Fusing tree-ring and forest inventory data to infer influences on tree growth

MARGARET E. K. EVANS,1,2† DONALD A. FALK,1,3 ALEXIS ARIZPE,1 TYSON L. SWETNAM,4 FLURIN BABST,5,6 AND KENT E. HOLSINGER7

1 Laboratory of Tree Ring Research, University of Arizona, Tucson, Arizona 85721 USA
2 Department of Ecology & Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 USA
3 School of Natural Resources and the Environment, University of Arizona, Tucson, Arizona 85721 USA
4 BIO5 Institute, University of Arizona, Tucson, Arizona 85719 USA
5 Dendro Sciences Group, Swiss Federal Research Institute WSL, 8903 Birmensdorf, Switzerland
6 W. Szafer Institute of Botany, Polish Academy of Sciences, 31-512 Krakow, Poland
7 Department of Ecology & Evolutionary Biology, University of Connecticut Storrs, Storrs, Connecticut 06269 USA

Citation: Evans, M. E. K., D. A. Falk, A. Arizpe, T. L. Swetnam, F. Babst, and K. E. Holsinger. 2017. Fusing tree-ring and forest inventory data to infer influences on tree growth. Ecosphere 8(7):e01889. 10.1002/ecs2.1889

Abstract. Better understanding and prediction of tree growth is important because of the many ecosystem services provided by forests and the uncertainty surrounding how forests will respond to anthropogenic climate change. With the ultimate goal of improving models of forest dynamics, here we construct a statistical model that combines complementary data sources, tree-ring and forest inventory data. A Bayesian hierarchical model was used to gain inference on the effects of many factors on tree growth—individual tree size, climate, biophysical conditions, stand-level competitive environment, tree-level canopy status, and forest management treatments—using both diameter at breast height (dbh) and tree-ring data. The model consists of two multiple regression models, one each for the two data sources, linked via a constant of proportionality between coefficients that are found in parallel in the two regressions. This model was applied to a data set of ~130 increment cores and ~500 repeat measurements of dbh at a single site in the Jemez Mountains of north-central New Mexico, USA. The tree-ring data serve as the only source of information on how annual growth responds to climate variation, whereas both data types inform non-climatic effects on growth. Inferences from the model included positive effects on growth of seasonal precipitation, wetness index, and height ratio, and negative effects of dbh, seasonal temperature, southerly aspect and radiation, and plot basal area. Climatic effects inferred by the model were confirmed by a dendroclimatic analysis. Combining the two data sources substantially reduced uncertainty about non-climate fixed effects on radial increments. This demonstrates that forest inventory data measured on many trees, combined with tree-ring data developed for a small number of trees, can be used to quantify and parse multiple influences on absolute tree growth. We highlight the kinds of research questions that can be addressed by combining the high-resolution information on climate effects contained in tree rings with the rich tree- and stand-level information found in forest inventories, including projection of tree growth under future climate scenarios, carbon accounting, and investigation of management actions aimed at increasing forest resilience.

Key words: climate; competition; data assimilation; dendrochronology; forest inventory; hierarchical Bayesian model; tree growth; tree-ring data.

Received 1 June 2017; accepted 7 June 2017. Corresponding Editor: Debra P. C. Peters.
Copyright: © 2017 Evans et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
† E-mail: mekevans@email.arizona.edu
INTRODUCTION

Improved understanding and prediction of tree growth is important because of the many ecosystem services provided by forests—global climate regulation via carbon sequestration, provisioning of drinking water, flood regulation, erosion control—in addition to the habitat they provide for many species (i.e., supporting biodiversity). Climate change is expected to change the geographic distribution and composition of the forest biome, with uncertain consequences with respect to these ecosystem services (Bonan 2008, Fettig et al. 2013). For example, a matter of great scientific uncertainty is whether forests will continue to be a carbon sink, sequestering ~25% of anthropogenic carbon emissions (Freidlingstein et al. 2010, Pan 2011), or become a carbon source in the future (Kurz et al. 2008, Luo et al. 2015), as the geographic distribution of the forest biome shifts, potentially shrinking in overall area. Forests in interior western North America may be at the leading edge of this change—with documented large-scale mortality events driven by warm drought, insect outbreaks, and increasingly large and severe fires (Allen 2010, Williams et al. 2012, Falk 2013, Fettig et al. 2013, Allen et al. 2015, Millar and Stephenson 2015)—and they are predicted to be especially vulnerable to the climate change projected over the course of the 21st century. Jiang et al. (2013) projected a loss of 50% of the needle-leaf evergreen forest in the western United States. Williams (2012) projected that by the 2050s, average forest drought stress in the southwestern United States will be more severe than the most severe drought conditions of the last 1000 yr. Charney et al. (2016) projected reduced growth of up to 70% for interior western North American trees in the second half of the 21st century compared to the first half of the 20th century.

These and other projections (Rehfeldt et al. 2006, Coops and Waring 2011, Notaro et al. 2012) derive from a diversity of data sources and/or modeling approaches, including dynamic vegetation models, tree-ring data, species distribution models, and physiological models, each of which has some inherent limitations (McMahon et al. 2011, Bellard et al. 2012, Bowman et al. 2013, Friend 2014). None of these previous studies combine different data sources together, or combine modeling approaches. More reliable prediction and greater insight into the complex of factors that influence individual tree growth could be gained by integrating multiple sources of data, with complementary information or sampling design (Evans et al. 2016). Specifically, tree-ring and forest inventory data are two powerful and complementary data sources that can be combined to make better inference on the role of forests in the global carbon cycle and what actions managers can take to maximize the resilience of forests to climate stress (Babst et al. 2014a, 2017). Tree-ring data have annual resolution and decadal- to centennial-length records, which provides rich information on the influence of climate on tree growth.

However, sampling has traditionally been biased toward the most climate-sensitive individuals (for the purpose of reconstruction of past climates), critical information on tree size and stand characteristics is missing in the public repository of tree-ring data (the International Tree-Ring Databank; https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring), and spatial replication is relatively limited (Babst et al. 2014a). By contrast, national forest inventory programs, such as the U.S. Forest Service’s Forest Inventory and Analysis (FIA; Gillespie 1999), are spatially comprehensive and unbiased with respect to tree size, providing rich forest structure information at the tree and stand level, but in the western United States, censuses of individual tree growth (remeasurement) are conducted on average once every 10 yr, forcing one to use summary statistics of climate over a 10-yr interval when investigating climate effects. Combining these two sources of data together would allow the strengths of both data types to inform our understanding of the drivers of variation in tree growth and ultimately forest ecosystem aboveground biomass accumulation, particularly how it may be influenced by climate change.

Precedents for using tree-ring and forest inventory data in parallel or in combination were set by Biondi (1999) and Clark et al. (2007). Biondi (1999) analyzed tree-ring and diameter at breast height (dbh) remeasurement data in parallel at the Gus Pearson Research Natural Area in northern Arizona, to better understand how high-density regeneration resulting from fire suppression affected the growth of large trees. This study was
ground-breaking in terms of comparing patterns in tree-ring vs. diameter remeasurement data, but it did not attempt to combine the two together. Clark et al. (2007) laid the groundwork for formal statistical fusion of tree-ring and forest inventory data using a hidden process model, in which the two data types were treated as observations (with error) of the true, underlying (hidden) process of individual tree growth. However, their process model did not include fixed effects: Tree growth was modeled as a function of year random effects and individual random effects. Modeling tree growth as a function of year random effects and individual random effects is thus the formal statistical fusion of tree-ring and forest inventory data to infer the inferences about disturbance, forest management, climate limitations, phenology, substrate, etc., providing a setting in which a complex multiple regression model problem can be unraveled with confidence. We test hypotheses about the factors influencing individual tree growth using a multiple regression approach, with several main effects, expected nonlinearities, and potential interactions among factors, to evaluate the hypotheses that growth is influenced by tree size, competitive conditions, climate, and other factors. Further, we ask whether effects inferred from the two data types are consistent with one another, and what advantage there is to combining them.

