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# Testing the performance of dendroclimatic process-based models at global scale with the PAGES2k tree-ring width database

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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 reconstructions based on data assimilation 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 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, 2017; Wilson et al. 2016; Anchukaitis et al. 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

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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, 1991; Cook and Kairiukstis 1990; 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 one 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 reconstructions based on data assimilation. 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 (Sect. 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 (1–15 cm; 15–30 cm; 30–65 cm; 65–100 cm) 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).

### 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

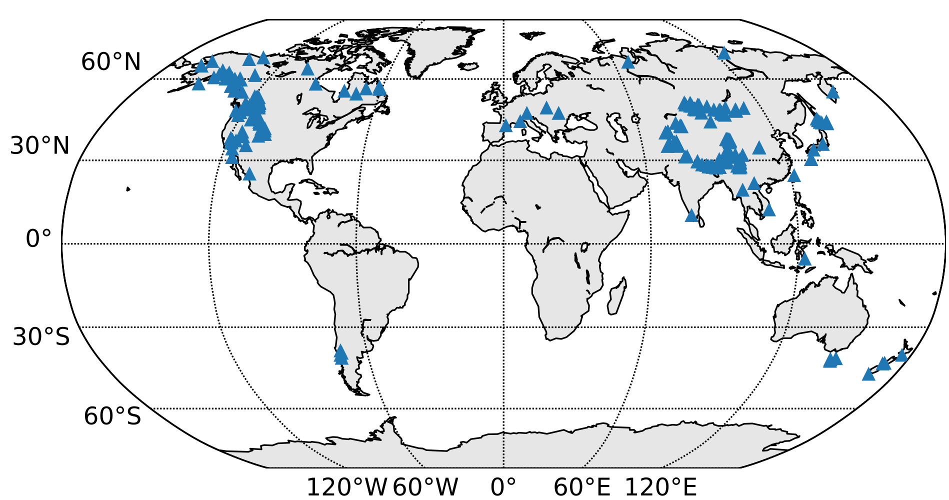


**Fig. 1** PAGES2k (PAGES 2k Consortium 2017) tree-ring width sites used in this study (302 sites). Background map from Hunter (2007)

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 be 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 reconstructions based on data assimilation. Finally, Sect. 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: (1) a significant (at the 95% confidence level) calibration (1950–2000) and verification (1901–1949) correlation ≥ 0.3; (2) 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 (Sects. 2.4.2, 2.5; Figs. S7, 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.

