Variable effects of climate on forest growth in relation to climate extremes, disturbance, and forest dynamics

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Abstract. Changes in the frequency, duration, and severity of climate extremes are forecast to occur under global climate change. The impacts of climate extremes on forest productivity and health remain difficult to predict due to potential interactions with disturbance events and forest dynamics—changes in forest stand composition, density, size and age structure over time. Such interactions may lead to non-linear forest growth responses to climate involving thresholds and lag effects. Understanding how forest dynamics influence growth responses to climate is particularly important given stand structure and composition can be modified through management to increase forest resistance and resilience to climate change. To inform such adaptive management, we develop a hierarchical Bayesian state space model in which climate effects on tree growth are allowed to vary over time and in relation to past climate extremes, disturbance events, and forest dynamics. The model is an important step toward integrating disturbance and forest dynamics into predictions of forest growth responses to climate extremes. We apply the model to a dendrochronology data set from forest stands of varying composition, structure, and development stage in northeastern Minnesota that have experienced extreme climate years and forest tent caterpillar defoliation events. Mean forest growth was most sensitive to water balance variables representing climatic water deficit. Forest growth responses to water deficit were partitioned into responses driven by climatic threshold exceedances and interactions with insect defoliation. Forest growth was both resistant and resilient to climate extremes with the majority of forest growth responses occurring after multiple climatic threshold exceedances across seasons and years. Interactions between climate and disturbance were observed in a subset of years with insect defoliation increasing forest growth sensitivity to water availability. Forest growth was particularly sensitive to climate extremes during periods of high stem density following major regeneration events when average inter-tree competition was high. Results suggest the resistance and resilience of forest growth to climate extremes can be increased through management steps such as thinning to reduce competition during early stages of stand development and small-group selection harvests to maintain forest structures characteristic of older, mature stands.

Key words: Bayesian state space model; climate; dendrochronology; disturbance; forest dynamics; forest tent caterpillar; hierarchical models; productivity; tree rings.

Introduction

Understanding the effects of climate on forest productivity is integral to predicting the response of forest ecosystems to global climate change. Changing climatic conditions have important implications for sustainable forest management, a fundamental goal of which is to maintain healthy and productive forests in perpetuity. Projected consequences of climate change, in addition to global warming trends, include changes in the frequency, severity, and duration of extreme climate or weather events (IPCC 2013). These extreme events have the potential to profoundly alter the productivity and health of forest ecosystems (Allen et al. 2010, 2015).

The increased frequency of droughts combined with warmer temperatures in the southwestern United States, for example, is projected to lead to growth declines in dominant coniferous species and in severe cases large-scale forest mortality (Breshears et al. 2005, Williams et al. 2010). Other analyses predict similar growth declines and mortality in mixed oak and pine forests of the southeastern United States and elsewhere around the globe (Klos et al.

2009, Berdanier and Clark 2016). The impact of droughts on forest health and productivity is compounded with potential interactions between drought and other abiotic and biotic disturbances such as wildfire and forest damaging insects (Dale et al. 2001). In particular, the occurrence of droughts may facilitate increased insect populations, or insect damage may exacerbate the effects of drought leading to more severe forest mortality (McDowell et al. 2008, Anderegg et al. 2015). Forest responses to interactions between climate extremes and disturbance are expected to be complex and exhibit non-linear behavior involving lags and threshold effects (Betancourt et al. 2004, Williams et al. 2010, Macalady and Bugmann 2014).

Forest sensitivity to climate extremes has been shown to vary depending on endogenous forest stand characteristics such as stem density, age, species composition, and developmental or successional stage (Laurent et al. 2003, Klos et al. 2009, D'Amato et al. 2013). Changes in these characteristics are driven by forest dynamics (e.g., Oliver and Larson 1996), altering forest responses to climate extremes over time and space. Further, stand characteristics can be modified through forest management to increase forest resistance and resilience to changing climatic conditions in the short term and facilitate forest adaptation to climate change in the long term (Millar et al. 2007, Puettmann 2011). Effective forest management in the face of global climate change requires understanding and predicting changes in the complex interactions between climate extremes, disturbance, and forest dynamics (Dale et al. 2001). New analytical approaches capable of dealing with non-linear forest responses to climate that change over time and space are needed to inform adaptive forest management (Betancourt et al. 2004).

Tree rings are valuable data for understanding the effects of climate and disturbance on forest productivity. In particular, tree rings can be used to infer relationships between inter-annual climate variability and tree growth and to identify past extreme climate/weather and disturbance events (Cook 1987, Cook and Kairiukstis 1990, Babst et al. 2014). In the current study, we are interested in the combined effects of past climate extremes, disturbance, and forest dynamics as observed in tree rings. Our goal was to develop a statistical model that allows for inference regarding if and how disturbance and stand characteristics driven by forest dynamics modify forest growth responses to climate extremes. Following from our goal, we developed a hierarchical Bayesian state space model that allows the effects of climate variables on radial tree growth to vary over time. We hypothesized tree growth responses to climate would change over time in relation to the occurrence of climate extremes, disturbance, and variation in stand characteristics. The model was motivated by the need to identify forest conditions that promote resistance and resilience to climate extremes, which can be used to inform forest management to minimize the impact of future extreme events on forest productivity.

The hypothesis that forest growth responses to climate vary over time is not new in forest ecology. Indeed, a number of dendrochronology methods exist to estimate time-varying climate response functions, most notably, applications of the Kalman filter to tree-ring analysis (Visser 1986, Visser and Molenaar 1988, Van Deusen 1989), and moving correlation analysis (Biondi 1997, 2000, Carrer and Urbinati 2006). The Kalman filter approach, in particular, has been applied to identify changes in the effects of climate on tree growth attributable to air pollution (Innes and Cook 1989), and to interactions with forest dynamics (Van Deusen 1987). The model developed herein nests the Kalman filter within a Bayesian hierarchical state space framework with several important model properties. First, the hierarchical model structure allows for changes in climate effects over time to be explicitly modeled as a function of past disturbance and forest dynamics (assuming suitable data are available). Secondly, the model can accommodate non-linear functions to model changing climate effects through time as well as non-normal error structures. Third, the hierarchical Bayesian approach provides explicit error quantification from posterior distributions as well as tractable error propagation across model components. We applied the state space model to a dendrochronology data set from northeastern Minnesota to demonstrate its potential to identify changes in forest growth responses to climate driven by interactions between climate extremes, disturbance, and forest dynamics. The data set includes radial growth measurements from individual trees located in 35 forest stands of varying age and size structure, species composition, and development stage.