**Methods**

**Study site**

Data were collected in the Monument Canyon Research Natural Area (RNA), in the Jemez Mountains of north-central New Mexico, USA (35.8°N, 106.6°W). The site was established as one of the earliest RNAs in the region (1935) and was thus protected from land uses such as logging or livestock grazing (Swetnam et al. 2015). Fire was excluded from the RNA and the surrounding landscape for most of the 20th century, which represents a significant deviation from the historical regime of high-frequency, low-intensity fire (Falk 2006, Falk et al. 2007). An 8 × 9 grid of 0.25-ha 50 × 50 m plots, centered 500 m apart, was established in 1999 and 2000 (described in Falk 2004, Farris et al. 2013). Fifteen of these plots were included in the present study, ranging in elevation from 2520 to 2590 m, with forest types ranging from essentially pure *Pinus ponderosa* ssp. *brachyptera* (Engelm.) Lemmon to dry mixed conifer stands. These plots vary with respect to substrate, slope, aspect (Table 1), and other variables.
Twentieth-century fire suppression led to dense regeneration, particularly on pumice-derived soils, such that a combined thinning (2006) and prescribed fire (2012) treatment was applied to restore forest structure. Our sample included three plots that experienced these treatments, one on each of the three substrate types present (tuff, pumice, and alluvium; Table 1). The site is characterized by cool winters and warm summers (mean January and July temperatures for the period 1982–2013 were −2.1° and 17.9°C, respectively), with wet winters (mean November–March total precipitation = 202 mm) and peak precipitation in July and August (mean total precipitation = 164 mm) associated with the North American monsoon (Fig. 1).

Growth increment data

At the time of plot establishment (1999 or 2000), all individuals of *P. ponderosa* >25 cm dbh were tagged and measured (>20 cm dbh threshold for all other species, including *Abies concolor* var. *concolor* (Gordon & Glend.) Lindl. ex. Hildebr., *Pinus flexilis* E. James, and *Pseudotsuga menziesii* var. *glauca* (Mayr) Franco). In a 10 x 10 m subplot, all trees (regardless of size) were tagged and measured at breast height. In February and April of 2015, a second measurement of dbh and first measurement of height (in m, by laser hypsometer) were collected from every tagged tree, capturing growth up to the end of the 2014 growth season (and not the 2015 growth season). Short increment cores were...
collected from ~10 trees per plot, randomly chosen within four size classes (0–20 cm, 20–35 cm, 35–50 cm, and 50+ cm dbh), irrespective of species identity. The choice to sample short cores rather than complete samples to pith reflected the decision to not tackle the fading record problem, as it is known in reconstructions of stand growth (Nehrbass-Ahles et al. 2014). That is, forest stand structure as it was recorded in plots in 1999 or 2000 becomes an increasingly inaccurate picture of stand structure going backward in time, until one runs the risk of attributing to climate some variation in individual tree growth actually caused by past stand structure, including the effect of either lower or higher stand density in the past. The samples were prepared following standard dendrochronological methods (mounted and sanded to achieve a smooth surface; Stokes and Smiley 1996, Speer 2010). Each tree ring was assigned to a calendar year referencing a chronology developed at Banco Bonito (Farella 2015); dating accuracy was statistically verified using the program COFECHA (Holmes 1983). Annual ring widths were then measured to the nearest μm, for the period 1950 to 2014, on a sliding stage micrometer. The majority of the data were derived from samples of P. ponderosa (87% of increment cores, 81% of dbh measurements), with limited representation of A. concolor, P. flexilis, and P. menziesii (7%, 5%, and 1% of increment cores and 10%, 4%, and 5% of dbh measurements, respectively).

Covariate data

Tree-level predictors of radial and diameter growth increments included size (BA at the time of the first dbh measurement, either 1999 or 2000) and height ratio (HR, the ratio of a given tree’s height compared to the tallest tree on the same plot in 2015). Plot-level predictors included plot BA at the time of the first dbh measurement, disturbance history (thinning and prescribed fire; Table 1), and several GIS-derived biophysical variables (substrate, slope, aspect, annual radiation, and a wetness index following Boehner et al. 2002). Plot BA was calculated by converting dbh data for each tree to BA (BA = π(dbh/2)^2). Total BA of large trees (those above the 20 cm dbh threshold for all species but P. ponderosa, above the 25 cm dbh threshold for P. ponderosa, censused in the 50 × 50 plot) was multiplied by 4 to convert to a per-hectare basis. Total BA of small trees (below species-specific size thresholds, censused in the 10 × 10 m inner plot) was multiplied by 100 to convert to a per-hectare basis. The two were summed and expressed in units of m²/ha. Plot BA ranged from 13.43 to 56.93 m²/ha among the 15 plots (Table 1). Time series data of monthly mean and maximum temperature (°C) and precipitation (mm) were derived from 4-km resolution AN81m PRISM data (January 1982–December 2013; PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu). All plots had the same climate data; that is, they all fall in the same PRISM cell. Vapor pressure deficit (VPD) data were derived from Climate Research Unit 3.21 products, as saturated minus actual vapor pressure (in hектopascals). All covariate data were centered and scaled (to a mean of zero and a standard deviation of 1.0), so that the magnitude of their effects could be compared.

Dendroclimatic analysis

We conducted a dendroclimatic analysis of the tree-ring data, to benchmark the output from the Bayesian multiple regression model (see Results: Bayesian fusion). In dendroclimatic studies, unwanted low-frequency variation in the absolute value of radial increments is traditionally removed (i.e., the long-term reduction in radial increment that results from distributing biomass over a continuously increasing stem diameter), a procedure known as detrending (Cook and Peters 1981, 1997, Cook and Briffa 1990, Speer 2010). We used two alternative cubic smoothing splines with a 50% frequency cutoff response at 30 yr vs. 60 yr (100% vs. 200% of the series length) to detrend the tree-level measurement series (function detrend, R package dplR; Bunn 2008, 2010). This retained interannual to interdecadal growth variability in the data while removing lower-frequency variation in the raw ring width measurements. A pre-whitened, site-level mean chronology was calculated from the total pool of 148 detrended series using a bi-weight robust mean (function chron {dplR}; Bunn 2008). Monthly correlation and response functions were calculated using the function dcc in the R package treeclim (Zang and Biondi 2015). The first were pairwise (univariate) Pearson’s correlations between the site-level chronology and monthly PRISM climate data.
spanning a 16-month window from the previous year’s May to the current year’s August. The second—response functions—use a principal components regression approach (Biondi and Waikul 2004, Zang and Biondi 2015) to examine drivers of tree-ring index variation while accounting for collinearity among climate variables.

