difference in the number of sites on which correlations are computed is due to the phenological criterion that has been applied to MAIDEN calibrated sites (see Sect. 2.4.1 for more details).

Model (version)	**Correlation**
Correlations between observed TRW and O-S P correlation and verification correlation	
MAIDEN (Ge2017; 189 sites)	0.114
MAIDEN (GI2015; 160 sites)	0.155
VS-Lite (302 sites)	0.149*
Correlations between observed TRW and annual T correlation and verification correlation	
MAIDEN (Ge2017; 189 sites)	0.074
MAIDEN (GI2015; 160 sites)	0.059
VS-Lite (302 sites)	0.467*
Correlations between observed TRW and JAS T correlation and verification correlation	
MAIDEN (Ge2017; 189 sites)	-0.039
MAIDEN (GI2015; 160 sites)	-0.097
VS-Lite (302 sites)	0.506*

3.3 Assessing the ability of MAIDEN and VS-Lite to reproduce climate relationship with tree-growth

One of the ultimate purposes of PSMs like VS-Lite and MAIDEN is to be used to reconstruct past climates, for example by including them in a data

assimilation procedure (Evans et al., 2013; Dee et al., 2016). Therefore, we have to assess if these models are able to reproduce well the climate signal recorded in TRW. In the previous section, we established if the models ability to reproduce tree-growth depends on the presence of a strong climate signal recorded in the tree rings. In this section, we want to evaluate if the simulated climate signal, whatever its predominance, is consistent with its recording by tree-ring indexes. This is based on the comparison of the correlations of different climate indicators with tree-growth in simulations and in observations: firstly, by means of scatterplots (Figs. 6, 7 and 8) and secondly, by means of correlations (Table 2).

For MAIDEN (Figs. 6 and 7), over- and underestimations of the climate dependencies of tree-growth are more balanced than for VS-Lite (Fig. 8) as the dots in the scatterplots tend to spread more equally around and are closer to the 1:1 line, particularly for temperature. Conversely, the scatterplots of VS-Lite (Fig. 8) show a stronger overestimation of the climate dependency of tree-growth at most sites, as most of the dots are far above the diagonal. This bias is particularly large for temperature. Indeed, for VS-Lite, the correlation for mean annual temperature is overestimated by more than 0.4 at 43% of the sites (12% for GI2015 and 18% for Ge2017), at 47% of the sites for mean July-August-September temperature (7% for GI2015 and 13% for Ge2017), and at 28% of the sites for October-September cumulative precipitation (17% for GI2015 and 12% for Ge2017). The same conclusion is still valid for VS-Lite when we restrict the analysis to the MAIDEN selected sites (Sect. 2.4.1) (Figs. S10–S15). This overestimation of the climate signal enhanced by the model is a crucial feature to consider when using such PSMs in paleoclimatology, as it can lead to biased climate reconstruction. Again, the structure of VS-Lite is likely responsible for the overestimation of the climate influence on tree-growth as tree-growth is not driven by any other internal or external drivers than limiting climatic factors. The very high correlations ($r>0.7$) between the VS-lite simulations and basic climate indicators on Fig. 8 at many sites indicate the simplicity of the climate dependence of tree-growth in this PSM. In MAIDEN, many biological processes are in play to frame the climate dependence of tree-growth. MAIDEN uses different functional rules specific to the ongoing phenological phase to allocate at a daily time step the available carbon from photosynthesis and stored non-structural carbohydrates to different tree compartments. The functional rules directly depend on climate factors, such as growing degree days, soil water content or temperature, and are specific to the phenological phase. Simultaneaously, the daily photosynthesis is simulated following the biochemical model of Farquhar et al. (1980) and dynamically interacts with the allocation module. The combination and interaction of these processes may smooth out the direct climate signal on tree-ring growth.

Correlations between observed and simulated (MAIDEN or VS-Lite) tree-growth dependency on climate at all sites are generally low (ranging from 0.053 to 0.515), particularly for temperature, even if mostly significant (Table 2). The correlations for VS-Lite when we restrict the analysis to the MAIDEN selected sites (Sect. 2.4.1) are in Table S8 and are similar to the results for

all 302 sites. In other words, when considering all sites, both models have low skill in reproducing correctly the actual climate signal observed in tree-rings. However the well-fitted sites (Sect. 3.1) have better correlations, ranging from 0.648 (annual temperature) to 0.759 (July-August-September temperature) for MAIDEN and 0.678 (annual temperature) to 0.837 (October-September precipitation) for VS-Lite. Both models are thus able to accurately mimic the climate signal in tree-ring observations if the sites are carefully selected (Sect. 3.1). When focusing on the common well-fitted sites between VS-Lite and MAIDEN, VS-Lite is slightly better at reproducing climate, specifically for annual temperature (0.608 correlation for MAIDEN and 0.772 for VS-Lite) and precipitation (0.747 for MAIDEN and 0.886 for VS-Lite).

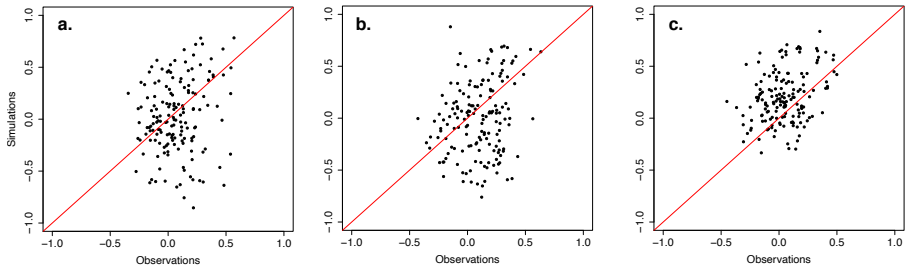

Fig. 6 Correlations between mean annual temperature (a), mean July-August-September temperature (b), October-September cumulative precipitation (c) and MAIDEN (GI2015) Dstem simulations as a function of correlations between the same climate indicators and TRW observations for selected sites (160 out of 302 sites; Sect. 2.4.1) over the 1901-1949 verification period.

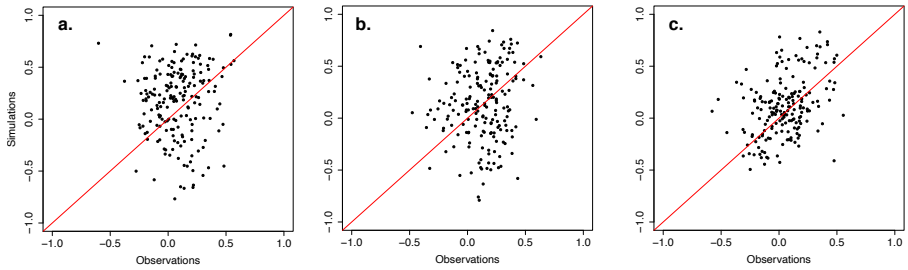

Fig. 7 Correlations between mean annual temperature (a), mean July-August-September temperature (b), October-September cumulative precipitation (c) and MAIDEN (Ge2017) Dstem simulations as a function of correlations between the same climate indicators and TRW observations for selected sites (189 out of 302 sites; Sect. 2.4.1) over the 1901-1949 verification period.

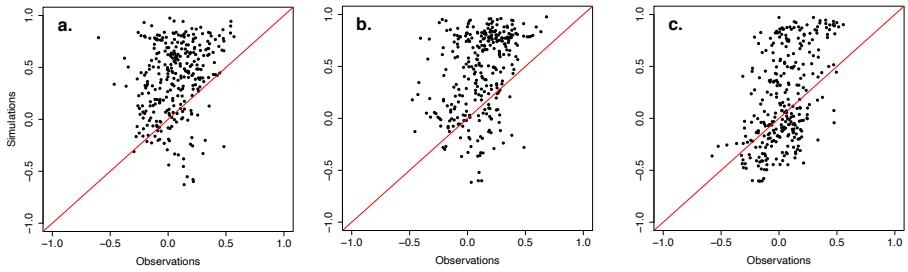

Fig. 8 Correlations between mean annual temperature (a), mean July-August-September temperature (middle), October-September cumulative precipitation (b) and VS-Lite tree-ring index simulations as a function of correlations between the same climate indicators and TRW observations for all sites (302) over the 1901-1949 verification period.

Table 2 Pearson correlations of correlations between different climate indicators and tree-ring width observations with correlations between the same climate indicators and MAIDEN or VS-Lite tree-growth simulations (1901-1949 verification period). O-S stands for the year starting from October (previous year) to September (current year); P for precipitation; JAS for July-August-September; T for temperature; TRindex for tree-ring index. Asterisks stand for significant correlations (p-value < 0.05). The difference in the number of sites on which correlations are computed is due to the phenological criterion that has been applied to MAIDEN calibrated sites (see Sect. 2.4.1 for more details).