Modeling Approach

We apply two models to estimate tree growth as a function of climate. The first model moves the analytical steps involved in a dendrochronology response function analysis, the objective of which is to estimate the average effects of a set of climate variables on annual tree growth over a fixed period, into an integrated hierarchical Bayesian model allowing for explicit error propagation across steps (Schofield et al. 2016). The second model extends the first, allowing climate effects on tree growth to vary annually over the study period using a hierarchical Bayesian state space approach. Throughout, we refer to the first model as the *fixed climate effects* model, and the second model as the *variable climate effects* model. Sources of uncertainty under the fixed climate effects model include steps to detrend/standardize individual tree growth records, generate composite growth records or chronologies, and random variability in individual and composite growth records. The variable climate effects model shares the same sources of uncertainty as the fixed climate effects model with additional uncertainty associated with the evolution of climate effects through time. An overview of the fixed and variable climate effects models are included in the following two subsections. Fig. 1 provides a schematic representation of the two models. The statistical details and
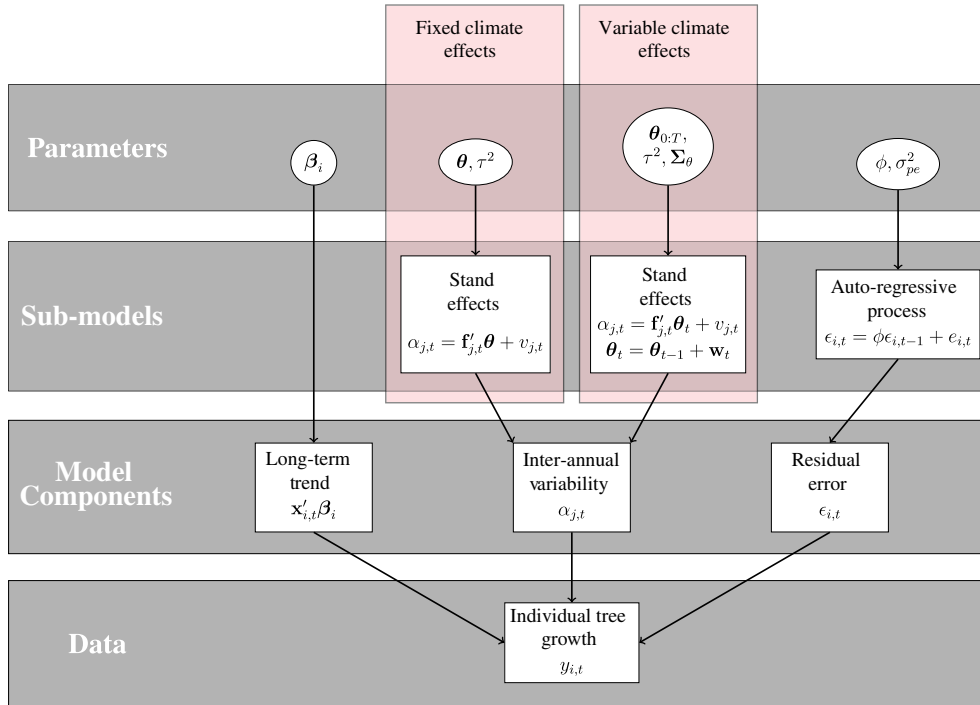
Fig. 1.   Schematic of fixed climate effects and variable climate effects in tree growth models. Note that fixed and variable climate effects sub-models are applied separately. Parameters include individual tree smoothing spline coefficients ($\boldsymbol{\beta}_i$), climate effects ($\boldsymbol{\theta}$ or $\boldsymbol{\theta}_{0:T}$), inter-annual variance (τ^2), process variance ($\boldsymbol{\Sigma}_\theta$), autocorrelation coefficient (ϕ), and pure-error variance (σ_{pe}^2). The $0{:}T$ subscript indicates all time points from 0 to T. [Colour figure can be viewed at wileyonlinelibrary.com]

discussion of Bayesian inference applied to estimate model parameters are provided in Appendix S1.

Fixed climate effects

We begin by decomposing individual tree growth measured in terms of radial growth increment (hereafter growth increment) into component sources of variability to explain the different submodels included in the fixed climate effects (FCE) model. Specifically,

$$
\begin{aligned}
\text{Individual Tree Growth} = {} & \text{Long-term Trend} \\
& + \text{Inter-annual Variablity} \\
& + \text{Random Error}
\end{aligned}
$$

where the long-term trend captures low-frequency changes in growth due to tree size and age, the inter-annual variability captures high-frequency changes in growth potentially driven by climate, and the random error term captures residual variability.

Long-term trend.—A smoothing spline is commonly applied in dendrochronology to model the long-term, low-frequency trend in individual growth attributable to tree size and age (Cook and Peters 1981). Smoothing splines are a highly flexible method to model natural phenomena using a set of polynomial basis functions (Wood 2006). We apply a penalized spline regression

submodel in the FCE model to capture long-term size and age effects, although a variety of smoothing approaches can be used here (see Appendix S1 for a complete discussion).

Inter-annual variability.—High-frequency, inter-annual variability in tree growth records is frequently attributed to the effects of climate and forest dynamics (Cook 1987). We model mean inter-annual growth variability with an additive annual stand effect that represents the average deviation of each tree within a stand from the tree's long-term growth trend within a given year (i.e., the stand effect is equivalent to the mean inter-annual variability across all trees in a stand after controlling for tree size and age). The additive stand effect is modeled as a function of observed climate. We model the mean stand-level variation rather than tree-level variation because individual trees within a stand are likely to exhibit differential responses to climate variability and forest dynamics.