**Bayesian fusion**

The hierarchical model comprised two regressions, predicting raw radial and diameter increments, respectively, constrained via a constant of proportionality between regression parameters on fixed effects common to both regressions. Motivating this design is the constant of proportionality between the two data types: Two times the radial increment is the diameter increment in a single year (setting aside sources of error in both measurements). Thus, we expect a constant of proportionality between (for example) the effect of plot-level radiation on annual radial increment vs. 10-yr diameter increment. The shared fixed effects linking the two regressions together included two tree-level variables (tree size (BA) and HR) and five plot-level variables (radiation, slope, aspect, wetness index, and plot BA; Table 2). In the following section, we detail each regression in turn and then the connection between them.

The tree-ring submodel was a multivariate normal Gaussian process model, which accounts explicitly for autocorrelation in the residuals $\varepsilon_t$ that is, lag effects in the time series of radial increments ($r_{\text{inc}}$) caused by, for example, physiological carry-over of resources that affect tree growth. Two tree-level predictors were included (according to the individual tree index $i$): tree size ($S$, BA at the time of the first dbh census) and HR (Table 2). Plot-level fixed effects were radiation, slope, aspect, wetness index, and plot BA ($rad$, $slope$, $asp$, $wet$, and $PBA$, respectively, using the plot index $j$). Because monthly mean temperature, maximum temperature, and VPD were strongly collinear (Appendix S1: Fig. S1a), and tree responses to these variables were similar (compare Fig. 2a to Appendix S1: Fig. S1b), we included monthly mean temperatures (vector $T$ with the year index $t$), along with monthly total precipitation (vector $P$), as predictors in the model. Plot random effects ($\varepsilon_{pi}$), normally distributed with a prior mean of zero and variance $\sigma_{.p}^2$ (the latter estimated from the data), were included to account for variation not captured by the plot-level fixed effects, for example, substrate that is known to vary among the plots (Table 1). Individual random effects ($\varepsilon_i$) were also included. Residual variation ($\varepsilon_{i}$) was modeled as multivariate normally distributed, with a mean of zero and variance–covariance matrix $\Sigma_{mn}$, where $m$ and $n$ refer to years, each ranging from 1 to 32; thus, $\Sigma_{mn}$ has

| Variables           | Fixed vs. random | Indexing | Scale  | Tree ring | dbh | Coupled |
|---------------------|------------------|----------|--------|-----------|-----|---------|
| Tree size (BA)      | Fixed            | Tree     | Continuous | X          | X   | 2       |
| Height ratio        | Fixed            | Tree     | Continuous | X          | X   | 2       |
| Plot BA             | Fixed            | Plot     | Continuous | X          | X   | 2       |
| Radiation           | Fixed            | Plot     | Continuous | X          | X   | 2       |
| Slope               | Fixed            | Plot     | Continuous | X          | X   | 2       |
| Aspect              | Fixed            | Plot     | Continuous | X          | X   | 2       |
| Wetness index       | Fixed            | Plot     | Continuous | X          | X   | 2       |
| Thinning + fire     | Fixed            | Plot     | Indicator  | –           | X   | –       |
| PRISM climate data  | Fixed            | Year     | Continuous | X          | –   | –       |
| Plot ID             | Random           | Plot     | Indicator  | X           | X   | –       |
| Tree ID             | Random           | Tree     | Indicator  | X           | –   | –       |
| Species ID          | Random           | Species  | Indicator  | –           | X   | –       |

**Notes:** Each variable is described as either a fixed or random effect, with respect to the sampling unit to which it applies, and as either continuous or an indicator. Tree size (BA) and plot BA, as predictors of growth increment, were measured at the time of the first census. Height ratio was based on heights exclusively measured at the time of the second census. Tree-ring and dbh columns indicate (X) which variables enter in the two submodels, respectively, and the column “coupled” indicates (with an a) those effects whose estimates were coupled to one another across the two submodels via a constant of proportionality. BA, basal area; dbh, diameter at breast height.
Fig. 2. Climate correlation function (a) and response function (b), based on a single, site-level tree-ring chronology and PRISM 4-km resolution monthly total precipitation and mean temperature time series data (1981–2014).
dimensions $32 \times 32$. The full tree-ring ($r_{inc_{ijt}}$) submodel is expressed as:

$$
r_{inc_{ijt}} = \beta_{0,r} + \beta_{s,r} S_i + \beta_{s,2,r} S_i^2 + \beta_{HR,r} HR_i + \beta_{PBA,r} PBA_j + \beta_{rad,r} rad_j + \beta_{slope,r} slope_j + \beta_{asp,r} asp_j + \beta_{wet,r} wet_j + b_p P_{ijt} + b_s P_{ij} + e_i + \epsilon_i
$$

$$
\epsilon_i \sim N(0, \sigma^2)
$$

$$
\epsilon_i \sim N(0, \sigma^2)
$$

$$
\sigma^2 \sim N(0, 1) I(0,)
$$

$$
\sigma^2 \sim N(0, 1) I(0,)
$$

$$
\epsilon_i \sim MVN(0, \Sigma)
$$

$$
\Sigma_{nn} = \begin{cases} \eta^2 e^{-\rho^2(i-j)^2}, & m \neq n \\ \eta^2 + \sigma^2 & \end{cases}
$$

$$
\sigma^2 \sim N(0, 1) I(0,)
$$

$$
\eta^2 \sim N(0, 1) I(0,)
$$

$$
\frac{1}{\rho^2} \sim N(0, 1) I(0,)
$$

where the parameter $\eta$ is within-year residual variation and the parameter $\rho$ is the rate at which covariance (among years) decays.

The diameter increment ($d_{inc_{ijkt}}$) submodel assumes a normally-distributed response, with the same tree-level and plot-level fixed and random effects as above, with the exception that thinning + prescribed fire ($thin_{fire}$) was included as a plot-level indicator variable (Table 2), there were no individual random effects, and there were species random effects (normally distributed with a prior mean of zero and variance $\sigma^2_{s}$, indicated by the index $k$). No climate predictors were included, since 4-km resolution PRISM climate data did not vary among the plots, and there was only one measurement of diameter increment per tree.

$$
d_{inc_{ijkt}} = \beta_{0,d} + \beta_{s,d} S_i + \beta_{s,2,d} S_i^2 + \beta_{HR,d} HR_i + \beta_{PBA,d} PBA_j + \beta_{rad,d} rad_j + \beta_{slope,d} slope_j + \beta_{asp,d} asp_j + \beta_{wet,d} wet_j + \beta_{thin_{fire},d} thin_{fire,j} + \epsilon_p + \epsilon_{s,k} + \epsilon
$$

$$
\epsilon_{p,j} \sim N(0, \sigma_{p,j}^2)
$$

$$
\epsilon_{s,k} \sim N(0, \sigma_{s,k}^2)
$$

$$
\epsilon \sim N(0, \sigma^2)
$$

$$
\sigma^2 \sim N(0, 1) I(0,)
$$

$$
\sigma^2_{p,j} \sim N(0, 1) I(0,)
$$

$$
\sigma^2_{s,k} \sim N(0, 1) I(0,)
$$

The two regressions were coupled via a constant of proportionality ($\alpha$) between shared fixed effects:

$$
\beta_{s,r} = \alpha \beta_{s,d}; \beta_{s,2,r} = \alpha \beta_{s,2,d}; \beta_{HR,r} = \alpha \beta_{HR,d};
$$

$$
\beta_{PBA,r} = \alpha \beta_{PBA,d}; \beta_{rad,r} = \alpha \beta_{rad,d}; \beta_{slope,r} = \alpha \beta_{slope,d};
$$

$$
\beta_{asp,r} = \alpha \beta_{asp,d}; \beta_{wet,r} = \alpha \beta_{wet,d}
$$

Prior distributions for the regression coefficients were normal with mean of zero and variance of 1.0. The prior for $\alpha$ was a positive half-normal, with a prior standard deviation of $\sqrt{2}$. The model was built and executed in R and Stan (package rstan; Gelman et al. 2015). Markov chain Monte Carlo (MCMC) simulations consisted of four chains run for 2500 iterations, with the first 1250 steps removed as burn-in. Markov chain Monte Carlo output was not thinned, leading to 5000 post-burn-in samples per model parameter, with the average effective number of samples per parameter ranging from 1913 to 3520 among alternative models (described in the following paragraph and Model comparison). Convergence among chains was evaluated using the $\hat{R}$ statistic (Gelman and Rubin 1992); for all model parameters, $0.99 > \hat{R} < 1.01$, indicating good mixing of the chains.