Model (version)	**Correlation**
Correlations between observed TRW and O-S P correlation and simulated TRindex and O-S P correlation	
MAIDEN (Ge2017; 189 sites)	0.388*
MAIDEN (GI2015; 160 sites)	0.322*
VS-Lite (302 sites)	0.515*
MAIDEN (well-fitted sites only)	0.694*
VS-Lite (well-fitted sites only)	0.837*
MAIDEN (common well-fitted sites only)	0.747*
VS-Lite (common well-fitted sites only)	0.886*
Correlations between observed TRW and annual T correlation and simulated TRindex and annual T correlation	
MAIDEN (Ge2017; 189 sites)	0.053
MAIDEN (GI2015; 160 sites)	0.171*
VS-Lite (302 sites)	0.241*
MAIDEN (well-fitted sites only)	0.648*
VS-Lite (well-fitted sites only)	0.678*
MAIDEN (common well-fitted sites only)	0.608*
VS-Lite (common well-fitted sites only)	0.772*
Correlations between observed TRW and JAS T correlation and simulated TRindex and JAS T correlation	
MAIDEN (Ge2017; 189 sites)	0.130
MAIDEN (GI2015; 160 sites)	0.216*
VS-Lite (302 sites)	0.338*
MAIDEN (well-fitted sites only)	0.759*
VS-Lite (well-fitted sites only)	0.704*
MAIDEN (common well-fitted sites only)	0.739*
VS-Lite (common well-fitted sites only)	0.787*

3.4 Sensitivity analysis of MAIDEN to atmospheric CO_2 concentration

In this section, we perform a sensitivity analysis of the MAIDEN model to atmospheric CO_2 concentration. The CO_2 concentration is a key driver of the forest carbon fluxes but its actual effects are still difficult to consider and evaluate in dendroecological studies (Körner et al., 2005; Silva et al., 2010; Peñuelas et al., 2011; Lévesque et al., 2014; Van Der Sleen et al., 2015; Girardin et al., 2016; Hararuk et al., 2019; Giguère-Croteau et al., 2019; Marchand et al., 2020). Yet, the CO_2 concentration has increased by 30% over the last 50 years and might increase up to 1000 ppm at the 2100 horizon (RCP 8.5; Myhre et al., 2013) relative to the current 414.49 ppm (December 2020, `https://www.esrl.noaa.gov/gmd/ccgg/trends/global.html`, last access: 19 March 2021), which will have an impact on the forest carbon fluxes. This effect should be taken into account in dendroecological analysis (Babst et al., 2018). In MAIDEN, the CO_2 influences the forest carbon fluxes through the coupled modelling of photosynthesis and stomatal conductance (Farquhar et al., 1980; Leuning, 1995) with environmental dependencies related to temperature and soil water content (Gea-Izquierdo et al., 2015; Gennaretti et al., 2017), and the feedbacks between the coupled photosynthesis-stomatal conductance system and the carbon allocation.

Here, we evaluate the influence of the inclusion of the CO_2 concentration increase in MAIDEN by comparing its performance in the standard configuration with a sensitivity experiment in which the CO_2 concentration is kept constant, for the 64 well-fitted sites (Sect. 3.1), with parameters calibrated based on the CO_2 increasing scenario. The CO_2 is fixed at its 1st January 1980 value for the Northern Hemisphere (339 ppm), and at its 1st July 1980 value for the Southern Hemisphere (340 ppm).

At each site, we computed the difference between normalized MAIDEN tree-ring growth simulations and normalized TRW observations from 1990 with increasing CO_2 and constant CO_2. We performed our analysis on the 60 sites out of 64 well-fitted sites that end at least in 1990. Note that both simulations were normalized over 1950-2000 based on the mean and standard deviation of the original simulation, i.e. with increasing CO_2, over the same time period. The density distributions of the difference for both experiments are shown on Fig. 9a. The Pearson's Chi-squared test indicates a significant difference between the two experiments distributions (p-value < 0.05). The mean for both experiments are -0.209 and 0.182 for the constant CO_2 and increasing CO_2 experiment, respectively. In other words, while not taking into account CO_2 tends to underestimate the actual tree-growth on average, taking into account the increase of CO_2 in MAIDEN leads to overestimate it. Ecophysiological models are indeed known to overestimate the actual effect of CO_2 (Peñuelas et al., 2011; Gea-Izquierdo et al., 2017). However, the CO_2 concentration has certainly an impact on the tree carbon assimilation (Marchand et al., 2020) that should be properly considered to avoid potential biases in climate and growth trend reconstructions derived from tree-ring data. This impact can be taken into account by ecophysiological models such as MAIDEN, but potential

overestimations must be carefully envisaged due to the generic default of such models.

The trend of simulated and observed tree-growth was also computed and compared at each of the 60 sites. It corresponds to the coefficient of regression of the normalized tree-growth simulations or observations from 1970 up to 1990 at least, versus the years. The simulated trend by MAIDEN may reproduce the generally positive trend that is observed from 1970 in TRW time series (Fig. 9b) in correlation with the increasing CO_2 concentrations.

Consequently, our results show that the growth trends simulated by MAIDEN are significantly influenced by the CO_2 increase and that MAIDEN simulated tree-growth is closer to the observed TRW when including the CO_2 concentration increase. This limited analysis is not sufficient to draw conclusions regarding CO_2 fertilization in trees but it highlights a potential CO_2 effect based on a model that takes into account a commonly used biochemical formulation of photosynthesis (Farquhar et al., 1980). Including the effect of CO_2 in a mechanistic model like MAIDEN is a potential advantage over statistical and simple process-based models such as VS-Lite that are not able to account for these processes strongly influencing the forest carbon fluxes. However, because of the remaining uncertainties on the associated processes, an improved representation of the effect of CO_2 in process-based dendroecological models is needed to analyse past and future growth trends and variability.

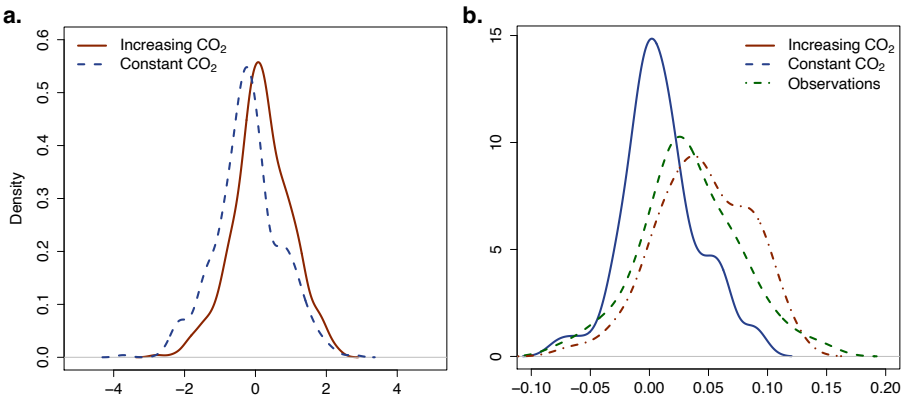

Fig. 9 Density distributions of (a) the difference between normalized tree-ring index simulations by MAIDEN and observed tree-ring width from 1990 with increasing CO_2 concentration (in red, i.e. the original configuration), and constant CO_2 concentration (in blue); (b) the trend from 1970 of normalized tree-ring index simulations by MAIDEN with increasing CO_2 concentration (in red, i.e. the original configuration) or with constant CO_2 concentration (in blue), and of normalized tree-ring width observations (in green); at 60 out of 64 well-fitted sites (Sect. 3.1).

4 Discussion and conclusions

In this paper, we have applied and compared two dendroclimatic process-based models of different complexity levels, VS-Lite and MAIDEN, using the global PAGES2k TRW database over the last century. We have evaluated their respective abilities and advantages to be used at the global scale as PSMs for paleoclimate data assimilation based reconstructions.

The models appear to be skillful for a similar number of mostly different sites (63 sites for VS-Lite and 64 sites for MAIDEN, 18 sites in common), spread over all continents. The performance of the models is comparable in terms of calibration and verification correlations. VS-Lite generally results in more stable correlations between the calibration and verification periods. When focusing on the factors that can drive the performance of both models, VS-Lite displays a strong correlation between its verification scores and tree-growth correlations with temperature, while MAIDEN does not. This means that VS-Lite tends to perform better at sites where observed tree-growth strongly correlates with temperature. In other words, the model's performance is improved in environments characterized by extreme temperatures. This feature hampers its application in many regions of the world away from the treeline, already rarely considered for paleoclimate reconstruction. In contrast, MAIDEN performance is less sensitive to the climate signal in TRW time series. We presume that MAIDEN performance is mainly limited by the lack of information needed to accurately calibrate and initialize the model at each specific site. As mentioned above, the information needed to calibrate MAIDEN is a key limitation of complex tree-growth models in general for use at a broader scale. This lack of data (for example, the observed Gross Primary Productivity data) also hinders a complete evaluation and identification of the factors driving the performance of MAIDEN.

At the sites where each model works well in terms of calibration and verification correlations, both VS-Lite and MAIDEN are on average able to successfully retrieve the climate signal in tree-rings. A careful selection of the tree-ring sites provides the opportunity to focus on the most robust simulated relationship between climate and tree-growth. However, VS-Lite appears to predominantly overestimate the observed dependence of tree-growth on climate, while there is no systematic bias for MAIDEN. The overestimation of the climate signal recorded in tree-rings has to be carefully taken into account when using such tree-growth models for data assimilation based reconstructions as it can result in biases. This is a clear disadvantage when using less complex dendroclimatic models, such as VS-Lite, in which the climate and tree-growth relationship is simplified.