Random error.—The residual error is modeled using an autoregressive process to explicitly account for temporal autocorrelation in annual tree growth increments. Specifically, we apply a first order autoregressive (AR1) model for the residual error. We note the residual error can also be modeled as a function of the mean growth increment to account for heteroscedasticity. We did not choose to do so here.

Log transformation.—We model growth increments on the log scale to ensure positive growth estimates consistent with Clark et al. (2007). Log transforming growth increments results in multiplicative errors equivalent to modeling non-transformed growth increments using a negative exponential model (Schofield et al. 2016). Log transforming growth increments also reduces the heteroscedasticity frequently observed in tree-ring records.

Combining the submodels, we model annual tree growth increments in a hierarchical Bayesian model as follows. Let i index individual trees ($i = 1, \ldots, n$), j index stands ($j = 1, \ldots, k$), and t index years ($t = 1, \ldots, T$) where n, k, and T are the total number of trees, stands, and years, respectively. Let $j(i)$ indicate the stand j in which the ith tree is located (e.g., $j(i) = 3$ indicates the ith tree is located in stand 3). Finally, define y to be the observed growth increment, such that $y_{i,t}$ is the observed growth increment for tree i in year t. Individual tree growth is modeled as,

$$\underbrace{log(y_{i,t})}_{\substack{\text{log-transformed} \\ \text{growth increment}}} = \underbrace{\mathbf{x}'_{i,t}\boldsymbol{\beta}_i}_{\substack{\text{long-term} \\ \text{trend}}} + \underbrace{\alpha_{j(i),t}}_{\substack{\text{inter-annual} \\ \text{variability}}} + \underbrace{\epsilon_{i,t}}_{\substack{\text{random} \\ \text{error}}} \quad (1)$$

where $\mathbf{x}_{i,t}$ includes tree age covariates, $\boldsymbol{\beta}_i$ is a set of tree-specific regression coefficients, $\alpha_{j(i),t}$ is the additive effect of being located in stand j during year t, and $\epsilon_{i,t}$ is the residual error modeled as an AR1 process. We assume the error term is normally distributed, $\epsilon_{i,t} \sim \mathcal{N}\left(0, \sigma_{pe}^2/(1-\phi^2)\right)$, where σ_{pe}^2 is the pure error variance and ϕ is the temporal autocorrelation coefficient. Stand effects reflecting mean inter-annual growth variability across all trees in a stand are modeled using observed climate as

$$\alpha_{j,t} = \mathbf{f}'_{j,t}\boldsymbol{\theta} + v_{j,t} \quad (2)$$

where $\mathbf{f}_{j,t}$ includes observed, standardized climate covariates, $\boldsymbol{\theta}$ is a set of stand-level regression coefficients, and $v_{j,t}$ is a random error term assumed to be independent with respect to time both within and across stands, $v_{j,t} \sim \mathcal{N}\left(0, \tau^2\right)$.

Variable climate effects

The variable climate effects (VCE) model extends the FCE model to allow climate regression coefficients ($\boldsymbol{\theta}$ in Eq. 2) to vary over time. The climate regression coefficients are treated as state variables in the VCE model and evolve over time such that a unique set of climate coefficients is estimated for each year in the study period ($\boldsymbol{\theta}_1, \boldsymbol{\theta}_2, \ldots, \boldsymbol{\theta}_T$). Annual climate coefficient estimates are updated using the Kalman filter and are informed by coefficient values for the previous and subsequent years ($t - 1$, $t + 1$) and annual stand effect estimates (Appendix S1; Fig. S1). Annual climate coefficients are estimated using stand effects for a 5-yr period centered on the current year ($t - 2$ through $t + 2$). The use of a 5-yr

moving window allows for partial temporal pooling of tree growth data similar to a moving correlation analysis (Biondi 1997), and provides increased sample size to estimate annual climate effects.

The tree-level model (Eq. 1) is unchanged in the VCE model. The stand-level model (Eq. 2) is updated to integrate time-varying climate coefficients

$$\alpha_{j,t} = \mathbf{f}'_{j,t}\boldsymbol{\theta}_t + v_{j,t}. \quad (3)$$

The evolution of climate coefficients over time is modeled using a random walk

$$\boldsymbol{\theta}_t = \boldsymbol{\theta}_{t-1} + \mathbf{w}_t. \quad (4)$$

We assume both the stand effect error and random walk error terms follow normal distributions, $v_{j,t} \sim \mathcal{N}(0, \tau^2)$, and $w_t \sim \mathcal{N}(\mathbf{0}, \boldsymbol{\Sigma}_\theta)$. Eqs. (3) and (4) define a state space or dynamic linear model framework with Eq. (3) serving as the observation equation and Eq. (4) the process or state equation (West and Harrison 1997). Details on the state space modeling approach and the numerical methods used to estimate model parameters including the application of the Kalman filter are provided in Appendix S1.

Criteria for evaluating variable climate effects.—Time-varying climate coefficients can be difficult to interpret. Understanding the factors that contribute to a significant forest growth response to a climate variable in a given year is especially challenging, particularly when multiple climate variables are considered. We applied the following criteria to evaluate time-varying climate coefficients and facilitate interpretation of VCE model results. A climate variable was considered to have no effect on mean annual growth at the stand scale in a given year if the 95% credible interval for the climate variable coefficient included zero. A climate variable was considered to have a weak effect in a given year if the 95% credible interval for its coefficient did not include zero, but the climate regression model (i.e., $\mathbf{f}'_{j,t}\boldsymbol{\theta}_t$ in Eq. (3)) explained less than 25% of the variability in the 5 yrs of annual stand effects centered on the current year (i.e., annual $r^2 < 0.25$). Mean annual growth at the stand scale was considered sensitive to a climate variable in a given year if the 95% credible interval for its coefficient did not include zero, and the climate regression model explained at least 25 percent of the variability in the 5 yrs of annual stand effects centered on the current year (in the remainder we use forest growth response to describe variable by year combinations for which forest growth sensitivity was observed).