To make the comparison between our multiple regression model (which does not detrend radial increments) and a dendroclimatic analysis, we
first included in the Bayesian regression 24 monthly climate variables (vectors $T_i$ and $P_i$). Climate data in a 12-month window from September of the previous year to August of the current year were used to predict tree growth, because the Gaussian process model of radial increments accounts for lag effects caused by climatic conditions in years $t - 1$, $t - 2$, etc. Correlations among the 24 monthly climate variables (12 months of mean temperature and precipitation) were generally low (Appendix S1: Fig. S2a) —only 6% of pairwise Pearson’s correlations exceed an absolute value of 0.50 (excluding correlations of 1.0 on the main diagonal of the correlation matrix)—suggesting that multicollinearity should not affect model stability. Principal components analysis of the monthly climate time series data shows little clustering, with only 42.2% of the total variance explained by the first three principal component axes (Appendix S1: Fig. S2b).

We then formed a second model of reduced complexity, that is, four seasonally-aggregated climate variables, and investigated interaction effects of a priori interest. The seasonal variables were formed based on the dendroclimatic analysis, which identified climate in certain seasons as limiting tree growth (see **Results**), and the literature suggesting a general climate response of tree growth across the southwestern and interior western United States (Littell et al. 2008, Chen et al. 2010, Williams et al. 2012, Dannenberg and Wise 2016). The four seasonal variables were warm season (previous September and October plus the current April–August) mean temperature and cumulative precipitation and cool season (previous November to current March) mean temperature and cumulative precipitation. These warm season months encompass the period when drought stress is most likely to occur, whereas the cool season months are when repeated frontal storms promote deep soil infiltration, fueling early-season tree growth (Breshears et al. 2009, Williams et al. 2012). These seasonal variables are significantly correlated (Appendix S1: Fig. S2c), although below the threshold value of $|r| = 0.70$ that is commonly considered problematic (Dormann et al. 2013). To verify model stability (in the face of collinearity between seasonal climate variables), we formed a variety of simpler vs. more complex multiple regression models, as well as splitting the data in half (randomly) and running the model on each half of the data, and examined the stability of parameter estimates.

In this second model, we tested the interaction between plot BA and climate, that is, two forms of stress, competition and climate, that are expected to exacerbate one another, such that individual tree growth should be more greatly reduced by climate stress (high temperature, low precipitation) if a tree is in a high-density stand than in a low-density stand. We also tested interactions between climate and HR (i.e., tree status in the canopy, relative to neighbors) and between climate and tree size (BA at the time of the first census). Code for executing the Bayesian model plus the original data files are available in a public GitHub repository (https://github.com/kholsinger/DBH).

### Model comparison
To evaluate whether a model that combines tree-ring and dbh data together outperforms separate models, we used a leave-one-out (LOO) cross-validation procedure. The principle of LOO cross-validation is to evaluate the log-likelihood of a single data point that was not included in parameter estimation, and repeat this for each data point, yielding an estimate of overall model out-of-sample predictive accuracy. Leave-one-out log-likelihoods of the tree-ring and dbh data were compared between the model described above, in which tree-ring and dbh submodels were coupled via the constant of proportionality $\alpha$ (coupled), vs. the case where they were uncoupled from one another (i.e., separate regressions; uncoupled). Similar to Akaike’s information criterion, a lower expected log pointwise predictive density (elpd) indicates better predictive accuracy; the standard error (SE) of the difference in elpd between two models can be used to assess whether one model has demonstrably better out-of-sample predictive performance than another (Vehtari et al. 2016). This LOO comparison was made using the R package loo, which implements Pareto smoothed importance sampling and conveniently takes as input MCMC simulation draws from a Stan model (Vehtari et al. 2016).

### Reduced data scenario
The data set we developed was exceptionally rich with respect to increment cores, 129 in a
small area, in contrast to a dendroclimatic sampling effort which is usually on the order of 10–40 increment cores per site. In order to better gauge the value of combining the two data sources (tree ring and dbh remeasurement), we created a more realistic data scenario in which the number of increment cores was small relative to forest inventory (diameter remeasurement) data. We randomly sampled a single increment core from each of the 15 plots, then reran the coupled and uncoupled models (model 1 with 24 climate variables and no interaction effects), and evaluated (1) the fit of the coupled vs. uncoupled models to the data (as measured by the leave-one-out information criterion [LOOIC]) and (2) the posterior distributions of effects.

RESULTS

Dendroclimatic analysis

Detrended radial increments were negatively correlated with temperature in the preceding September–October and current year April–July, and positively correlated with precipitation in similar months (Fig. 2a), indicating that tree growth is precipitation-limited at this site. This is a typical climate signal for tree growth in the southwestern United States (Williams et al. 2012). Correlations between growth and (1) maximum temperature or (2) VPD were very similar to the correlations with mean temperature (compare Appendix S1: Fig. S1b to Fig. 2a). The response function also indicates that growth is positively sensitive to precipitation and (to a lesser degree) negatively sensitive to temperature, although these effects are not significant based on bootstrapping of a 30-yr time series (Fig. 2b).

Bayesian fusion

The Bayesian multiple regression model that included 24 monthly climate variables inferred univariate associations very similar to the dendroclimatic analysis: positive effects of precipitation and negative effects of temperature, especially at the end of the previous year’s growing season and the beginning of the current year’s growing season (compare Fig. 3a to Fig. 2a). Partial regression coefficients, which account for the effects of the other 23 climate variables and correlations with them (Fig. 3b), were similar to the dendroclimatic response function (Fig. 2b) in that they showed strong positive effects of precipitation vs. weaker effects of temperature, including both negative and positive temperature effects.

Of all the predictors in the model, including the 24 climate variables, tree size had the strongest effect on radial and diameter increments: Growth increments declined with tree size, but this slowed with increasing size (negative and positive first-order and second-order terms, respectively; Fig. 4). Height ratio (i.e., canopy status) had a positive effect on growth increments, and plot BA had a negative effect (Fig. 4). Aspect had a negative effect on growth, as did radiation, whereas the wetness index had a positive effect (Fig. 4). The effect of slope on diameter and radial increments was indistinguishable from zero. The effect of canopy removal (thinning followed by fire) on diameter increments was relatively large (the second largest effect by magnitude, after the effect of size), but the posterior distribution of this effect overlaps zero considerably. Investigation of the interaction between thinning + fire and substrate, via plot random effects, showed that growth was somewhat elevated in plots on (1) pumice and alluvium soils that experienced thinning and prescribed fire, compared to (2) thinned and burned plots on tuff soils, and (3) plots that were not thinned and burned (Fig. 5), consistent with the knowledge that Pueblo farmers in the area planted crops on pumice soils for their productivity (Gauthier et al. 2007).