Consequently, we may recommend using MAIDEN especially when the relationship between climate and tree-growth is complex with interacting limiting factors. VS-Lite would be a good candidate if tree-growth is mostly limited by only one climatic factor (e.g. summer temperature), although it may overestimate these climate dependences, particularly for temperature, leading to overconfident reconstructions. In this case, MAIDEN should produce more

plausible results. However, if not enough data are available to properly set and calibrate MAIDEN (for example long daily climate data or soil characteristics), VS-Lite should be preferred. As shown in Rezsöhazy et al. (2020), MAIDEN cannot be properly calibrated if used with short and low-replicated TRW time series (periods shorter than 50 years).

It has also been shown in this study that the inclusion of atmospheric CO_2 concentration has a significant impact on the MAIDEN simulations. More generally, MAIDEN appears as a potential good candidate to account for the non-stationarity of the tree-growth-to-climate relationship linked to changing CO_2 conditions in paleoclimate reconstructions. In particular, ecophysiological models, such as MAIDEN, could be useful tools to solve the so-called divergence problem in dendroclimatology (D'Arrigo et al., 2008). Conversely, from a paleoclimate perspective, not taking into account changing CO_2 concentration when using PSMs for data assimilation based reconstructions could lead to inaccurate climate reconstructions. More specifically, models such as VS-Lite could wrongly assign a trend in TRW series due to CO_2 concentration changes to the effect of rising temperatures. In turn, this will lead to an overestimation of the climate sensitivity of tree-growth and thus to an overestimation of the amplitude of past reconstructions. However, the impact of CO_2 concentration on tree carbon assimilation in more complex ecophysiological models should be evaluated carefully to properly take this process into account.

Consequently, future reconstructions and data assimilation could benefit from the use of complex ecophysiological models such as MAIDEN. Despite the obvious challenges that are associated with the calibration of such models, their potential for improving the quality of the reconstructions makes their complexity worthy. In particular, they widen the range of environments where tree-ring observations can be used for dendroclimatic reconstructions, including regions where the relationship between TRW and climate is more complex. They also account for the potential non-stationarity of tree-growth, for example due to increasing CO_2 concentration. Finally, they can prevent from systematic bias in the reconstruction of the climate signal recorded in TRW observations. Additionally, ecophysiological models like MAIDEN are continuously benefiting from improvements made in ecophysiology, in particular in the modelling of the links between climate and tree-growth through complex biological processes. However, in order to optimally use these complex models, we need to (1) have additional site knowledge to properly initialize the model such as data on the root profile, (2) use additional observations to verify specific processes such as phenology and photosynthetic rates, and (3) verify that the tree-ring chronologies are not affected by sampling biases that can distort the growth trends or are linked to non-climatic processes such as tree ontogeny and demographic changes in the sampled stands (Duchesne et al., 2019). Finally, to properly calibrate a complex model such as MAIDEN at the global scale, multiple data information sources should be mixed in the future. For example, tree phenology is hard to set with tree-ring data only. The phenology of MAIDEN could be informed more efficiently using satellite data (e.g. NDVI). On the other hand, simple dendroclimatic models like

VS-Lite, through their ease of use and calibration, coupled with a satisfying performance in reproducing tree-growth, are also appealing candidates for paleoclimate data assimilation based reconstructions. VS-Lite and MAIDEN thus bring complementary assets for reconstructing past climates. The user must select the model according to the goal of the study (temperature or hydroclimate reconstruction), the data availability at the proxy site and the climate dependence of the TRW observations (one or multiple climate drivers).

More generally, the simultaneous evaluation of tree-growth PSMs of different complexity is essential for any future paleoclimate data assimilation exercises willing to use TRW proxy data and tree-ring PSMs at the global scale. Such study helps to select the adequate PSM and identify the limitations and the advantages of mechanistic modelling in a paleoclimate perspective compared to statistical methods. It is thus a necessary step to increase our ability to robustly reconstruct past climates from tree-rings. In particular, our work sheds light on how process-based dendroclimatic models can improve the skill of reconstructions of past climate from tree-rings in comparison with the commonly used linear reconstruction methods. We have shown that the mechanistic approach has great potential to enhance our understanding of the past climate variability. Consequently, the next step will be to include such models in a data assimilation procedure to reconstruct the climate of the last millennium in regions where the models perform well. On this basis, we will be able to fully evaluate how process-based dendroclimatic models can contribute to the improvement of large-scale reconstructions of past climate variability and justify the added complexity of the procedure compared to linear regressions.

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Conflict of interest

The authors declare that they have no conflict of interest.

References

Acevedo W, Fallah B, Reich S, Cubasch U (2017) Assimilation of pseudo-Tree-ring-width observations into an atmospheric general circulation model. Climate of the Past 13(5):545–557, DOI 10.5194/cp-13-545-2017

689 Anchukaitis KJ, Wilson R, Briffa KR, Büntgen U, Cook ER, D'Arrigo R,
690 Davi N, Esper J, Frank D, Gunnarson BE, Hegerl G, Helama S, Klesse
691 S, Krusic PJ, Linderholm HW, Myglan V, Osborn TJ, Zhang P, Rydval
692 M, Schneider L, Schurer A, Wiles G, Zorita E (2017) Last millennium
693 Northern Hemisphere summer temperatures from tree rings: Part II, spa-
694 tially resolved reconstructions. Quaternary Science Reviews 163:1–22, DOI
695 10.1016/j.quascirev.2017.02.020
696 Anderson DM, Tardif R, Horlick K, Erb MP, Hakim GJ, Noone D, Perkins WA,
697 Steig E (2019) Additions to the Last Millennium Reanalysis Multi-Proxy
698 Database. Data Science Journal 18(1):2, DOI 10.5334/dsj-2019-002, URL
699 https://datascience.codata.org/article/10.5334/dsj-2019-002/
700 Babst F, Bodesheim P, Charney N, Friend AD, Girardin MP, Klesse S, Moore
701 DJ, Seftigen K, Björklund J, Bouriaud O, Dawson A, DeRose RJ, Dietze
702 MC, Eckes AH, Enquist B, Frank DC, Mahecha MD, Poulter B, Record S,
703 Trouet V, Turton RH, Zhang Z, Evans ME (2018) When tree rings go global:
704 Challenges and opportunities for retro- and prospective insight. Quaternary
705 Science Reviews 197:1–20, DOI 10.1016/j.quascirev.2018.07.009
706 Boucher E, Guiot J, Hatté C, Daux V, Danis PA, Dussouillez P (2014) An
707 inverse modeling approach for tree-ring-based climate reconstructions un-
708 der changing atmospheric CO_2 concentrations. Biogeosciences 11(12):3245–
709 3258, DOI 10.5194/bg-11-3245-2014
710 Breitenmoser P, Brönnimann S, Frank D (2014) Forward modelling of tree-
711 ring width and comparison with a global network of tree-ring chronologies.
712 Climate of the Past 10(2):437–449, DOI 10.5194/cp-10-437-2014
713 Briffa KR, Schweingruber FH, Jones PD, Osborn TJ, Harris IC, Shiyatov
714 SG, Vaganov EA, Grudd H (1998) Trees tell of past climates: but are they
715 speaking less clearly today? Philosophical Transactions of the Royal Society
716 of London Series B: Biological Sciences 353(1365):65–73, DOI 10.1098/rstb.
717 1998.0191, URL https://doi.org/10.1098/rstb.1998.0191
718 Cook ER, Kairiukstis L (1990) Methods of dendrochronology: Applications
719 in the Environmental Sciences. Kluwer Academic, Boston, DOI 10.1016/
720 0048-9697(91)90076-q
721 Danis PA, Hatté C, Misson L, Guiot J (2012) MAIDENiso: a multiproxy bio-
722 physical model of tree-ring width and oxygen and carbon isotopes. Canadian
723 Journal of Forest Research 42(9):1697–1713, DOI 10.1139/x2012-089, URL
724 http://www.nrcresearchpress.com/doi/abs/10.1139/x2012-089
725 D'Arrigo R, Wilson R, Liepert B, Cherubini P (2008) On the 'Divergence
726 Problem' in Northern Forests: A review of the tree-ring evidence and pos-
727 sible causes. Global and Planetary Change 60(3-4):289–305, DOI 10.1016/
728 j.gloplacha.2007.03.004
729 Dee SG, Steiger NJ, Emile-Geay J, Hakim GJ (2016) On the utility of proxy
730 system models for estimating climate states over common era. Journal of
731 Advances in Modeling Earth Systems 8:1164–1179, DOI https://doi.org/10.
732 1002/2016MS000677
733 Drew DM, Downes GM, Battaglia M (2010) CAMBIUM, a process-based
734 model of daily xylem development in Eucalyptus. Journal of Theoreti-