We partitioned years during which there was evidence of growth sensitivity for one or more climate variables into four categories. First, we defined climatic thresholds as the upper quantiles of observed mean annual climate variable values across stands (quantile values used varied depending on the climate variable to ensure identification of at least 1 yr with a growth response; Fig. 5). Growth sensitivity to a climate variable in a given year was

attributed to a threshold exceedance if the threshold for a variable was exceeded within the 5-yr moving window of annual stand effects used to estimate climate coefficients. Growth sensitivity to a climate variable was attributed to a persistent exceedance effect if there were continued years of growth sensitivity following the 5-yr period centered on a climatic threshold exceedance. Growth sensitivity was attributed to interactions with disturbance if years of growth sensitivity coincided with forest tent caterpillar outbreak years for known host species. Finally, growth sensitivity to a climate variable in a given year was attributed to unknown sources if it did not meet any of the previous criteria.

Data

Tree growth data

We applied the FCE and VCE models to previously published tree growth data collected in 2010 from 35 forest stands in and around Superior National Forest in northeastern Minnesota (Fig. 2; Foster et al. 2014, 2016). The current analysis differs from previous applications of the northeastern Minnesota tree growth data set in that the VCE model estimates time-varying climate coefficients based on stand-level growth to understand the effects of past forest disturbance and dynamics on growth responses to climate extremes. The study region has a continental climate defined by cold winters (mean January temperature −15°C) and short summers (mean July temperature 19°C). Mean annual precipitation is 600–800 mm with much of the total precipitation falling as snow. Stands were selected to represent the predominant forest communities in the broader geographical area based on National Forest Inventory and Analysis data from 2004 to 2008 and included a mixture of species compositions, age structures, and development stages. The study region spans the temperate-boreal forest ecotone and sampled forest types reflected this biogeographic setting ranging from common temperate forest types, such as *Acer saccharum*-dominated northern hardwood forests, to boreal forests dominated by *Pinus banksiana*, *Populus tremuloides*, and *Picea* spp. Three replicate 400-m^2 circular plots were established within each stand. Increment cores were collected at breast height (1.3 m) from all live trees with a diameter at breast height (DBH) larger than 10 cm. Increment cores were measured using a Velmex measuring stage and cross-dated according to standard dendrochronological techniques (Holmes 1983, Yamaguchi 1991). The most-recent year in which growth data was available for all study trees was 2007.
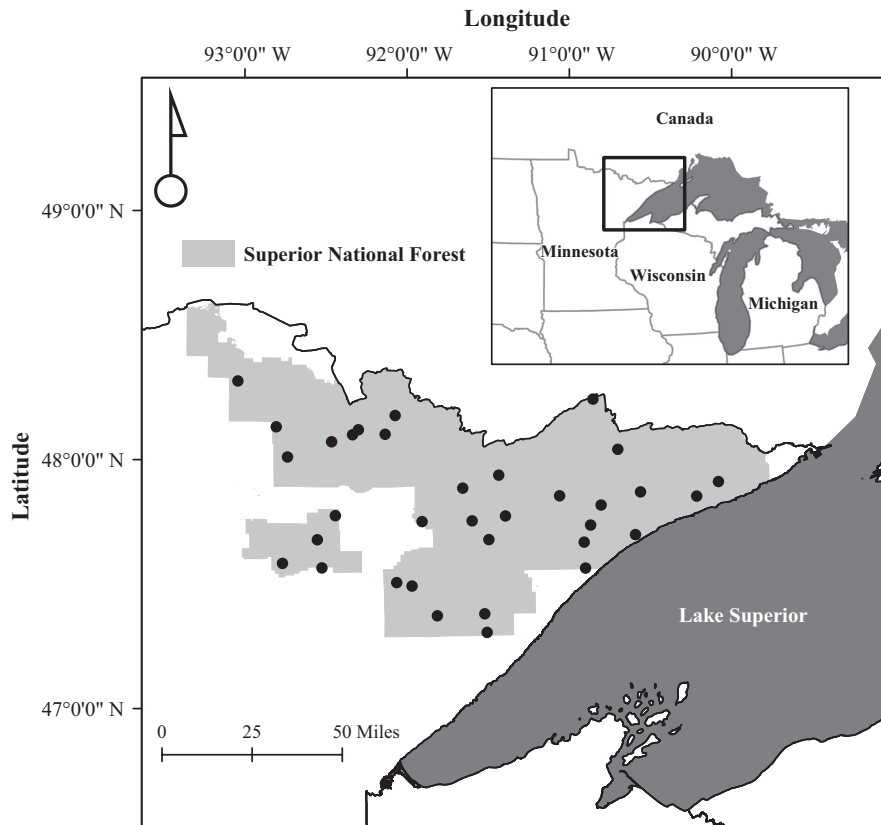

Fig. 2. Location of 105 forest plots (35 stands, 3 plots per stand; 1 mile = 1.61 km) in relation to Superior National Forest in northeastern Minnesota, USA.

TABLE 1. Summary of species sampled.

Species	Species code	No. of trees	No. of plots	First year observed	Relative basal area (%)
Abies balsamea	ABBA	365	59	1897	9 (0, 62)
Acer rubrum	ACRU	87	30	1899	3 (0, 23)
Acer saccharum	ACSA	175	16	1899	9 (0, 97)
Betula papyrifera	BEPA	273	50	1897	13 (0, 70)
Fraxinux nigra	FRNI	132	9	1897	7 (0, 97)
Larix laricina	LALA	10	6	1903	1 (0, 16)
Picea glauca	PIGL	96	30	1929	5 (0, 50)
Picea mariana	PIMA	400	36	1897	13 (0, 98)
Pinus banksiana	PIBA	383	23	1919	13 (0, 93)
Pinus resinosa	PIRE	33	9	1903	3 (0, 47)
Pinus strobus	PIST	56	15	1898	5 (0, 77)
Populus grandidentata	POGR	23	4	1927	2 (0, 33)
Populus tremuloides	POTR	93	25	1925	6 (0, 66)
Quercus rubra	QURU	118	11	1919	7 (0, 91)
Thuja occidentalis	THOC	47	12	1897	6 (0, 68)

Notes: Number of plots is the number of plots in which each species is found out of a maximum of 105 plots. First year observed is the first year in the study period a growth record exists for a tree of the corresponding species (several trees have records that date back prior to 1897). Mean percent relative basal area is the mean calculated across all study stands based on tree diameters in 2007; the minimum and maximum relative basal areas across study stands are provided in parentheses.