Seasonally-defined precipitation effects on growth were positive and temperature effects negative. Cool- and warm-season precipitation had the strongest effects on tree growth. Warm-season temperature had a weaker but non-zero effect on growth. Cool-season temperature did not affect growth. Other main effects were as before: Size and size² had negative and positive effects, respectively, HR had a positive effect, plot BA had a negative effect, aspect and radiation had negative effects, wetness had a positive effect, and slope did not consistently affect growth (the effect of thinning + fire was not tested, since this effect proved indistinguishable from zero in the model with 24 monthly climate variables). Interaction effects between seasonal climate variables and tree size, plot BA, as well as HR, were indistinguishable from zero.
Model comparison

The difference in LOO log-likelihoods of radial increments between the coupled and uncoupled models was 0.31 (SE of 2.41), indicating that the out-of-sample predictive performance of the two models was indistinguishable with these data (model 1, with 24 climate variables and no interaction effects). The same was true with respect to the diameter increments: The difference between LOO log-likelihoods (coupled-uncoupled) was 0.11 (SE = 1.62). The predictive performance of the coupled vs. uncoupled models was also statistically indistinguishable from one another when only 15 increment cores were analyzed (rather than 129): The difference between LOO log-likelihoods (coupled-uncoupled) was 0.38 (SE = 0.65) for the radial increments (tree-ring data) and −0.15 (SE = 0.52) for the diameter increments (dbh data). Posterior distributions of climate effects (partial regression coefficients) were noticeably broader under the reduced data scenario (Fig. 3d), as expected, since only the tree-ring data inform estimates of climate effects. The same was true of non-climate fixed effects estimated from the tree-ring data, under the uncoupled model (Fig. 4b). In contrast, under the coupled model, posterior distributions of non-climate effects on radial growth were similar (mean and variance) to what was obtained using the much larger sample of increment cores (Fig. 4c).

Fig. 3. Posterior distributions of climate effects from the “uncoupled” version of the Bayesian multiple regression model. (a) Bivariate associations, calculated from partial regression coefficients and correlations between each variable and the other 23 monthly climate variables and their effects. (b) Partial regression coefficients. (c) Bivariate associations and (d) partial regression coefficients under the reduced data scenario of a single increment core randomly selected from each plot (n = 15). Note that the y-scale in panel d is larger than in panel b.
Fig. 4. Posterior distributions of non-climatic fixed effects on diameter growth (diameter at breast height [dbh])
DISCUSSION

The Bayesian hierarchical model that we present is capable of taking advantage of the strengths of two widely available and complementary data sources—tree ring and forest inventory—to estimate the influence of many factors on tree growth. That is, the model formally combines the two data sources and accommodates the complexity of individual tree growth, including influences at multiple scales (tree level and stand level) that jointly result in variation in growth among individual trees. This merging of two data sources represents a bridge across two research approaches with very different histories and insufficient crosstalk. Dendroclimatological approaches have historically focused on relative, year-to-year, site-level composite variation in tree growth, viewing the tree as an instrument to reconstruct past climate. Mensurational approaches have focused on absolute variation in forest productivity, where the tree itself, its response as an organism, and projections of its future behavior are the subject of interest. Here, we offer a model that folds the strength of tree-ring data into a mensurational context. As new uses for tree-ring data emerge, including carbon accounting (Babst et al. 2014a, b, 2017, Dye et al.

![Plot random effects](image)

Fig. 5. Posterior distributions of plot random effects, grouped according to whether the plot was thinned (2006), then burned (2012) vs. substrate (alluvium, pumice, or tuff).
2016, Klesse et al. 2016), projection of future tree growth (Chen et al. 2010, Martin-Benito et al. 2011, Williams et al. 2012, Charney et al. 2016), and projection of forest dynamics under climate scenarios (Crookston et al. 2010), it becomes increasingly important to understand the influence of climate on tree growth in the context of several other factors that also influence tree growth, such as the size of the tree, its position in the forest canopy, and the density of the stand it is found in (Foster et al. 2016, Rollinson et al. 2016, Buechling et al. 2017). In particular, these latter factors are ones that forest managers can influence, whereas they cannot influence climate itself. Thus, explicitly modeling multiple influences on absolute tree growth is critical to be able to answer global change and forest management questions, and doing so with more and higher-resolution data is better than doing so with less, lower-resolution data.

Specifically, we show how tree-ring and diameter remeasurement data can be combined to quantify and parse the effects of tree size, climate, and competition on tree growth. The most important influence on growth increments is tree size, followed by a negative effect of plot BA and positive effect of HR, as well as a suite of effects consistent with precipitation-limited tree growth—negative effects of radiation, aspect, and average temperature, combined with positive effects of a wetness index and cumulative precipitation (Figs. 3, 4). The fact that tree size had the strongest effect on radial and diameter growth increments (see also Michaletz et al. 2014, Foster et al. 2016) is, all else being equal, driven by geometry. Given a certain amount of photosynthate (biomass) produced by a tree, with increasing BA each year, the new biomass is spread out over a larger and larger circumference. The result is a negative effect of BA on radial and diameter increments, weakening with increasing size (negative and positive first-order and second-order terms, respectively; Fig. 4). It should be noted, however, that while tree growth in the radial or diameter dimension declines with tree size, tree-level, absolute aboveground woody biomass increment is known to increase with tree size (Stephenson 2014, Foster et al. 2016). With respect to managing a forest for carbon sequestration, the implication is that large trees are the most valuable trees on the landscape and, at the same time, that the single most important characteristic of trees governing their rate of carbon sequestration is one that managers cannot change in a short time frame—they cannot make trees large, though they can remove smaller trees. Large trees not only accumulate more biomass than small trees, they also, by virtue of their longevity, delay the return of carbon back to the atmosphere (Korner 2017). We caution, however, that physiological limitations (Darcy’s Law; McDowell and Allen 2015) imply that with warming temperatures, these same large, old trees are likely to be the most vulnerable to drought stress.

Climatic influences on growth detected by the Bayesian multiple regression model were very similar to results from a dendroclimatic analysis, in terms of tree response and its seasonality, increasing our confidence in the Bayesian model output (Fig. 2a vs. Fig. 3a). We note, however, that the error bars in Fig. 2a are not directly comparable to error bars in Fig. 3a, because the former were created by bootstrapping a 30-yr time series of climate data with respect to a single site-level chronology (Zang and Biondi 2015), whereas the latter indicate Bayesian credible intervals of fixed effects in a multiple regression model (which includes factors not in the dendroclimatic analysis: non-climatic fixed effects, plot random effects, etc.). The results from these two approaches were also broadly similar with respect to analyses that take into account correlations between climate variables (Figs. 2b, 3b), although they differ in details, which is not surprising given that they are derived from different methods (principal components regression of detrended data vs. a hierarchical multiple regression of raw growth increments).

The estimated effect of thinning followed by prescribed fire on diameter increments was positive and large—a posterior mean of 0.291 (see horizontal line, Fig. 4a). But this effect was not distinguishable from zero (standard deviation of 0.217), either because of parameter uncertainty or because of process variability (or both). Our ability to detect any effect of canopy removal on diameter increments was compromised by the fact that the treatments (thinning in 2006, prescribed fire in 2012) occurred part-way through the diameter remeasurement interval (starting in either year 1999 or 2000 and ending in year
2014); thus, only a fraction of the observed diameter increment in a given tree reflects this treatment. Process variability might arise with respect to the effect of prescribed fire, since individual trees can have either a positive or negative response to fire: positive if they are not damaged by fire and fire removes competitors, but negative (at least in the short term) if fire does incur significant damage.