### 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

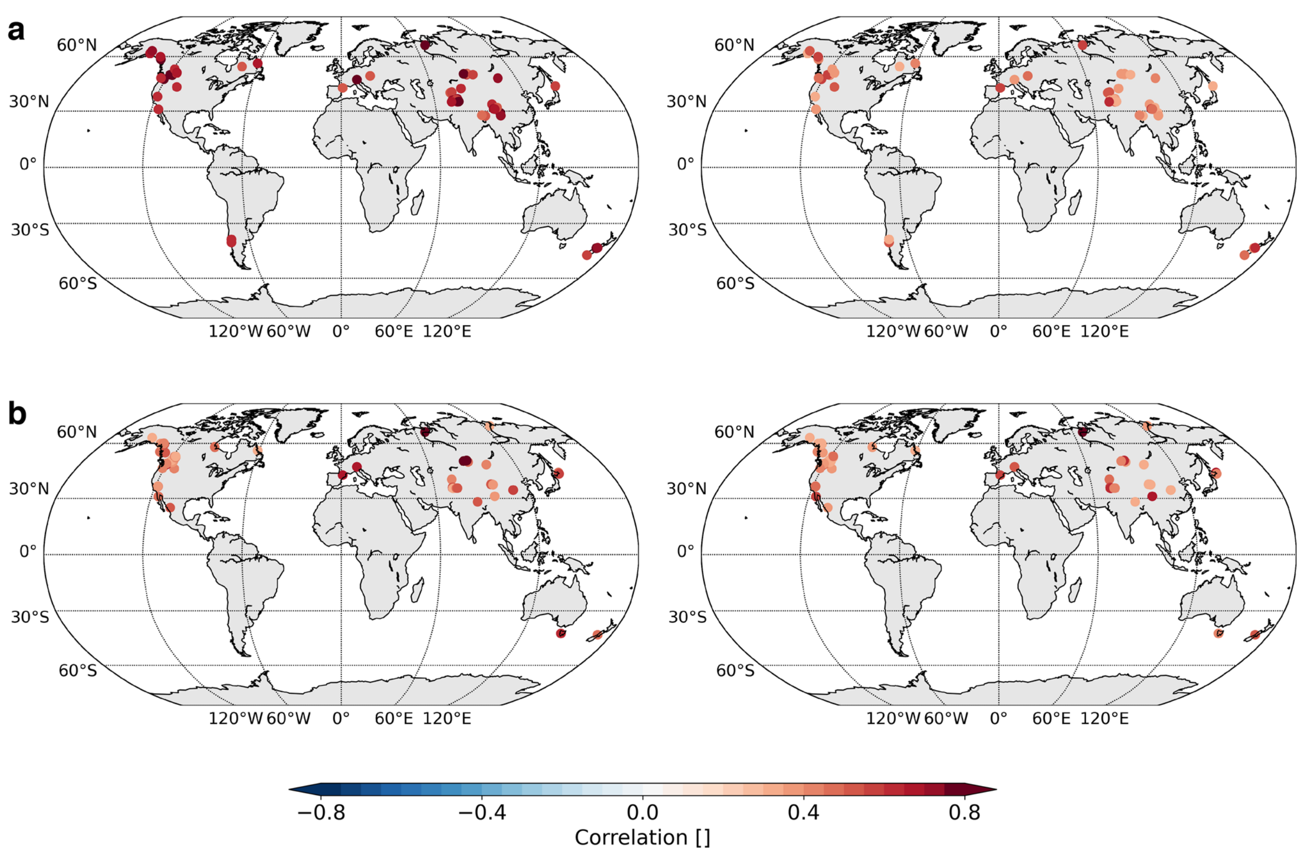


**Fig. 2** **a** MAIDEN (64 sites) and **b** VS-Lite (63 sites) calibration (left) and verification (right) correlations for well-fitted sites (Sect. 3.1). All correlations are significant at the 95% confidence level. Background maps from Hunter (2007)

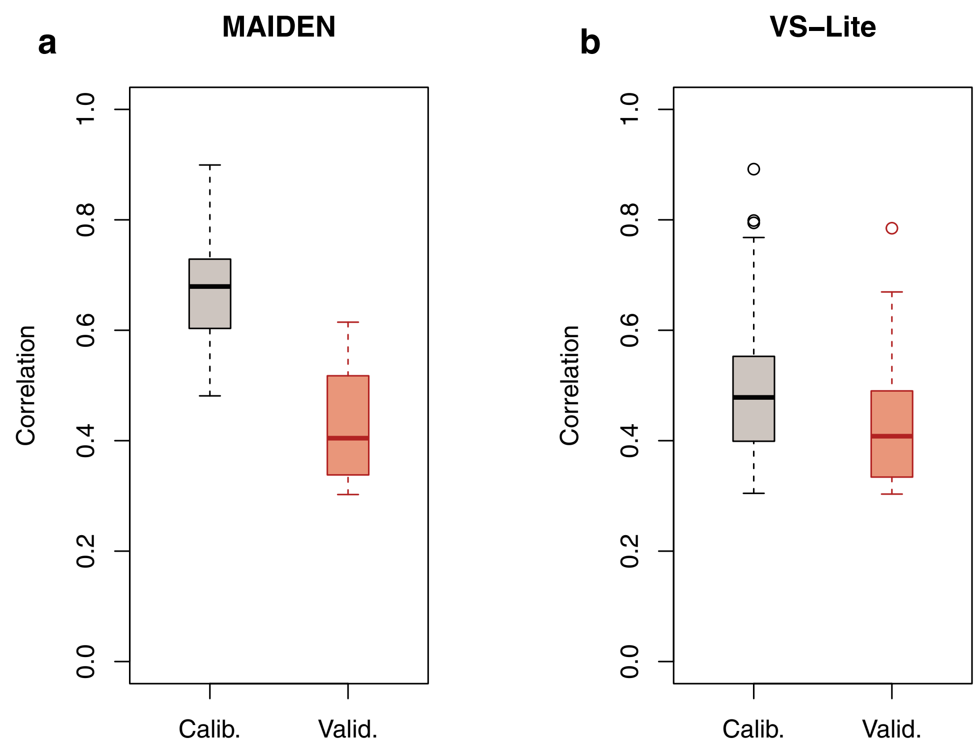


**Fig. 3** **a** MAIDEN (64 sites) and **b** VS-Lite (63 sites) calibration (1950–2000) and verification (1901–1949) correlations (all significant at the 95% confidence level) boxplots for well-fitted sites (Sect. 3.1)