735 cal Biology 264(2):395–406, DOI 10.1016/j.jtbi.2010.02.013, URL http:
736 //dx.doi.org/10.1016/j.jtbi.2010.02.013
737 Duchesne L, Houle D, Ouimet R, Caldwell L, Gloor M, Brienen R (2019)
738 Large apparent growth increases in boreal forests inferred from tree-rings
739 are an artefact of sampling biases. Scientific Reports 9(1):1–9, DOI 10.1038/
740 s41598-019-43243-1
741 Dufrêne E, Davi H, François C, Le Maire G, Le Dantec V, Granier A (2005)
742 Modelling carbon and water cycles in a beech forest. Part I: Model de-
743 scription and uncertainty analysis on modelled NEE. Ecological Modelling
744 185(2-4):407–436, DOI 10.1016/j.ecolmodel.2005.01.004
745 Esper J, George SS, Anchukaitis K, D'Arrigo R, Ljungqvist F, Luter-
746 bacher J, Schneider L, Stoffel M, Wilson R, Büntgen U (2018) Large-
747 scale, millennial-length temperature reconstructions from tree-rings. Den-
748 drochronologia 50:81–90, DOI 10.1016/j.dendro.2018.06.001, URL http:
749 //linkinghub.elsevier.com/retrieve/pii/S1125786518300687
750 Evans MN, Tolwinski-Ward SE, Thompson DM, Anchukaitis KJ (2013) Appli-
751 cations of proxy system modeling in high resolution paleoclimatology. Qua-
752 ternary Science Reviews 76:16–28, DOI 10.1016/j.quascirev.2013.05.024,
753 URL http://dx.doi.org/10.1016/j.quascirev.2013.05.024
754 Fang M, Li X (2019) An Artificial Neural Networks-Based Tree Ring
755 Width Proxy System Model for Paleoclimate Data Assimilation. Jour-
756 nal of Advances in Modeling Earth Systems 11(4):892–904, DOI 10.1029/
757 2018MS001525
758 FAO/IIASA/ISRIC/ISSCAS/JRC (2012) Harmonized World Soil Database
759 (version 1.2). FAO, Rome, Italy and IIASA, Laxenburg, Austria
760 Farquhar GD, Caemmerer S, Berry JA (1980) A biochemical model of photo-
761 synthetic CO_2 assimilation in leaves of C_3 species. Planta 149(1):78–90–90,
762 URL http://dx.doi.org/10.1007/BF00386231
763 Fatichi S, Leuzinger S, Körner C (2014) Moving beyond photosynthesis:
764 From carbon source to sink-driven vegetation modeling. New Phytologist
765 201(4):1086–1095, DOI 10.1111/nph.12614
766 Fatichi S, Pappas C, Zscheischler J, Leuzinger S (2019) Modelling carbon
767 sources and sinks in terrestrial vegetation. New Phytologist 221(2):652–668,
768 DOI 10.1111/nph.15451
769 Franke J, Brönnimann S, Bhend J, Brugnara Y (2017) A monthly global paleo-
770 reanalysis of the atmosphere from 1600 to 2005 for studying past climatic
771 variations. Scientific Data 4:1–19, DOI 10.1038/sdata.2017.76
772 Fritts HC (1976) Tree rings and climate. Academic Press, London
773 Fritts HC (1991) Reconstructing large-scale climatic patterns from tree-ring
774 data: A diagnostic analysis. University of Arizona Press, Tucson, Arizona,
775 USA
776 Gea-Izquierdo G, Guibal F, Joffre R, Ourcival JM, Simioni G, Guiot J (2015)
777 Modelling the climatic drivers determining photosynthesis and carbon allo-
778 cation in evergreen Mediterranean forests using multiproxy long time series.
779 Biogeosciences 12(3):2745–2786, DOI 10.5194/bgd-12-2745-2015

780 Gea-Izquierdo G, Nicault A, Battipaglia G, Dorado-Liñán I, Gutiérrez E,
781 Ribas M, Guiot J (2017) Risky future for Mediterranean forests unless they
782 undergo extreme carbon fertilization. Global Change Biology 23(7):2915–
783 2927, DOI 10.1111/gcb.13597, 0608246v3
784 Gennaretti F, Gea-Izquierdo G, Boucher E, Berninger F, Arseneault D, Guiot
785 J (2017) Ecophysiological modeling of the climate imprint on photosynthesis
786 and carbon allocation to the tree stem in the North American boreal forest.
787 Biogeosciences 14:4851–4866, DOI 10.5194/bg-2017-51
788 Giguère-Croteau C, Boucher É, Bergeron Y, Girardin MP, Drobyshev I, Silva
789 LC, Hélie JF, Garneau M (2019) Correction: Plant biology, earth, atmo-
790 spheric, and planetary sciences (Proceedings of the National Academy of
791 Sciences of the United States of America (2019) 116 (2749–2754) DOI:
792 10.1073/pnas.1816686116). Proceedings of the National Academy of Sci-
793 ences of the United States of America 116(10):4748, DOI 10.1073/pnas.
794 1902083116
795 Girardin MP, Bouriaud O, Hogg EH, Kurz W, Zimmermann NE, Metsaranta
796 JM, De Jong R, Frank DC, Esper J, Büntgen U, Guo XJ, Bhatti J (2016) No
797 growth stimulation of Canada's boreal forest under half-century of combined
798 warming and CO_2 fertilization. Proceedings of the National Academy of
799 Sciences of the United States of America 113(52):E8406–E8414, DOI 10.
800 1073/pnas.1610156113
801 Goosse H, Crespin E, Dubinkina S, Loutre MF, Mann ME, Renssen H, Sallaz-
802 Damaz Y, Shindell D (2012) The role of forcing and internal dynamics in ex-
803 plaining the "Medieval Climate Anomaly". Climate Dynamics 39(12):2847–
804 2866, DOI 10.1007/s00382-012-1297-0
805 Guiot J, Torre F, Jolly D, Peyron O, Boreux JJ, Cheddadi R (2000) Inverse
806 vegetation modeling by Monte Carlo sampling to reconstruct palaeoclimates
807 under changed precipitation seasonality and CO_2 conditions: Application to
808 glacial climate in Mediterranean region. Ecological Modelling 127(2-3):119–
809 140, DOI 10.1016/S0304-3800(99)00219-7
810 Guiot J, Boucher E, Gea-Izquierdo G (2014) Process models and model-data
811 fusion in dendroecology. Frontiers in Ecology and Evolution 2:1–12, DOI 10.
812 3389/fevo.2014.00052, URL http://journal.frontiersin.org/article/
813 10.3389/fevo.2014.00052/abstract
814 Hararuk O, Campbell EM, Antos JA, Parish R (2019) Tree rings provide
815 no evidence of a CO_2 fertilization effect in old-growth subalpine forests of
816 western Canada. Global Change Biology 25(4):1222–1234, DOI 10.1111/gcb.
817 14561
818 Hartig F, Minunno F, Paul S (2019) BayesianTools: General-Purpose MCMC
819 and SMC Samplers and Tools for Bayesian Statistics. R package version
820 0.1.6. URL https://github.com/florianhartig/BayesianTools
821 Hunter JD (2007) Matplotlib: A 2D graphics environment. Computing in Sci-
822 ence and Engineering 9(3):90–95, DOI 10.1109/MCSE.2007.55
823 Jones PD, Briffa KR, Barnett TP, Tett SFB (1998) High-resolution palaeocli-
824 matic records for the last millennium. The Holocene 4:455–471

825 Jones PD, Briffa KR, Osborn TJ, Lough JM, Van Ommen TD, Vinther BM,
826 Luterbacher J, Wahl ER, Zwiers FW, Mann ME, Schmidt GA, Ammann
827 CM, Buckley BM, Cobb KM, Esper J, Goosse H, Graham N, Jansen E,
828 Kiefer T, Kull C, Küttel M, Mosley-Thompson E, Overpeck JT, Riedwyl
829 N, Schulz M, Tudhope AW, Villalba R, Wanner H, Wolff E, Xoplaki E
830 (2009) High-resolution palaeoclimatology of the last millennium: A review
831 of current status and future prospects. Holocene 19(1):3–49, DOI 10.1177/
832 0959683608098952
833 Konecky B, McKay N, Churakova (Sidorova) O, Comas-Bru L, Dassié E, De-
834 Long K, Falster G, Fischer M, Jones M, Jonkers L, Kaufman D, Leduc G,
835 Managave S, Martrat B, Opel T, Orsi A, Partin J, Sayani H, Thomas E,
836 Thompson D, Tyler J, Abram N, Atwood A, Conroy J, Kern Z, Porter T,
837 Stevenson S, von Gunten L (2020) The Iso2k Database: A global compilation
838 of paleo-δ18O and δ2H records to aid understanding of Common Era climate.
839 Earth System Science Data (12):2261–2288, DOI 10.5194/essd-12-2261-2020
840 Körner C (2015) Paradigm shift in plant growth control. Current Opinion in
841 Plant Biology 25:107–114, DOI 10.1016/j.pbi.2015.05.003
842 Körner C, Asshoff R, Bignucolo O, Hättenschwiler S, Keel SG, Peláez-
843 Riedl S, Pepin S, Siegwolf RT, Zotz G (2005) Ecology: Carbon flux and
844 growth in mature deciduous forest trees exposed to elevated CO_2. Science
845 309(5739):1360–1362, DOI 10.1126/science.1113977
846 Lavergne A, Daux V, Villalba R, Barichivich J (2015) Temporal changes
847 in climatic limitation of tree-growth at upper treeline forests: Contrasted
848 responses along the west-to-east humidity gradient in Northern Patago-
849 nia. Dendrochronologia 36:49–59, DOI 10.1016/j.dendro.2015.09.001, URL
850 http://dx.doi.org/10.1016/j.dendro.2015.09.001
851 Lavergne A, Gennaretti F, Risi C, Daux V, Savard M, Naulier M, Villalba R,
852 Begin C, Lavergne A, Gennaretti F, Risi C, Daux V, Boucher E, Lavergne
853 A, Gennaretti F, Risi C, Daux V, Boucher E, Savard MM (2017) Modelling
854 tree ring cellulose δ18O variations in two temperature-sensitive tree species
855 from North and South America. Climate of the Past (13):1515–1526
856 Leuning R (1995) A critical appraisal of a combined stomatal-
857 photosynthesis model for C_3 plants. Plant, Cell & Environment 18(4):339–
858 355, DOI https://doi.org/10.1111/j.1365-3040.1995.tb00370.x, URL
859 https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-3040.
860 1995.tb00370.x
861 Lévesque M, Siegwolf R, Saurer M, Eilmann B, Rigling A (2014) Increased
862 water-use efficiency does not lead to enhanced tree growth under xeric and
863 mesic conditions. New Phytologist 203(1):94–109, DOI 10.1111/nph.12772
864 Mann ME, Bradley RS, Hughes MK (1999) Northern Hemisphere tempera-
865 tures during the past millennium. Climate Change: Evaluating recent and
866 future climate change 26(6):759–762
867 Mann ME, Zhang Z, Hughes MK, Bradley RS, Miller SK, Rutherford S, Ni F
868 (2008) Proxy-based reconstructions of hemispheric and global surface tem-
869 perature variations over the past two millennia. Proceedings of the National
870 Academy of Sciences 105(36):13252–13257, DOI 10.1073/pnas.0805721105