The DBH and species of sample trees were recorded and tree locations were mapped (relative to plot center coordinates). Tree age was estimated by defining the pith as the recruitment year and counting the number of growth rings from recruitment to present. Data suitable for climate modeling exist for 2,291 trees representing 15 unique species located across 105 forest plots (Table 1). Sampled trees are assumed to have established as a new cohort following a large disturbance event (e.g., timber harvest or fire). The year of new cohort establishment (or initiation) was set equal to the 25th percentile of the tree recruitment year distribution for each stand to account for the presence of trees from older cohorts (additional details provided in Foster et al. 2014). The start of the study period was set to 1897 to be consistent with the earliest available climate data, although the growth records for a subset of trees date back before 1897 (study period 1897–2007). As is the case with nearly all dendrochronology data sets, the number of trees and stands observed each year increases with time reflecting trees that established between the start and end of the study period (Fig. 4).

Forest tent caterpillar

The forest tent caterpillar (*Malacosoma disstria*) is an important native defoliating insect in eastern North America. There have been several forest tent caterpillar (FTC) outbreaks in the study region between 1987 and 2007. Most notably, FTC outbreaks resulted in significant defoliation of susceptible trees during the following periods: 1951–1959; 1964–1972; 1989–1995; 2000–2006 (Reinikainen et al. 2012). FTC defoliation in 2001 was particularly severe with greater than 7.5 million acres of susceptible hardwood forests in the state suffering defoliation (Albers et al. 2014). Study species that are known FTC hosts include *Acer saccharum*, *Betula papyrifera*, *Populus grandidentata*, *P. tremuloides*, and *Quercus rubra*.

Climate data

Mean monthly temperature and precipitation estimates were obtained for the study period at a 4-km resolution from PRISM (PRISM Climate Group 2013). Climate data were assigned to individual stands by intersecting plot centroids with the PRISM grid and averaging climate observations across the three stand plots if they fell within different grid cells (occurs for 3 out of 35 stands). A number of studies have shown that temperature and precipitation are poorly correlated with plant distribution and growth in comparison to water balance metrics that translate raw climate observations into variables with direct physiological relevance to plant function (Stephenson 1998, Dyer 2004, Lutz et al. 2010). We derived monthly values of potential evapotranspiration (PET), actual evapotranspiration (AET), climatic water deficit (DEF: PET-AET), and mean snow pack using a modified Thornthwaite-type water balance model (Lutz et al. 2010; see Appendix S2 for details). We calculated seasonal aggregations for each variable where relevant as detailed in Table 2 for a total of 28 climate variables.

Bayesian variable selection.—We applied the Bayesian Lasso to select a reduced set of climate variables with the greatest effect on annual tree growth (Park and Casella 2008). While not a formal model-based variable selection technique, the Bayesian Lasso shrinks the coefficient values for unimportant variables to zero in a regression model (Hooten and Hobbs 2015). We chose to apply the Bayesian Lasso given its ability to accommodate collinear variables since many of our climate variables were correlated. Additional details on the Bayesian Lasso and its implementation are provided in Appendix S1. Applying the Bayesian Lasso, the 28 climate variables were pared down to a final set of five climate variables: fall deficit (FAL-DEF), spring deficit (SPR-DEF), summer

TABLE 2. Summary of seasonal aggregations of climate variables.

Variable	Fall (Sep–Nov)$_{t-1}$	Winter (Dec–Feb)$_t$	Spring (Mar–May)$_t$	Summer (Jun–Aug)$_t$	Summer Lag (Jun–Aug)$_{t-1}$
Mean Tmin	•	•	•	•	•
Mean Tmean	•	•	•	•	•
Mean Tmax	•	•	•	•	•
Total AET	•		•	•	•
Total PET	•		•	•	•
Total DEF	•		•	•	•
Mean SNOW		•			

Notes: Bullets indicate that a seasonal aggregation is calculated for a given variable.Tmin, Tmean, Tmax indicate minimum, mean, and maximum temperature, AET and PET indicate actual and potential evapotranspiration, DEF indicates climatic water deficit (PET - AET), SNOW indicates snow pack; t, year of growth, $t-1$, year preceding growth.

deficit (SUM-DEF), summer deficit in the previous growing season (SUM-DEF-LAG), and mean annual snow pack (SNOW). All model results are restricted to this final set of climate variables. Intuitively, we expected water deficit variables to have a negative effect on tree growth. Snow pack, reflecting spring soil water recharge given the parametrization of the water balance model (see Appendix S2), was expected to have a positive effect on tree growth, though reduced growing season length due to prolonged snow cover could negatively affect growth.

RESULTS

Fixed Climate Effects (FCE) model

Mean annual stand-level tree growth was sensitive to all five water balance variables in the model as indicated by the 95% credible intervals not overlapping with zero (Fig. 3). Specifically, the four variables representing seasonal climatic water deficit (FAL-DEF, SPR-DEF, SUM-DEF, SUM-DEF-LAG), where larger values indicate greater water deficit, were negatively related to mean annual growth at the stand level, while snow pack was positively related to mean annual growth. Climatic deficit in the fall, summer, and summer before the year of growth were most related to mean annual growth at the stand level (credible interval bounds are farthest from zero). The climate coefficient estimates in the FCE model represent the average effects of the five climate variables over the study period.

Posterior variance estimates for the FCE model are provided in Appendix S1; Table S1. Notably, the first-order autocorrelation coefficient was roughly 0.37 indicating that tree-ring records were moderately autocorrelated even after detrending. The individual-tree variance was approximately 0.29, while the inter-annual variance (capturing stand-level variability) was approximately 0.05, both on the log scale. The individual tree growth variance was roughly six times the stand-level growth variance on the log scale.