Interaction effects between individual tree size and seasonal climate variables were not significant. Keeping in mind that our sampling design targeted trees above a fairly large size threshold (>25 cm dbh for Pinus ponderosa), we still might have expected the largest trees in our sample to be more negatively impacted by climate stress than smaller (but still moderately-sized) trees (McDowell and Allen 2015, Rollinson et al. 2016), but we did not detect such an effect. The empirical literature on interactions between size and climate effects is mixed, with some studies showing significant interaction effects and others not (Chhin et al. 2008, Carnwath et al. 2012, NehrBass-Ahles et al. 2014). We also would have expected competition and climate stress to interact. Existing literature suggests that thinning can mitigate drought stress (Laurent et al. 2003, Klos et al. 2009, Martin-Benito et al. 2011, D’Amato et al. 2013, Magrunder et al. 2013, Sanchez-Salgueo 2015, Rollinson et al. 2016). Even without a statistically-detectable interaction effect, reducing one negative effect (stand density) would increase carbon capture of remaining trees, increasing their vigor and presumably their potential resilience to other forms of stress. We see a need for further investigation of climate sensitivity across tree sizes and stand conditions.

Estimates of effects from the tree-ring data vs. dbh data were consistent with one another, even based on the uncoupled model, in which the parallel fixed effects ($\beta_{s, r}$ vs. $\beta_{s, d}$, $\beta_{HR, r}$ vs. $\beta_{HR, d}$) were free to differ (Fig. 4a). That is, the two data sources do not tell different stories about effects on tree growth. Our sampling of increment cores did not follow standard dendroclimatological practices that target large, isolated trees. It is reassuring that when sampling is targeted at the same statistical population, that is, all trees above a minimum size threshold, the two data sources agree with respect to the sign and magnitude of influences on radial (diameter) increments. Biondi (1999) reported larger growth increments inferred from diameter remeasurement data compared to increment cores, particularly for smaller trees; we see no evidence of such a pattern.

Tree rings are arguably the better data source, because of their annual resolution and temporal depth, but they are relatively expensive to develop, especially in places where false rings and missing rings make cross-dating an essential part of sample processing (3.3% of rings were missing in our data set, and false ring formation was strongly prevalent). This makes the idea of combining the two data sources appealing, that is, few tree-ring data with more forest inventory data. In particular, at a single site and with only one diameter remeasurement interval, increment cores are the only source of information on how climate variation influences tree growth, and their annual resolution is powerful. With respect to non-climatic effects, model comparison showed no advantage to fusing the two data types together in terms of fit to the data (the LOOIC), either when a very large sample of increment cores was used ($n = 129$) or when a much reduced sample size was used ($n = 15$ increment cores). However, there was a clear advantage to the combined use of the two data sets (i.e., the coupled model) in terms of uncertainty about the effects that could be estimated from both data sets (size, plot BA, HR, radiation, topographic wetness index), when there were few increment cores and many dbh remeasurements. Estimates of these effects from the tree-ring data overlapped zero when the uncoupled model was used on a reduced tree-ring data set (Fig. 4b), but when the estimates of effects from the two data sources were coupled to one another, the posterior distributions of non-climatic effects were forced to resemble one another (tree-ring vs. dbh data, Fig. 4c); thus, the coupled model was able to borrow strength from the rich dbh data, and substantially reduce uncertainty about those effects (Fig. 4c compared to 4b). In other words, there is strength in numbers. More data are better: It reduces uncertainty about effects. The performance of our Bayesian fusion model under a data scenario where strength can be borrowed across tree-ring vs. forest inventory data with respect to climate effects is a target of further investigation, that is, whether the annual resolution of tree-ring data leads to different estimates of climate effects.
compared to the 10-yr resolution of inventory data (see Rohner et al. 2016).

Tree-ring data have traditionally been detrended (or standardized; Cook and Peters 1981, 1997; Cook and Briffa 1990) to remove low-frequency variation in radial increments caused by changing tree size. It has long been recognized that this practice removes low-frequency variation regardless of the cause (Fritts 1976: 267–268, Cook et al. 1995, Biondi 1999, Sullivan et al. 2016), be it the increasing size of the tree or long-term trends in temperature, atmospheric carbon dioxide concentration, or other factors (e.g., stand dynamics). Here, we offer an alternative approach to modeling tree-ring data, noting that it depends on knowledge of the absolute size of the tree (e.g., when the increment core was collected) and preferably information on other factors as well. Explicitly and jointly modeling the effects of tree size, climate, stand conditions, and other factors represents an emerging methodological alternative to the traditional practice of detrending, one that is attractive in the context of research questions focused on absolute rather than relative growth. A small number of recent papers have analyzed tree-ring data (not in combination with diameter remeasurement data) in terms of absolute growth with a multiple regression approach, rather than standardizing the data (Foster et al. 2016, Rollinson et al. 2016, Buechling et al. 2017).

We note that in our analysis, we treated tree size and proxies for competition (plot BA, HR) as invariant, when in fact we know that they evolve over time. We found sensible, significant (non-zero) effects of these predictors, because we chose to analyze relatively short time series of growth increment data (32 yr). To better take advantage of the long time series provided by tree-ring data, it will be necessary to treat tree size and stand conditions as dynamic. The former problem (changing tree size) is easy to solve within the modeling framework we present, especially if a pith date is known (the same is true for the hidden process model of Clark et al. 2007). The second problem, sometimes referred to as the “ghost of competition past” or the “fading record,” is more challenging. A possible solution is the marriage of a model of stand dynamics (e.g., the Forest Vegetation Simulator; Crookston and Dixon 2005) with a model of individual tree growth, to properly account for both tree-level and stand-level influences on tree growth across decades of forest development (M. Itter, personal communication). That would require forest inventory data on stand conditions of greater temporal depth than are available at the Monument Canyon RNA (but are available at a variety of other forest sites, e.g., Gus Pearson RNA, Harvard Forest, and Hubbard Brook and Penobscot Experimental Forests).

Combining tree-ring and forest plot data together to explicitly model drivers of absolute tree growth in a multiple regression context has great potential to improve models of forest dynamics, including projections of future forest carbon sequestration and investigation of forest management actions that might increase the resistance or resilience of forests to climate stress. At a single, small-scale site, as in our case, tree-ring data may serve as the only source of information on how monthly to seasonal climate variation influences tree growth, and blending that information with other sources has great value. At the other end of the spectrum, new tree-ring data networks, such as the U.S. Forest Service’s Interior West-FIA network (DeRose et al. 2016), will enable global change questions to be addressed with the combination of tree-ring and forest inventory data at a much larger scale. Such nationally-coordinated efforts can then be combined to form a global network of tree-ring and forest inventory data (Babst et al. 2017). We have only begun to scratch the surface of what can be done by bringing tree-ring data into a mensurational context—much remains to be gained by combining these two sources of information on forest change.

ACKNOWLEDGMENTS

Our thanks go to Tom and Suzanne Swetnam, David Frank, and Susan Harrelson for facilitating this research. Laura Marshall, Chris Guiterman, Ben Olimpio, Craig Allen, Park Williams, Justin DeRose, and Jeff Oliver provided data or helpful feedback. MEKE acknowledges the support of the College of Science, University of Arizona, and USDA-AFRI Grant 2016-67003-24944. FB acknowledges funding from the EU Horizon 2020 Project “BACT” (Grant 640176) and the Swiss National Science Foundation (Grant P300P2_154543). The authors declare no conflicts of interest.
Literature Cited

Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6:1–55.