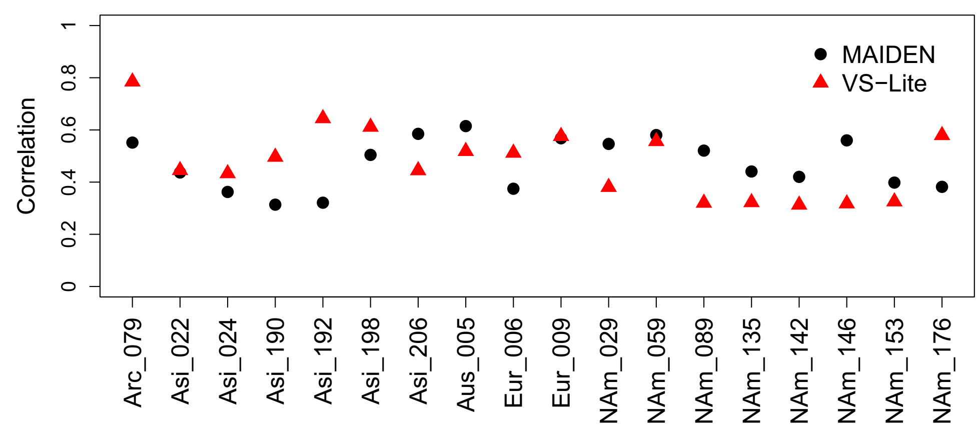


**Fig. 4** MAIDEN and VS-Lite verification (1901-1949) correlations (all significant at the 95% confidence level) for common well-fitted sites (Sect. 3.1) (18 sites, with names from the PAGES2k database: *NAm* for North American sites; *Asi* for Asian sites; *Eur* for European sites; *Arc* for Arctic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

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 model 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, 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

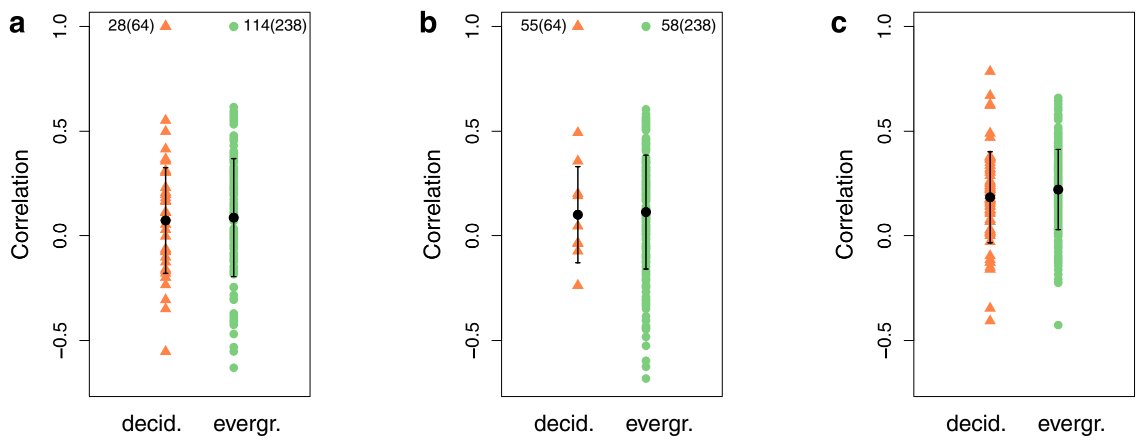


**Fig. 5** Verification correlations, mean and standard deviation by tree types (deciduous or evergreen) for the MAIDEN version of GI2015 (**a**) and Ge2017 (**b**), for selected sites (160 sites for GI2015 and 189 for Ge2017, Sect. 2.4.1; others have been put to 1; the number of sites that have been 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**)

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

**Table 1** Pearson correlations between correlations of observed TRW with different climate indicators and MAIDEN or VS-Lite verification correlations (1901–1949)

| 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* |

*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) 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.