Mann ME, Zhang Z, Rutherford S, Bradley RS, Hughes MK, Shindell D, Ammann C, Faluvegi G, Ni F (2009) Global Signatures and Dynamical Origins of the Little Ice Age and Medieval Climate Anomaly. Science 326:1256–1260, DOI 10.1126/science.1166349

Marchand W, Girardin MP, Hartmann H, Depardieu C, Isabel N, Gauthier S, Boucher É, Bergeron Y (2020) Strong overestimation of water-use efficiency responses to rising CO_2 in tree-ring studies. Global Change Biology 26(8):4538–4558, DOI 10.1111/gcb.15166

Misson L (2004) MAIDEN: a model for analyzing ecosystem processes in dendroecology. Canadian Journal of Forest Research 34(4):874–887, DOI 10.1139/x03-252, URL http://www.nrcresearchpress.com/doi/abs/10.1139/x03-252

Myhre G, Shindell D, Bréon FM, Collins W, Fuglestvedt J, Huang J, Koch D, Lamarque JF, Lee D, Mendoza B, Nakajima T, Robock A, Stephens G, Takemura T, Zhang H (2013) Anthropogenic and Natural Radiative Forcing. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom and New York, USA., DOI 10.1017/CBO9781107415324.018

PAGES 2k Consortium (2013) Continental-scale temperature variability during the past two millennia. Nature Geoscience 6(5):339–346, DOI 10.1038/ngeo1797

PAGES 2k Consortium (2017) A global multiproxy database for temperature reconstructions of the Common Era. Scientific Data 4(170088):1–33, DOI DOI:10.1038/sdata.2017.88

Peñuelas J, Canadell JG, Ogaya R (2011) Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. Global Ecology and Biogeography 20(4):597–608, DOI 10.1111/j.1466-8238.2010.00608.x

Rezsöhazy J, Goosse H, Guiot J, Gennaretti F, Boucher E, André F, Jonard M (2020) Application and evaluation of the dendroclimatic process-based model MAIDEN during the last century in Canada and Europe. Climate of The Past 16:1043–1059, DOI 10.5194/cp-16-1043-2020

Seftigen K, Frank DC, Björklund J, Babst F, Poulter B (2018) The climatic drivers of normalized difference vegetation index and tree-ring-based estimates of forest productivity are spatially coherent but temporally decoupled in Northern Hemispheric forests. Global Ecology and Biogeography 27(11):1352–1365, DOI 10.1111/geb.12802

Sheffield J, Goteti G, Wood EF (2006) Development of a 50-year high-resolution global dataset of meteorological forcings for land surface modeling. Journal of Climate 19(13):3088–3111, DOI 10.1175/JCLI3790.1

Silva LC, Anand M, Leithead MD (2010) Recent widespread tree growth decline despite increasing atmospheric CO_2. PLoS ONE 5(7), DOI 10.1371/journal.pone.0011543

St George S, Esper J (2019) Concord and discord among Northern Hemisphere paleotemperature reconstructions from tree rings. Quaternary Science Reviews 203:278–281, DOI S0277379118307170

Steiger NJ, Smerdon JE (2017) A pseudoproxy assessment of data assimilation for reconstructing the atmosphere-ocean dynamics of hydroclimate extremes. Climate of the Past 13(10):1435–1449, DOI 10.5194/cp-13-1435-2017

Steiger NJ, Smerdon JE, Cook ER, Cook BI (2018) A reconstruction of global hydroclimate and dynamical variables over the Common Era. Scientific Data 5:1–15, DOI 10.1038/sdata.2018.86

Tardif R, Hakim GJ, Perkins WA, Horlick KA, Erb MP, Emile-Geay J, Anderson DM, Steig EJ, Noone D (2019) Last Millennium Reanalysis with an expanded proxy database and seasonal proxy modeling. Climate of the Past 15(4):1251–1273, DOI 10.5194/cp-15-1251-2019

Tolwinski-Ward SE, Evans MN, Hughes MK, Anchukaitis KJ (2011) An efficient forward model of the climate controls on interannual variation in tree-ring width. Climate Dynamics 36(11-12):2419–2439, DOI 10.1007/s00382-010-0945-5

Tolwinski-Ward SE, Anchukaitis KJ, Evans MN (2013) Bayesian parameter estimation and interpretation for an intermediate model of tree-ring width. Climate of the Past 9(4):1481–1493, DOI 10.5194/cp-9-1481-2013

Vaganov EA, Hughes MK, Shashkin A (2006) Growth dynamics of conifer tree rings, springer edn. New York

Van Der Sleen P, Groenendijk P, Vlam M, Anten NP, Boom A, Bongers F, Pons TL, Terburg G, Zuidema PA (2015) No growth stimulation of tropical trees by 150 years of CO_2 fertilization but water-use efficiency increased. Nature Geoscience 8(1):24–28, DOI 10.1038/ngeo2313

Wilson R, Elling W (2004) Temporal instability in tree-growth/climate response in the Lower Bavarian Forest region: Implications for dendroclimatic reconstruction. Trees - Structure and Function 18(1):19–28, DOI 10.1007/s00468-003-0273-z

Wilson R, D'Arrigo R, Buckley B, Büntgen U, Esper J, Frank D, Luckman B, Payette S, Vose R, Youngblut D (2007) A matter of divergence: Tracking recent warming at hemispheric scales using tree ring data. Journal of Geophysical Research Atmospheres 112(17):1–17, DOI 10.1029/2006JD008318

Wilson R, Anchukaitis K, Briffa KR, Büntgen U, Cook E, D'Arrigo R, Davi N, Esper J, Frank D, Gunnarson B, Hegerl G, Helama S, Klesse S, Krusic PJ, Linderholm HW, Myglan V, Osborn TJ, Rydval M, Schneider L, Schurer A, Wiles G, Zhang P, Zorita E (2016) Last millennium northern hemisphere summer temperatures from tree rings: Part I: The long term context. Quaternary Science Reviews 134:1–18, DOI 10.1016/j.quascirev.2015.12.005

S1 Supplementary materials

Table S1 Main constants linked to site conditions and control parameters in the MAIDEN model.

Parameter	**Meaning**	**Units**
exp_site	Indicates if the species at the site is a deciduous (1) or evergreen (2) tree	no unit (1 or 2)
base_elev_cst	Station elevation	meters
base_isoh_cst	Station isohyet	centimeters
site_lat_cst	Site latitude	degrees
site_elev_cst	Site elevation	meters
site_slp_cst	Site slope	degrees
site_asp_cst	Site aspect	degrees
site_isoh_cst	Site isohyet	centimeters
site_ehoriz_cst	Site East slope	degrees
site_whoriz_cst	Site West slope	degrees
thick1-2-3 or 4	Soil layer thickness	meters
finefrac1-2-3 or 4	% of fine roots in the soil layer	Coeff. between 0-1
clay1-2-3 or 4	% of clay in the soil layer	%
sand1-2-3 or 4	% of sand in the soil layer	%

Table S2 Calibrated parameters of the MAIDEN model (Gennaretti et al., 2017).