Variable climate effects (VCE) model

Estimates of annual effects for each of the five water balance variables were obtained applying the VCE
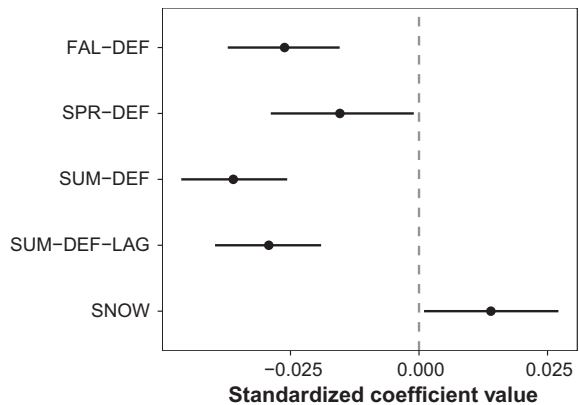

FIG. 3. Standardized coefficient values for fixed climate effects model. Points represent posterior median coefficient estimates; black lines indicate 95% credible interval bounds; a dashed gray line at a coefficient value of zero is provided for reference. Variable abbreviations are as follows: fall deficit (FAL-DEF), spring deficit (SPR-DEF), summer deficit (SUM-DEF), summer deficit in the previous growing season (SUM-DEF-LAG), and mean annual snow pack (SNOW)

model. The evolution of each variable over the study period is presented in Fig. 4. While the FCE model demonstrated that mean annual growth at the stand level was sensitive to all five water balance variables, there is evidence under the VCE model that the sensitivity of mean annual growth to each variable changed in strength and, in some cases, direction over the study period following the sensitivity criteria described in *Modeling approach: Variable climate effects* (Fig. 4). Table 3 summarizes the results shown in Fig. 4 partitioning sensitive years for each climate variable into different response categories. The most common source of growth sensitivity to any climate variable was a threshold exceedance, either during the exceedance year (~41% of all sensitive growth years) or in the years following an exceedance, i.e., a persistent response (~13% of all sensitive growth years; Figs. 4 and 5). Growth sensitivity to one or more climate variables coincided with forest tent caterpillar defoliation of host species in 20% of all sensitive growth years. There is evidence that trees driving large stand-level growth decreases (indicative of defoliation) during
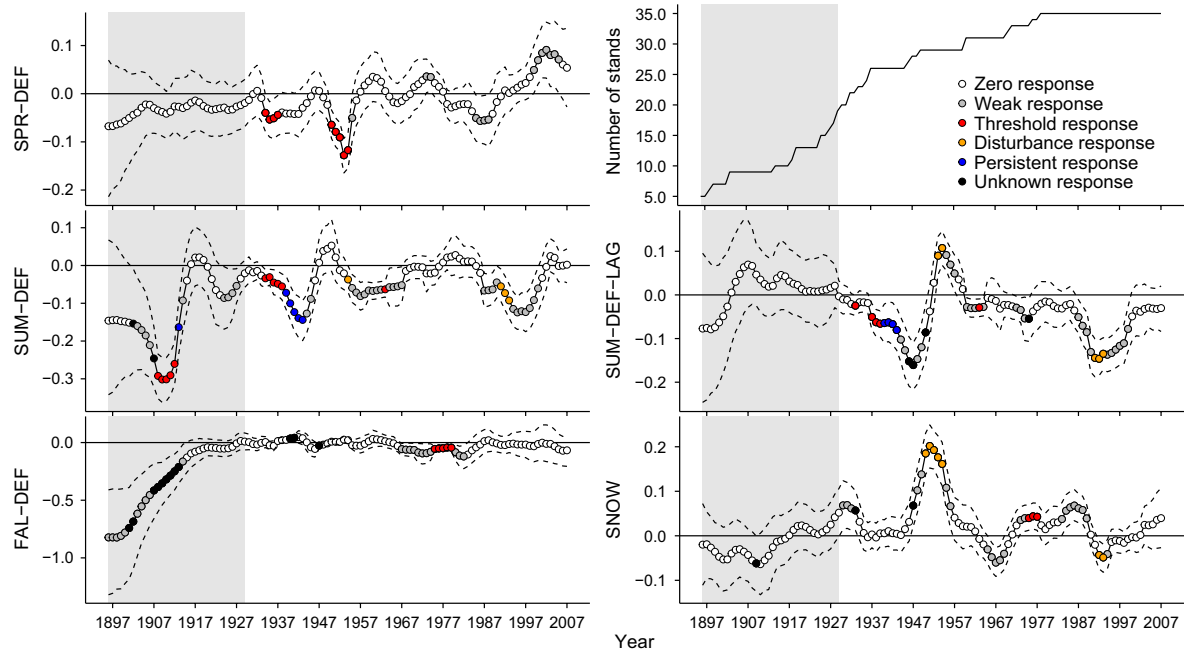
Fig. 4. Evolution of climate coefficient values for each climate variable over the study period (1897–2007). Solid black line and points indicate posterior mean coefficient values. Dashed lines delineate 95% credible intervals. Points are colored to indicate different response categories. Zero response, credible interval includes zero; weak response, credible interval does not contain zero, but annual $r^2 < 0.25$; threshold response, strong response to climate (credible interval does not contain zero and annual $r^2 \geq 0.25$) within 2 yrs of threshold exceedance; persistent response, strong response to climate in years immediately following a threshold exceedance; disturbance response, strong response to climate in years where forest tent caterpillar is present in study region; unknown response, strong response to climate not attributable to threshold exceedance, persistent response, or disturbance. The upper right panel indicates the number of study stands from which tree growth data exist in relation to the study period. The gray shading in each panel indicates the period during which tree growth data from fewer than 20 study stands are available (1897–1929). Variable abbreviations are as follows: fall deficit (FAL-DEF), spring deficit (SPR-DEF), summer deficit (SUM-DEF), summer deficit in the previous growing season (SUM-DEF-LAG), and mean annual snow pack (SNOW). [Colour figure can be viewed at wileyonlinelibrary.com]

periods of regional forest tent caterpillar defoliation and growth sensitivity to climate were forest tent caterpillar hosts (Fig. 6). Finally, growth sensitivity to one or more climate variables was due to unknown sources (i.e., could not be attributed to a climatic threshold exceedance or

forest tent caterpillar defoliation event) for roughly 26% of all sensitive growth years.