### 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, 8) and secondly, by means of correlations (Table 2).

For MAIDEN (Figs. 6, 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

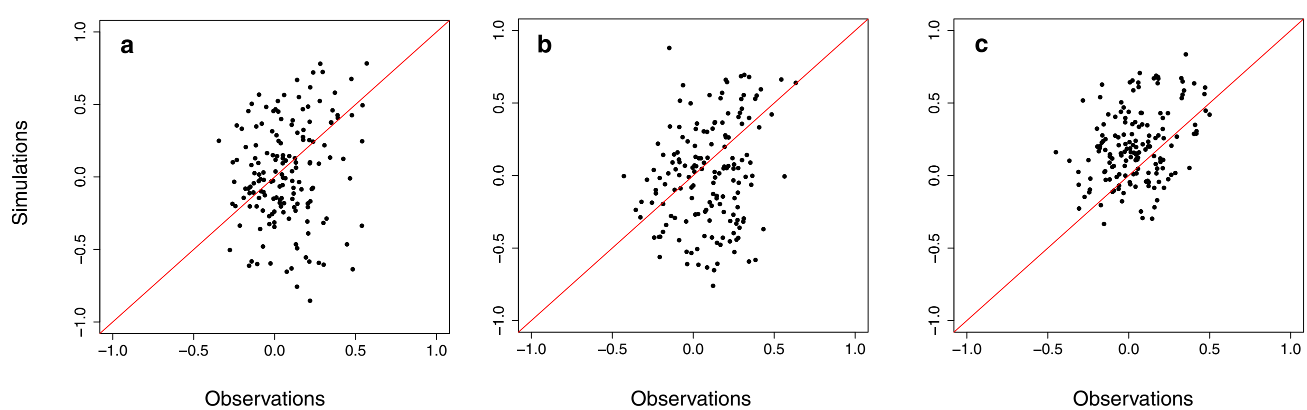


**Fig. 6** Correlations between mean annual temperature (**a**), mean July–August–September temperature (**b**), October–September cumulative precipitation (**c**) and MAIDEN (GI2015) Dstem simulations as a function of correlations between the same climate indicators and TRW observations for selected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

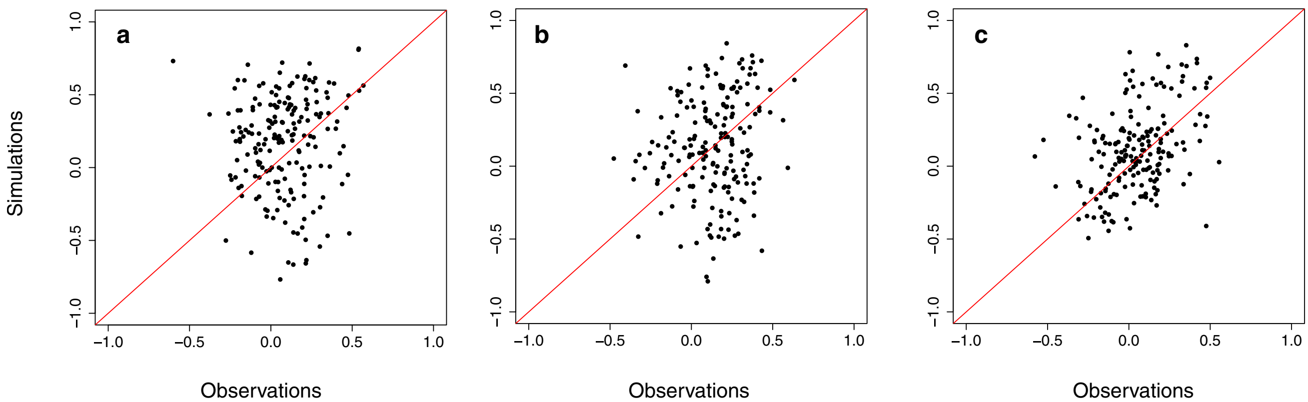


**Fig. 7** Correlations between mean annual temperature (**a**), mean July–August–September temperature (**b**), October–September cumulative precipitation, (**c**) and MAIDEN (Ge2017) Dstem simulations as a function of correlations between the same climate indicators and TRW observations for selected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