	Process		Parameter	Units
Photosynthesis	Temperature dependence of photosynthesis	Asymptote	V_{max}	μmol C.m^{-2} of leaves . s^{-1}
		Slope	V_b	°C^{-1}
		Inflection point	V_{ip}	°C
	Water stress dependence of stomatal conductance	Slope	$soil_b$	mm^{-1}
		Inflection point	$soil_{ip}$	mm
	Acclimation to temperature of photosynthesis	Needed days	τ	days
Carbon allocation	Definition of canopy maximum amount of carbon	Slope of temperature dependence	*CanopyT*	°C^{-1}
		Slope of precipitation dependence	*CanopyP*	mm^{-1}
	Start of the growing season (budburst)	GDD sum threshold	GDD_1	°C
		Day before the later start	*vegphase23*	day of the year
		Acclimation to changing GDD sums	*day23_flex*	years
	Daily available carbon from buds reservoir	Storage C used by the tree	C_{bud}	gC.m^{-2} of stand . day^{-1}
	Partition of carbon to different tree compartments during growing season	Portion allocated to canopy and roots	*h3*	fraction (0-1)
	Partition of carbon to different tree compartments during summer period	Inflection point of the temperature dependence	st_{4temp}	°C
	Photoperiod for transition from summer to fall season	Photoperiod threshold	*photoper*	hours
	Carbon losses from the canopy (evergreen only)	Yearly canopy turnover rate	*PercentFall*	fraction (0-1)
		Approximate day of the year with maximum losses	*OutMax*	day of the year
		Index proportional to the length of the period with losses	*OutLength*	NA

Table S3 Calibrated parameters of the MAIDEN model (Gea-Izquierdo et al., 2015).

	Process		Parameter	Units
Photosynthesis	Temperature dependence of photosynthesis	Asymptote	V_{max}	μmol C.m^{-2} of leaves . s^{-1}
		Slope	V_b	$^{\circ}$C^{-1}
		Inflection point	V_{ip}	$^{\circ}$C
	Water stress dependence of stomatal conductance	Slope	$soil_b$	mm^{-1}
		Inflection point	$soil_{ip}$	mm
Carbon allocation	Definition of canopy maximum amount of carbon	Slope of temperature dependence	$perc_{LAI}$	$^{\circ}$C^{-1}
	Start of the growing season (budburst)	GDD sum threshold	GDD_1	$^{\circ}$C
		Day before the later start	*vegphase23*	day of the year
	Daily available carbon from buds reservoir	Storage C used by the tree	C_{bud}	gC.m^{-2} of stand . day^{-1}
	Partition of carbon to different tree compartments during growing season	Definition of carbon allocated to the stem as a function of soil water	p_{3moist}	mm^{-1}
		Definition of carbon allocated to the stem as a function of maximum temperature	p_{3temp}	$^{\circ}$C
			p_{3sd}	$^{\circ}$C
		Definition of carbon allocated to the stem as a function of soil water	st_{3moist}	mm^{-1}
		Definition of carbon allocated to the stem as a function of maximum temperature	st_{3temp}	$^{\circ}$C
			st_{3sd_temp}	$^{\circ}$C
	Partition of carbon to different tree compartments during summer period	Definition of carbon allocated to stem or storage as a function of maximum temperature	st_{4temp}	$^{\circ}$C^{-1}
		Definition of carbon allocated to stem or storage as a function of soil water	st_{4sd_moist}	mm
	Photoperiod for transition from summer to fall season	Photoperiod threshold	*photoper*	hours

Table S4 Ranges of calibrated parameters prior uniform distributions, for the MAIDEN model (Gennaretti et al., 2017). See Table S2 for details on calibrated parameters.

	Parameter	Lower bound	Upper bound
Photosynthesis	V_{max}	5	150
	V_b	-0.3	-0.05
	V_{ip}	5	30
	$soil_b$	-0.06	-0.005
	$soil_{ip}$	3	400
	τ	1	20
Carbon allocation	$CanopyT$	0	20
	$CanopyP$	0	20
	GDD_1	10	250
	$vegphase23$	90	190
	$day23\_flex$	1	10
	C_{bud}	1	16
	$h3$	0	1
	st_{4temp}	1	100
	$photoper$	9	14
	$PercentFall$	0.09	0.5
	$OutMax$	120	250
	$OutLength$	2	15

Table S5 Ranges of calibrated parameters prior uniform distributions, for the MAIDEN model (Gea-Izquierdo et al., 2015). See Table S3 for details on calibrated parameters.

	Parameter	Lower bound	Upper bound
Photosynthesis	V_{max}	5	150
	V_b	-0.3	-0.05
	V_{ip}	5	30
	$soil_b$	-0.06	-0.005
	$soil_{ip}$	3	400
Carbon allocation	$perc_{LAI}$	40	250
	GDD_1	10	250
	vegphase23	90	190
	C_{bud}	1	16
	p_{3moist}	-0.7	-0.001
	p_{3temp}	-160	185
	p_{3sd}	5	200
	st_{3moist}	-0.8	-0.005
	st_{3temp}	-170	230
	st_{3sd_temp}	5	300
	st_{4temp}	0.008	0.95
	st_{4sd_moist}	45	1090
	photoper	9	14

Table S6 Pearson correlations between different climate indicators and MAIDEN or VS-Lite verification correlations (1901-1949). O-S stands for the year starting from October (previous year) to September (current year); P for precipitation; JAS for July-August-September; T for temperature. Asterisks stand for significant correlations (p-value < 0.05). The difference in the number of sites on which correlations are computed is due to the phenological criterion that has been applied to MAIDEN calibrated sites (see Sect. 2.4.1 for more details).

Model (version)	**Correlation**
Correlations between O-S mean cumulative P correlation and verification correlation	
MAIDEN (Ge2017; 189 sites)	0.073
MAIDEN (GI2015; 160 sites)	0.076
VS-Lite (302 sites)	-0.067
Correlations between annual mean T correlation and verification correlation	
MAIDEN (Ge2017; 189 sites)	0.036
MAIDEN (GI2015; 160 sites)	0.036
VS-Lite (302 sites)	-0.052
Correlations between JAS mean T correlation and verification correlation	
MAIDEN (Ge2017; 189 sites)	0.027
MAIDEN (GI2015; 160 sites)	0.049
VS-Lite (302 sites)	-0.053

Table S7 Pearson correlations between correlations of observed TRW with different climate indicators and MAIDEN or VS-Lite verification correlations (1901-1949). O-S stands for the year starting from October (previous year) to September (current year); P for precipitation; JAS for July-August-September; T for temperature. Asterisks stand for significant correlations (p-value < 0.05). The difference in the number of sites on which correlations are computed is due to the phenological criterion that has been applied to MAIDEN calibrated sites (see Sect. 2.4.1 for more details).

Model (version)	**Correlation**
Correlations between observed TRW and O-S P correlation and verification correlation	
MAIDEN (Ge2017; 189 sites)	0.114
MAIDEN (GI2015; 160 sites)	0.155
VS-Lite (302 sites)	0.149*
VS-Lite (189 Ge2017 selected sites)	0.190*
VS-Lite (160 GI2015 selected sites)	0.091
Correlations between observed TRW and annual T correlation and verification correlation	
MAIDEN (Ge2017; 189 sites)	0.074
MAIDEN (GI2015; 160 sites)	0.059
VS-Lite (302 sites)	0.467*
VS-Lite (189 Ge2017 selected sites)	0.471*
VS-Lite (160 GI2015 selected sites)	0.503*
Correlations between observed TRW and JAS T correlation and verification correlation	
MAIDEN (Ge2017; 189 sites)	-0.039
MAIDEN (GI2015; 160 sites)	-0.097
VS-Lite (302 sites)	0.506*
VS-Lite (189 Ge2017 selected sites)	0.496*
VS-Lite (160 GI2015 selected sites)	0.494*

Table S8 Pearson correlations of correlations between different climate indicators and tree-ring width observations with correlations between the same climate indicators and MAIDEN or VS-Lite tree-growth simulations (1901-1949 verification period). O-S stands for the year starting from October (previous year) to September (current year); P for precipitation; JAS for July-August-September; T for temperature; TRindex for tree-ring index. Asterisks stand for significant correlations (p-value < 0.05). The difference in the number of sites on which correlations are computed is due to the phenological criterion that has been applied to MAIDEN calibrated sites (see Sect. 2.4.1 for more details).

Model (version)	**Correlation**
Correlations between observed TRW and O-S P correlation and simulated TRindex and O-S P correlation	
MAIDEN (Ge2017; 189 sites)	0.388*
MAIDEN (GI2015; 160 sites)	0.322*
VS-Lite (302 sites)	0.515*
VS-Lite (189 Ge2017 selected sites)	0.552*
VS-Lite (160 GI2015 selected sites)	0.552*
MAIDEN (well-fitted sites only)	0.694*
VS-Lite (well-fitted sites only)	0.837*
MAIDEN (common well-fitted sites only)	0.747*
VS-Lite (common well-fitted sites only)	0.886*
Correlations between observed TRW and annual T correlation and simulated TRindex and annual T correlation	
MAIDEN (Ge2017; 189 sites)	0.053
MAIDEN (GI2015; 160 sites)	0.171*
VS-Lite (302 sites)	0.241*
VS-Lite (189 Ge2017 selected sites)	0.203*
VS-Lite (160 GI2015 selected sites)	0.291*
MAIDEN (well-fitted sites only)	0.648*
VS-Lite (well-fitted sites only)	0.678*
MAIDEN (common well-fitted sites only)	0.608*
VS-Lite (common well-fitted sites only)	0.772*
Correlations between observed TRW and JAS T correlation and simulated TRindex and JAS T correlation	
MAIDEN (Ge2017; 189 sites)	0.130
MAIDEN (GI2015; 160 sites)	0.216*
VS-Lite (302 sites)	0.338*
VS-Lite (189 Ge2017 selected sites)	0.329*
VS-Lite (160 GI2015 selected sites)	0.328*
MAIDEN (well-fitted sites only)	0.759*
VS-Lite (well-fitted sites only)	0.704*
MAIDEN (common well-fitted sites only)	0.739*
VS-Lite (common well-fitted sites only)	0.787*

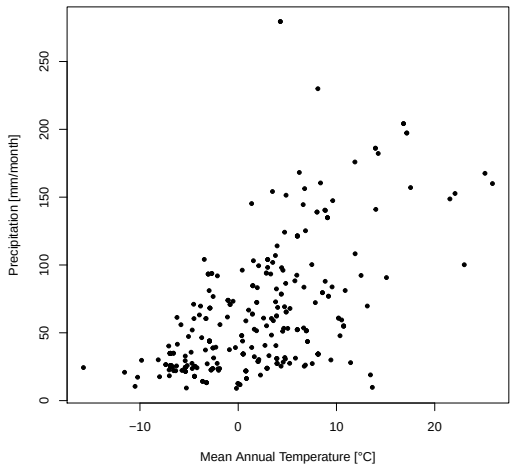


Fig. S1 Mean monthly cumulative precipitation (in millimeters per month) as a function of mean annual temperature (in °C) at the 302 PAGES2k TRW sites used in this study. The climate data are from the *Global Meteorological Forcing Dataset for land surface modelling* (v2) at 0.5° resolution (Section 2.3) over the 1901-2000 time period.