Posterior variance estimates for the VCE model are provided in Appendix S1; Table S1. The variance estimates were consistent with the FCE model, except

TABLE 3. Summary of tree growth sensitivity to climate variables (Fig. 4).

Variable	Threshold exceedance	Persistent response threshold exceedance	Disturbance	Other
SPR-DEF	1934–1937 1950–1954	NA	NA	NA
SUM-DEF	1908–1912 1934–1938 1963	1913 1939–1943	1954 1991–1993	1902 1907
SUM-DEF-LAG	1933 1937–1939 1963	1940–1943	1953–1954 1991–1993	1946–1947 1950, 1975
FAL-DEF	1975–1979	NA	NA	1901–1902 1908–1913 1940–1941 1947
SNOW	1975–1977	NA	1950–1954 1992–1993	1909, 1933 1947
Growth responses (%)	41.25	12.5	20	26.25

Notes: Variable abbreviations are as follows: fall deficit (FAL-DEF), spring deficit (SPR-DEF), summer deficit (SUM-DEF), summer deficit in the previous growing season (SUM-DEF-LAG), and mean annual snow pack (SNOW), NA, not applicable.
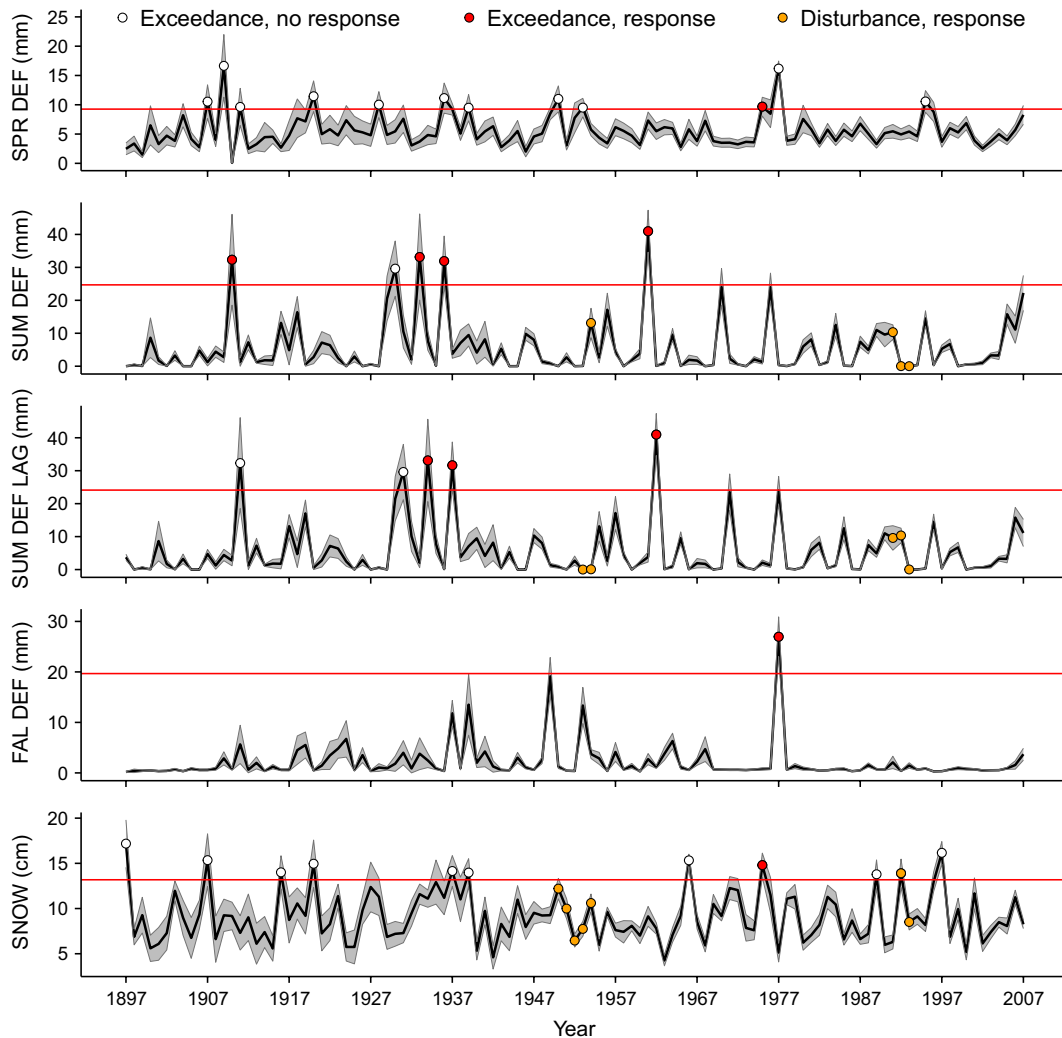
FIG. 5.   Observed climate variable values over the study period (1897–2007). Black lines indicate mean climate variable values across study stands along with uncertainty levels equal to two times the standard error (gray shading). The horizontal red line indicates the estimated climate threshold for each variable (thresholds correspond to the following quantiles: 0.95, summer deficit, lagged summer deficit; 0.98, fall deficit; 0.85, spring deficit, snow). White filled points indicate threshold exceedances with no growth response. Red filled points indicate threshold exceedances for which a growth response was observed in the 5-yr period centered on the year of exceedance. Orange filled points indicate a disturbance response. Variable abbreviations are as follows: fall deficit (FAL-DEF), spring deficit (SPR-DEF), summer deficit (SUM-DEF), summer deficit in the previous growing season (SUM-DEF-LAG), and mean annual snow pack (SNOW) [Colour figure can be viewed at wileyonlinelibrary.com]

inter-annual stand-level variance, which was slightly smaller under the VCE model (0.042 vs. 0.05). As in the FCE model, individual-tree growth variance was roughly six times the stand-level growth variance on the log scale. The large tree-level variance relative to stand-level variance in both the FCE and VCE models is consistent with previous analyses (Foster et al. 2016).