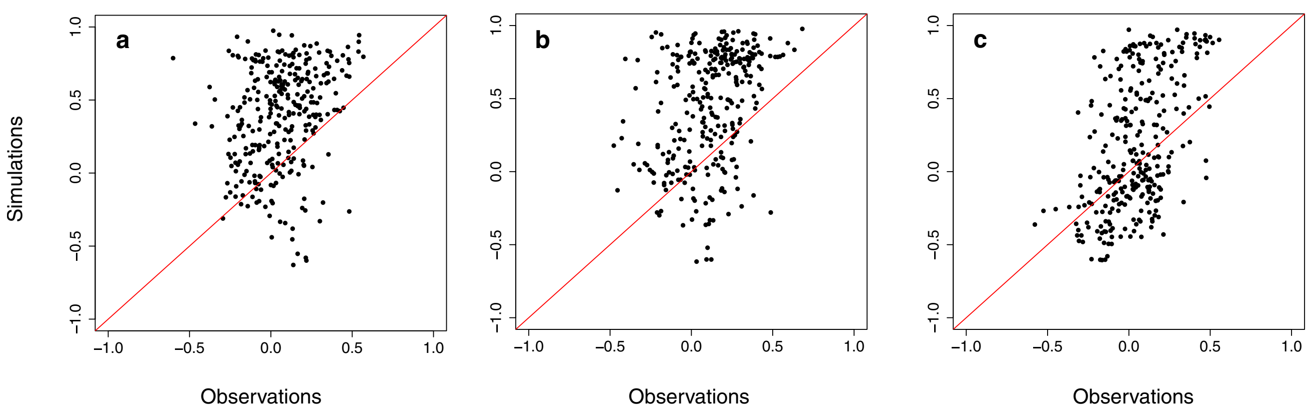


**Fig. 8** Correlations between mean annual temperature (**a**), mean July–August–September temperature (middle), October–September cumulative precipitation (**b**) and VS-Lite tree-ring index simulations as a function of correlations between the same climate indicators and TRW observations for all sites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

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 (referred to as correlations of correlations in Table 2) are generally low (ranging from 0.053 to 0.515), particularly for temperature, even if mostly significant. 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

**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)

| 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* |

*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)

0.772 for VS-Lite) and precipitation (0.747 for MAIDEN and 0.886 for VS-Lite).

### 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.

## 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 reconstructions based on data assimilation.

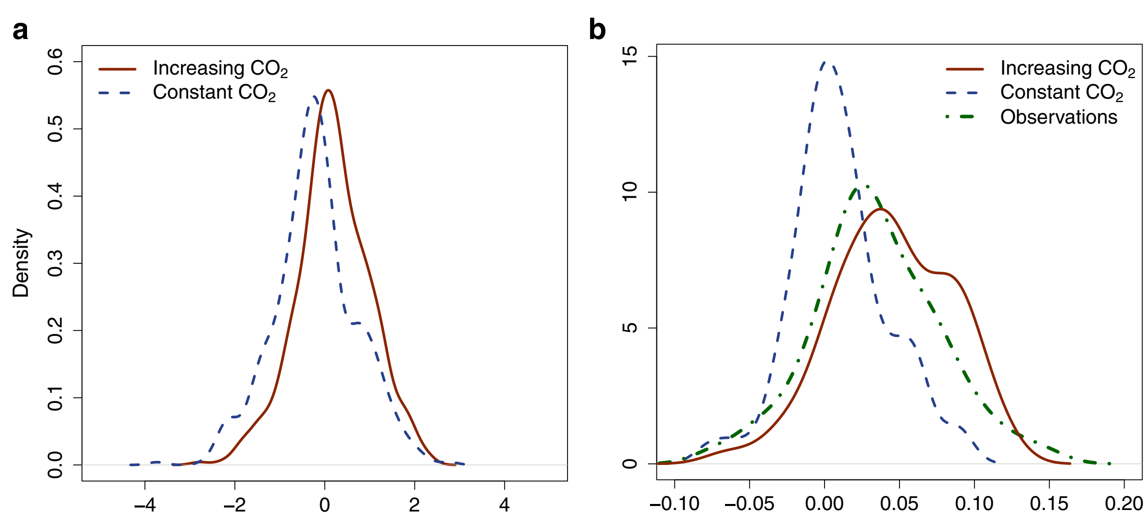


**Fig. 9** Density distributions of (**a**) the difference between normalized tree-ring index simulations by MAIDEN and observed tree-ring width from 1990 with increasing $CO_2$ concentration (red solid line, i.e. the original configuration), and constant $CO_2$ concentration (blue dashed line); (**b**)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

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 reconstructions based on data assimilation. 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 a necessary step to increase our ability to robustly reconstruct past climates from tree-rings. In particular, our study has shown that the mechanistic approach has great potential to enhance the skill of reconstructions of past climate variability from tree-rings. 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 the linear regressions classically used up to now.

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## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

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