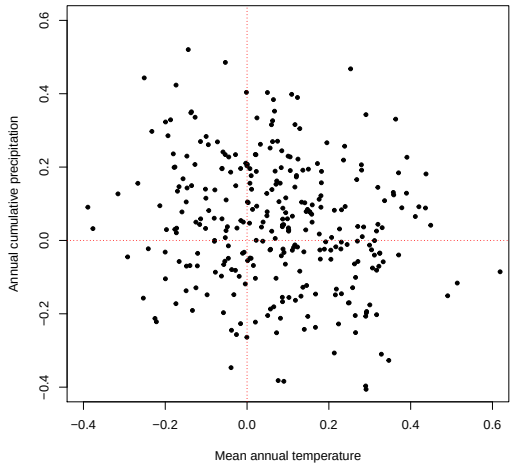


Fig. S2 Correlations between annual cumulative precipitation and TRW observations as a function of correlations between mean annual temperature and TRW observations at the 302 PAGES2k TRW sites used in this study, over the 1901-2000 period. The climate data are from the *Global Meteorological Forcing Dataset for land surface modelling* (v2) at 0.5° resolution (Section 2.3).

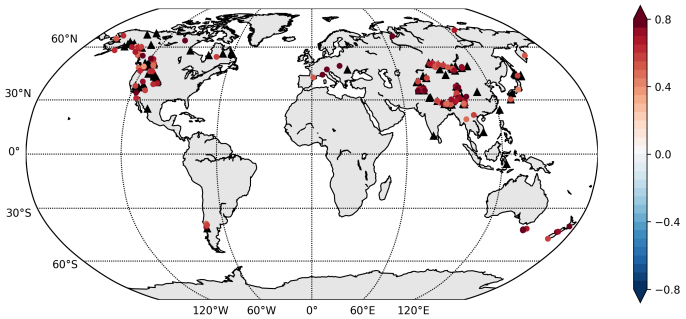


Fig. S3 MAIDEN (Gea-Izquierdo et al., 2015) calibration correlations for selected sites (Sect. 2.4.1; 160 sites out of 302). Background map from Hunter (2007).

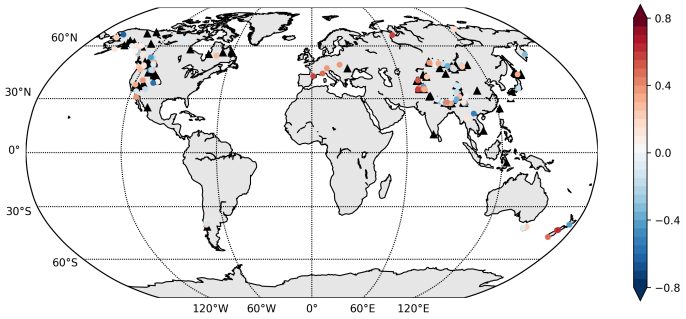


Fig. S4 MAIDEN (Gea-Izquierdo et al., 2015) verification correlations for selected sites (Sect. 2.4.1; 160 sites out of 302). Background map from Hunter (2007).

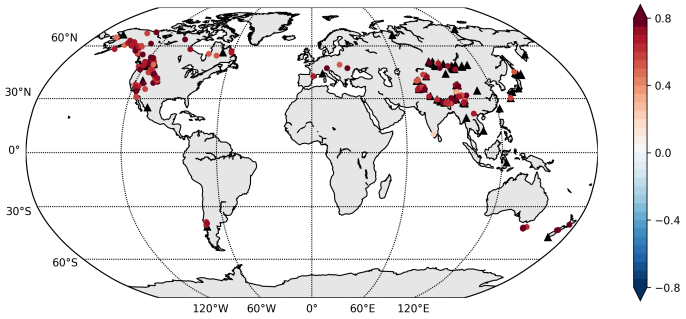


Fig. S5 MAIDEN (Gennaretti et al., 2017) calibration correlations for selected sites (Sect. 2.4.1; 189 sites out of 302). Background map from Hunter (2007).

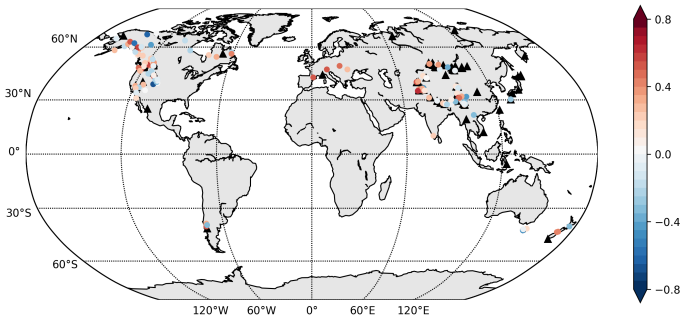


Fig. S6 MAIDEN (Gennaretti et al., 2017) verification correlations for selected sites (Sect. 2.4.1; 189 sites out of 302). Background map from Hunter (2007).

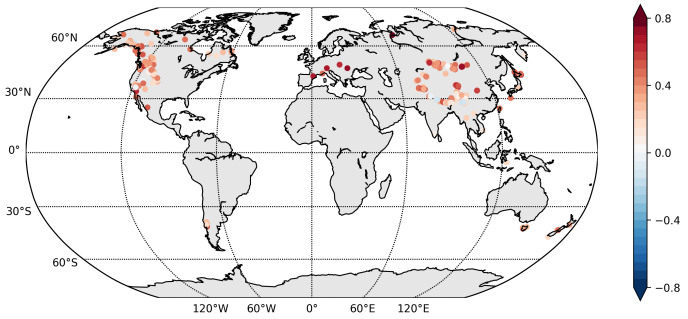


Fig. S7 VS-Lite calibration correlations for 302 sites. Background map from Hunter (2007).

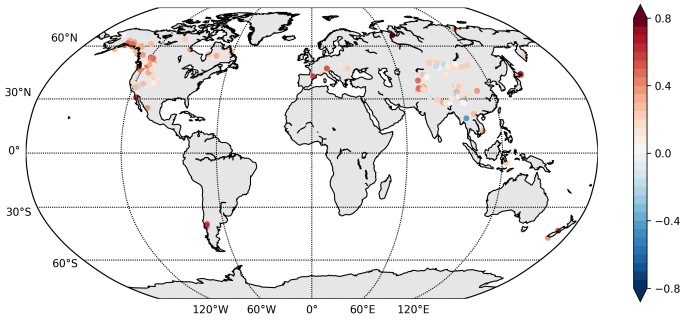
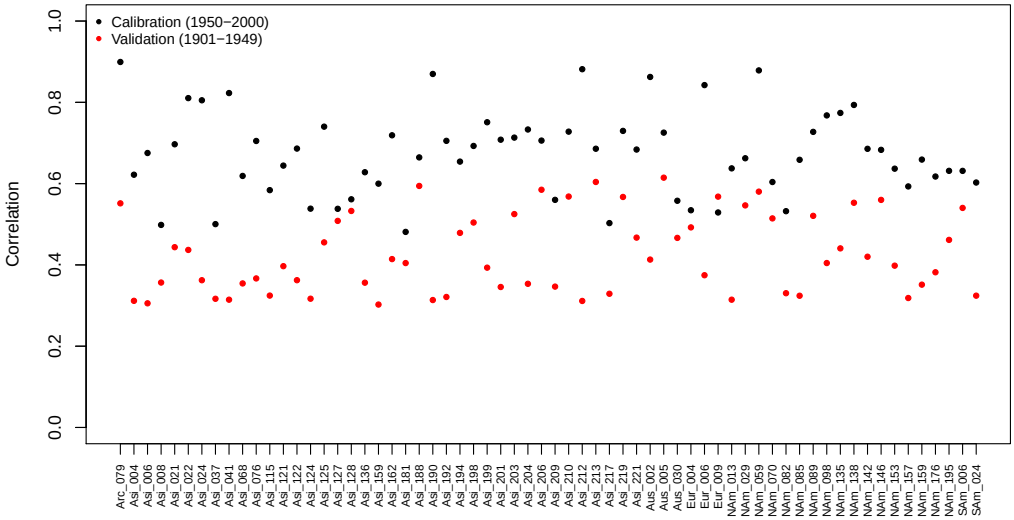
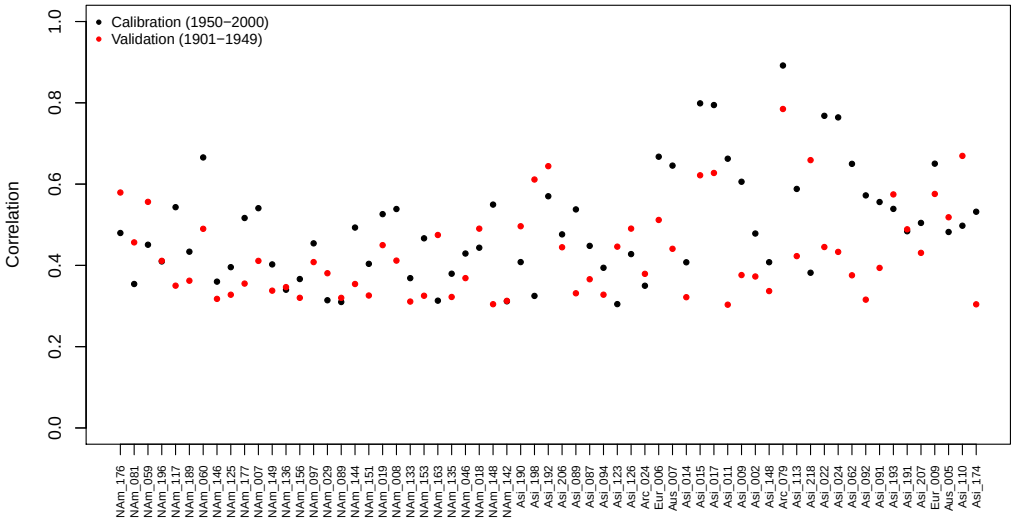