Babst, F., et al. 2014a. A tree-ring perspective on the terrestrial carbon cycle. Oecologia 176:307–322.

Babst, F., O. Bouriaud, R. Alexander, V. Trouet, and D. Frank. 2014b. Towards consistent measurement of carbon accumulation: a multi-site assessment of biomass and basal area increments across Europe. Dendrochronologia 32:153–161.

Babst, F., B. Poulter, P. Bodesheim, M. D. Mahecha, and D. C. Frank. 2017. Improved tree-ring archives will support earth-system science. Nature Ecology and Evolution 1:0008. https://doi.org/10.1038/s41559-016-0008

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Cottam. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15:365–377.

Biondi, F. 1999. Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. Ecological Applications 9:216–227.

Biondi, F., and K. Waikul. 2004. DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. Computers and Geosciences 30:303–311.

Boehner, J., R. Koethe, O. Conrad, J. Gross, A. Ringeler, and T. Selige. 2002. Soil regionalisation by means of terrain analysis and process parameterisation. Pages 213–222 in E. Micheli, F. Nachtgeraele, and L. Montanarella, editors. Soil classification 2001. Research Report Number 7, EUR 20398 EN. European Soil Bureau, Luxembourg, Germany.

Bonan, G. B. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320:1444–1449.

Bowman, D. M. J. S., R. J. W. Buijenen, E. Gloor, O. L. Phillips, and L. D. Prior. 2013. Detecting trends in tree growth: not so simple. Trends in Plant Science 18:11–17.

Breshears, D. D., O. B. Myers, and F. J. Barnes. 2009. Horizontal heterogeneity in the frequency of plant-available water with woodland intercanopy-canopy vegetation patch type rivals that occurring vertically by soil depth. Ecohydrology 2:503–519.

Buechling, A., P. H. Martin, and C. D. Canham. 2017. Climate and competition effects on tree growth in Rocky Mountain forests. Journal of Ecology. https://doi.org/10.1111/1365-2745.12782

Bunn, A. G. 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26:115–124.

Bunn, A. G. 2010. Statistical and visual crossdating in R using the dplR library. Dendrochronologia 28:251–258.

Carnwath, G. C., D. W. Peterson, and C. R. Nelson. 2012. Effect of crown class and habitat type on climate–growth relationships of ponderosa pine and Douglas-fir. Forest Ecology and Management 285:44–52.

Charney, N., F. Babst, B. Poulter, S. Record, V. Trouet, B. Enquist, and M. Evans. 2016. Observed forest sensitivity to climate implies large changes in 21st century North American forest growth. Ecology Letters 19:1119–1128.

Chen, P.-Y., C. Welsh, and A. Hamann. 2010. Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. Global Change Biology 16:3374–3385.

Chhin, S., E. H. Hogg, V. J. Lieffers, and S. Huang. 2008. Potential effects of climate change on the growth of lodgepole pine across diameter size classes and ecological regions. Forest Ecology and Management 256:1692–1703.

Clark, J. S. 2005. Why environmental scientists are becoming Bayesians. Ecology Letters 8:2–14.

Clark, J. S., M. Wolosin, M. Dietze, I. Ibanez, S. LaDeau, M. Welsh, and B. Kloeppel. 2007. Tree growth inference and prediction from diameter censuses and ring widths. Ecological Applications 17:1942–1953.

Cook, E. R., and K. Briffa. 1990. Data analysis. Chapter 3 in E. R. Cook and L. A. Kairiukstis, editors. Methods of dendrochronology: applications in the environmental sciences. Springer, New York, New York, USA.

Cook, E. R., K. R. Briffa, D. M. Meko, D. A. Graybill, and G. Funkhouser. 1995. The ‘segment length curse’ in long tree-ring chronology development for paleoclimatic studies. Holocene 5:229–237.

Cook, E. R., and K. Peters. 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. Tree-Ring Bulletin 41:45–53.

Cook, E. R., and K. Peters. 1997. Calculating unbiased tree-ring indices for the study of climatic and environmental change. Holocene 7:361–370.

Coops, N. C., and R. H. Waring. 2011. Estimating the vulnerability of fifteen tree species under changing climate in Northwest North America. Ecological Modelling 222:2119–2129.
Crookston, N. L., and G. E. Dixon. 2005. The forest vegetation simulator: a review of its structure, content, and applications. Computers and Electronics in Agriculture 49:60–80.

Crookston, N. L., G. E. Rehfeldt, G. E. Dixon, and A. R. Weiskittel. 2010. Addressing climate change in the forest vegetation simulator to assess impacts on landscape forest dynamics. Forest Ecology and Management 260:1198–1211.

D’Amato, A. W., J. B. Bradford, S. Fraver, and B. J. Palik. 2013. Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. Ecological Applications 23:1735–1742.

Dannenberg, M. P., and E. K. Wise. 2016. Seasonal climate signals from multiple tree-ring metrics: a case study of *Pinus ponderosa* in the upper Columbia River basin. Journal of Geophysical Research: Biogeosciences 121:1178–1189.

DeRose, R. J., J. D. Shaw, and J. N. Long. 2016. Building the forest inventory and analysis tree-ring data set. Journal of Forestry 114: https://doi.org/10.5849/jof.15-097

Dormann, C., F. J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. García Marqués, B. Gruber, et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

Dye, A., A. B. Plotkin, D. Bishop, N. Pederson, B. Poult-er, and A. Hessl. 2016. Comparing tree-ring and permanent plot estimates of aboveground net primary production in three eastern U.S. forests. Ecosphere 7:e01454.

Evans, M. E. K., C. Merow, S. Record, S. M. McMahon, and B. J. Enquist. 2016. Towards process-based range modeling of many species. Trends in Ecology and Evolution 31:860–871.

Falk, D. A. 2004. Scaling rules for fire regimes. Dissertation. University of Arizona, Tucson, Arizona, USA.

Falk, D. A. 2006. Process-centred restoration in a fire-adapted ponderosa pine forest. Journal for Nature Conservation 14:140–151.

Falk, D. A. 2013. Are Madrean ecosystems approaching tipping points? Anticipating interactions of landscape disturbance and climate change. USDA Forest Service Proceedings RMRS-P-67. Pages 40–47 in G. J. Gottfried, P. F. Frolliott, B. S. Gebow, L. G. Eskew, and L. C. Collins, editors. Merging science and management in a rapidly changing world: biodiversity and management of the Madrean Archipelago III and 7th Conference on Research and Resource Management in the Southwestern Deserts, 2012 May 1–5, Tucson, Arizona, USA. Proceedings. RMRS-P-67. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Falk, D. A., C. Miller, D. M. McKenzie, and A. E. Black. 2007. Cross-scale analysis of fire regimes. Ecosystems 10:809–823.

Farella, J. 2015. *Terminus ante quem* constraint of Pueblo occupation periods in the Jemez Province, New Mexico. Thesis. University of Arizona, Tucson, Arizona, USA.

Farris, C. A., C. H. Baisan, D. A. Falk, M. L. Van Horne, P. Z. Fulé, and T. W. Swetnam. 2013. A comparison of targeted and systematic fire-scar sampling for estimating historical fire frequency in south-western ponderosa pine forests. International Journal of Wildland Fire 22:1021–1033.

Fettig, C. J., M. L. Reid, B. J. Bentz, S. Sevanto, D. L. Spittlehouse, and T. Wang. 2013. Changing climates, changing forests: a western North American perspective. Journal of Forestry 111:214–228.