Fig. S8 VS-Lite verification correlations for 302 sites. Background map from Hunter (2007).



(a) MAIDEN



(b) VS-Lite

Fig. S9 (a) MAIDEN (64 sites) and (b) VS-Lite (63 sites) calibration (1950-2000) and verification (1901-1949) correlations (all significant at the 95% confidence level) for well-fitted sites (Sect. 3.1) (with names from the PAGES2k database: *NAm* for North American sites; *Asi* for Asian sites; *Eur* for European sites; *Arc* for Arctic sites; *Aus* for Australian, Tasmanian or New Zealand sites; *SAm* for South American sites).

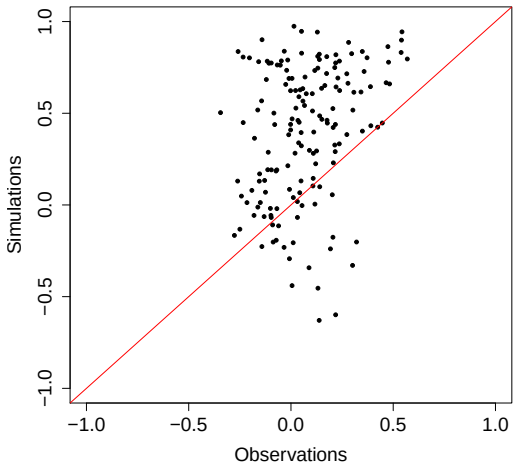


Fig. S10 Correlations between mean annual temperature and VS-Lite tree-ring index simulations as a function of correlations between mean annual temperature and TRW observations for MAIDEN (Gea-Izquierdo et al., 2015) selected sites (Sect. 2.4.1; 160 sites out of 302), over the 1901-1949 verification period.

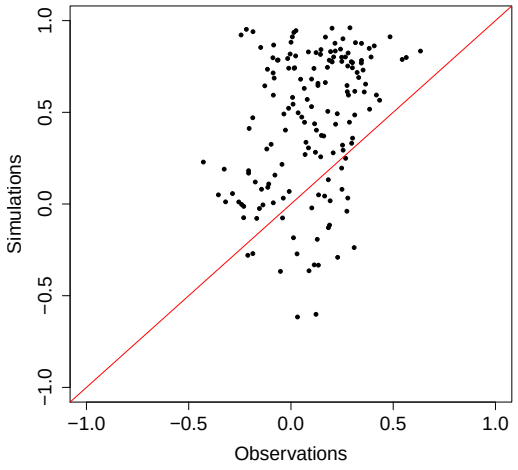


Fig. S11 Correlations between mean July-August-September temperature and VS-Lite tree-ring index simulations as a function of correlations between mean July-August-September temperature and TRW observations for MAIDEN (Gea-Izquierdo et al., 2015) selected sites (Sect. 2.4.1; 160 sites out of 302), over the 1901-1949 verification period.

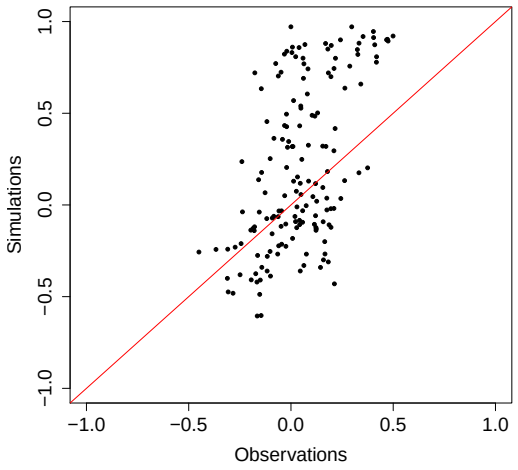


Fig. S12 Correlations between October-September cumulative precipitation and VS-Lite tree-ring index simulations as a function of correlations between October-September cumulative precipitation and TRW observations for MAIDEN (Gea-Izquierdo et al., 2015) selected sites (Sect. 2.4.1; 160 out of 302), over the 1901-1949 verification period.

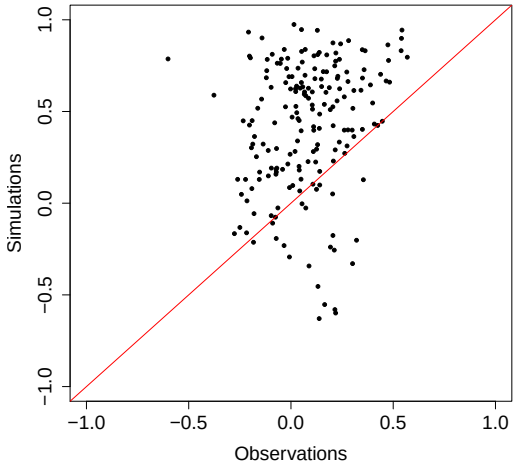


Fig. S13 Correlations between mean annual temperature and VS-Lite tree-ring index simulations as a function of correlations between mean annual temperature and TRW observations for MAIDEN (Gennaretti et al., 2017) selected sites (Sect. 2.4.1; 189 sites out of 302), over the 1901-1949 verification period.

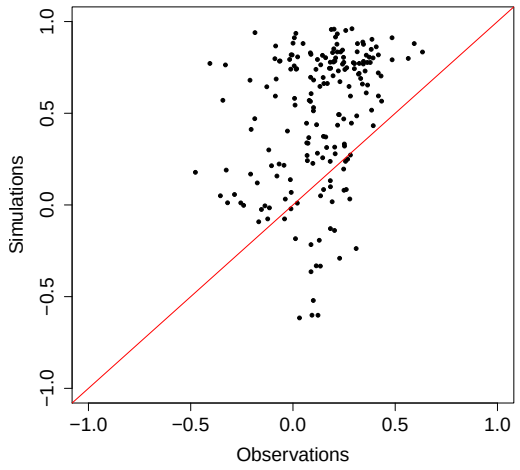


Fig. S14 Correlations between mean July-August-September temperature and VS-Lite tree-ring index simulations as a function of correlations between mean July-August-September temperature and TRW observations for MAIDEN (Gennaretti et al., 2017) selected sites (Sect. 2.4.1; 189 sites out of 302), over the 1901-1949 verification period.

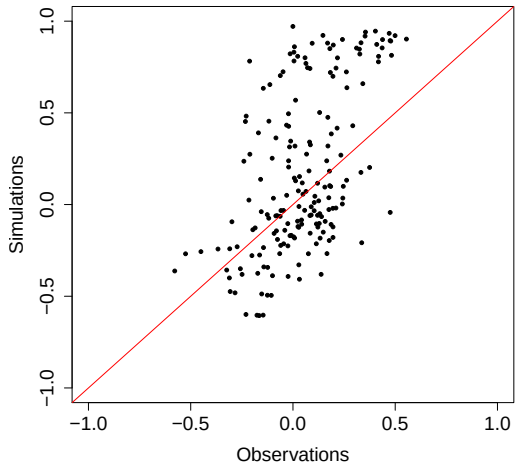


Fig. S15 Correlations between October-September cumulative precipitation and VS-Lite tree-ring index simulations as a function of correlations between October-September cumulative precipitation and TRW observations for MAIDEN (Gennaretti et al., 2017) selected sites (Sect. 2.4.1; 189 out of 302), over the 1901-1949 verification period.