Foster, J. R., A. O. Finley, A. W. D’Amato, J. B. Bradford, and S. Banerjee. 2016. Predicting tree biomass growth in the temperate-boreal ecotone: Is tree size, age, competition, or climate response most important? Global Change Biology 22:2138–2151.

Freifeldstein, P., R. A. Houghton, G. Marland, J. Hacket, T. A. Boden, T. J. Conway, J. G. Canadell, M. R. Raupach, P. Ciais, and C. Le Quéré. 2010. Update on CO₂ emissions. Nature Geoscience 3:811–812.

Friend, A. D., et al. 2014. Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO₂. Proceedings of the National Academy of Sciences of the United States of America 111:3280–3285.

Fritts, H. C. 1976. Tree rings and climate. Academic Press, Cambridge, Massachusetts, USA.

Gauthier, R. O. R. Y., R. Powers, C. Herhahn, M. Bremer, and F. Goff. 2007. Dry farming El Cajete Pumice: Pueblo farming strategies in the Jemez Mountains, New Mexico. Pages 469–474 in New Mexico geological society guidebook. 58th Field Conference, Geology of the Jemez Mountains Region II. New Mexico Geological Society, Socorro, New Mexico, USA.

Gelman, A., D. Lee, and J. Guo. 2015. Stan: a probabilistic programming language for Bayesian inference and optimization. Journal of Educational and Behavioral Statistics 40:530–543.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–511.

Gillespie, A. J. R. 1999. Rationale for a national annual forest inventory program. Journal of Forestry 97:16–20.
Holmes, R. L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43:69–78.

Jiang, X., S. A. Rauscher, T. D. Ringler, D. M. Lawrence, A. P. Williams, C. D. Allen, A. L. Steiner, D. M. Cai, and N. G. McDowell. 2013. Projected future changes in vegetation in western North America in the twenty-first century. Journal of Climate 26:3671–3687.

Kelley, S., K. A. Kempter, F. Goff, M. Rampey, B. Osburn, and C. A. Ferguson. 2003. Geologic map of the Jemez Springs 7.5-minute quadrangle. New Mexico Bureau of Geology. http://geoinfo.nmt.edu/statemap

Klesse, S., S. Etzold, and D. Frank. 2016. Integrating tree-ring and inventory-based measurements of above-ground biomass growth: research opportunities and carbon cycle consequences from a large snow breakage event in the Swiss Alps. European Journal of Forest Research 135:297–311.

Klos, R. J., G. G. Wang, W. L. Bauerle, and J. R. Rieck. 2009. Drought impact on forest growth and mortality in the southeast USA: an analysis using forest health and monitoring data. Ecological Applications 19:699–708.

Korner, C. 2017. A matter of tree longevity. Science 355:130–131.

Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452:987–990.

Laurent, M., N. Antoine, and G. Joël. 2003. Effects of different thinning intensities on drought response in Norway spruce. Forest Ecology and Management 183:47–60.

Littell, J. S., D. L. Peterson, and M. Tjoelker. 2008. Douglas-fir growth in mountain ecosystems: Water limits tree growth from stand to region. Ecological Monographs 78:349–368.

Luo, Y., T. F. Keenan, and M. Smith. 2015. Predictability of the terrestrial carbon cycle. Global Change Biology 21:1737–1751.

Magruder, M., S. Chhin, B. Palík, and J. B. Bradford. 2013. Thinning increases climate resilience of red pine. Canadian Journal of Forest Research 43:878–889.

Martin-Benito, D., V. Kint, M. del Rio, B. Muys, and I. Canellas. 2011. Growth responses of West-Mediterranean Pinus nigra to climate change are modulated by competition and productivity: past trends and future perspectives. Forest Ecology and Management 262:1030–1040.

McDowell, N. G., and C. Allen. 2015. Darcy’s Law predicts widespread forest mortality under climate warming. Nature Climate Change. https://doi.org/10.1038/NCLIMATE2641

McMahom, S. M., S. P. Harrison, W. S. Armbruster, P. J. Bartlein, C. M. Beale, M. E. Edwards, J. Kattge, G. Midgley, X. Morin, and I. C. Prentice. 2011. Improving assessment and modeling of climate change impacts on global terrestrial biodiversity. Trends in Ecology and Evolution 26:249–259.

Michaletz, S. T., D. Cheng, A. J. Kerkoff, and B. J. Enquist. 2014. Convergence of terrestrial plant production across global climate gradients. Nature 512:39–52.

Millar, C. I., and N. L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. Science 349:823–826.

Nehrbass-Ahles, C., F. Babst, S. Klesse, M. Nötzel, O. Bouriaud, R. Neukom, M. Dobbertin, and D. Frank. 2014. The influence of sampling design on tree-ring-based quantification of forest growth. Global Change Biology 20:2867–2885.

Notaro, M., A. Mauss, and J. W. Williams. 2012. Projected vegetation changes for the American Southwest: combined dynamic modeling and bioclimatic-envelope approach. Ecological Applications 22:1365–1388.

Paine, C. E. T., T. R. Matthews, D. R. Vogt, D. Purves, M. Rees, A. Hector, and L. A. Turnbull. 2011. How to fit nonlinear plant growth models and calculate growth rates: an update for ecologists. Methods in Ecology and Evolution 3:245–256.

Pan, Y., et al. 2011. A large and persistent carbon sink in the world’s forests. Science 333:988–993.

Rehfeldt, G. E., N. L. Crookston, M. V. Warwell, and J. S. Evans. 2006. Empirical analysis of plant–climate relationships for the western United States. International Journal of Plant Sciences 167:1123–1150.

Rohner, B., P. Weber, and E. Thürig. 2016. Bridging tree rings and forest inventories: how climate effects on spruce and beech growth aggregate over time. Forest Ecology and Management 360:159–169.

Rollinson, C. R., M. W. Kaye, and C. D. Canham. 2016. Interspecific variation in growth responses to climate and competition of five eastern tree species. Ecology 97:1003–1011.

Sanchez-Salgueiro, R., et al. 2015. Disentangling the effects of competition and climate on individual tree growth: a retrospective and dynamic approach in Scots pine. Forest Ecology and Management 358:12–25.

Speer, J. H. 2010. Fundamentals of tree-ring research. University of Arizona Press, Tucson, Arizona, USA.

Stephenson, N. L., et al. 2014. Rate of tree carbon accumulation increases continuously with tree size. Nature 507:90–93.
Stokes, M. A., and T. L. Smiley. 1996. An introduction to tree-ring dating. University of Arizona Press, Tucson, Arizona, USA.

Sullivan, P. F., R. R. Pattison, A. H. Brownlee, S. M. P. Cahoon, and T. N. Hollingsworth. 2016. Effect of tree-ring detrending method on apparent growth trends of black and white spruce in interior Alaska. Environmental Research Letters 11:114007.

Swetnam, T. L., A. M. Lynch, D. A. Falk, S. R. Yool, and D. P. Guertin. 2015. Discriminating disturbance from natural variation with LiDAR in semi-arid forests in the southwestern USA. Ecosphere 6:1–13.

Vehtari, A., A. Gelman, and J. Gabry. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Journal of Statistical Computing 27:1413.

Williams, A. P., et al. 2012. Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change 3:292–297.

Zang, C., and F. Biondi. 2015. Treeclim: an R package for the numerical calibration of proxy–climate relationships. Ecography 38:431–436.

**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1889/full