DISCUSSION

Climate change and associated extreme drought events are expected to fundamentally alter the structure and functioning of forest ecosystems across wide portions of the globe (Clark et al. 2016). The localized impacts of these

events on forest processes, such as productivity, are likely to vary as a function of tree- and stand-level characteristics including species, size, age, and density leading to differential effects across a landscape and over time. Most approaches to modeling climate effects on forest growth have focused on "average species" responses limiting our understanding of how differences in forest conditions may affect the severity of climate impacts. This study presents a modeling framework that underscores the importance of forest dynamics in predicting forest growth responses to climate extremes and disturbance, and highlights the potential for management regimes focused on manipulating stand structure and density to increase resistance and resilience to future climate change. The current analysis
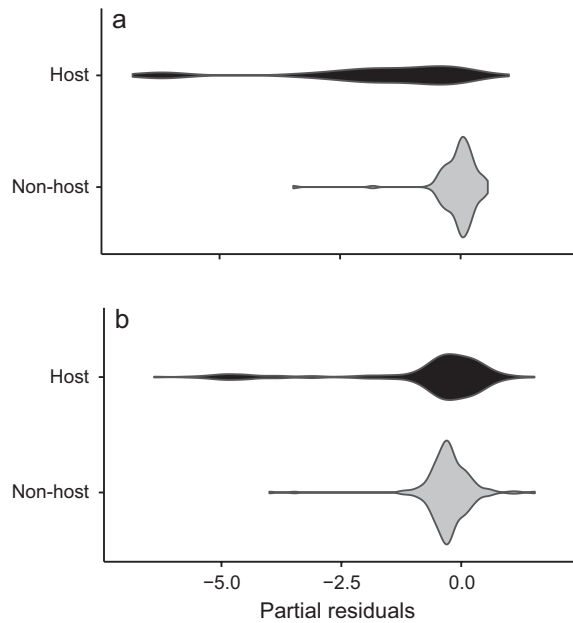
FIG. 6.　Violin plots of partial residuals (observed log annual growth increment minus spline-based estimate) for forest tent caterpillar (FTC) host and non-host individuals located in stands in the 5th percentile for growth in years (a) 1950–1954 and (b) 1991–1993. Stands in the lowest 5th percentile for growth are considered likely to have been affected by FTC. Black shading indicates FTC host trees; grey shading indicates non-FTC host trees.

focuses on the interactive effects of climate extremes, disturbance, and forest dynamics on growth in mesic forests in northeastern Minnesota. We note the modeling approach developed herein may prove even more useful for understanding forest growth responses to drought and disturbance in drier ecosystems such as in the southwestern United States. We begin this section with a discussion of the FCE and VCE model results. We then discuss the broader implications of the VCE model results to advance understanding of forest growth responses to climate extremes and potential forest management applications.

Fixed climate effects

We defined a set of 28 climate variables that may affect tree growth in northeastern Minnesota indicative of temperature, precipitation, evaporative water demand, and climatic water deficit (Table 2). The Bayesian Lasso provides an objective method to identify the subset of variables to which tree growth is most sensitive by shrinking the coefficient values of unimportant climate variables to zero (Hooten and Hobbs 2015; see Appendix S1; Fig. S2). The value of such a tool in analyses of the effects of climate on ecological processes is great and has not been previously employed in tree-ring analyses. We found water balance variables (climatic water deficit and snow pack) had the largest impact on inter-annual tree growth in northeastern Minnesota. Results indicate that tree

growth was sensitive to all five water balance variables selected by the Bayesian Lasso over the study period with climatic water deficit exhibiting negative growth effects regardless of season, and snow pack (a measure of spring soil water recharge) exhibiting positive growth effects (Fig. 3). Water availability is important in the study region where summers can be dry and soils are generally shallow and formed largely from glacial till with poor water retention. The climatic water deficit and snow pack variables reflect the interaction between temperature, precipitation, and soil water holding capacity (Appendix S2). The FCE model results indicate that tree growth in the study region was more sensitive to these interactions than to raw temperature and precipitation values (Appendix S1; Fig. S2) underscoring the importance of translating climate data into physiologically-relevant variables in studies of tree growth as noted in previous studies (Stephenson 1998).

Variable climate effects

We developed the VCE model to better understand the role of past disturbance and forest dynamics in shaping forest growth responses to climate extremes. Application of the VCE model to tree growth data from northeastern Minnesota indicates tree growth was sensitive to water balance variables in punctuated intervals of one to several years. We partitioned periods of tree growth sensitivity into four categories to identify climate extremes and elucidate potential interactions between climate extremes and past forest tent caterpillar defoliation (as defined in *Modeling approach: Variable climate effects*).

Climatic threshold exceedance.—The thresholds set for each climate variable in the model were used to identify extreme climate values (large climatic water deficits), which might lead to a forest growth response (Fig. 5). In particular, we sought to identify a threshold for each climate variable above which a forest growth response is always observed. Forest growth responses to climate variable threshold exceedances occurred in several ways. There were strong responses to singular exceedances, e.g., the observed growth response to summer deficit in 1910, a pronounced drought year in the region (Clark 1989), and the response to large fall deficit in 1977 (Figs. 4 and 5). There were also responses to an exceedance that closely followed several exceedances in a short period, e.g., the observed response to summer deficit exceedances in 1933 and 1936 following an exceedance in 1930 (Fig. 5, Table 3). Finally, there were several instances of a response to an exceedance of one climate variable when exceedances of multiple climate variables occurred coincidentally, e.g., the negative response to fall deficit in 1977 and the positive response to a large snow pack in 1975 coincided with large spring deficits in the same year (Fig. 5).

Fig. 5 demonstrates that we cannot establish a threshold for each climate variable, above which, there is a high probability of a growth response. Rather, there were a

number of threshold exceedances for each variable (except fall deficit) with no forest growth response (Fig. 5). This may be due to the study period (111 yrs) being too short to observe sufficient variability in water balance variables to establish meaningful thresholds. It also suggests the stands in the study area are relatively resistant to the effects of isolated climate extremes. As highlighted above, responses to threshold exceedances coincided with multiple exceedances in a short period or exceedances of multiple variables.

The persistent response category provides a measure of forest growth resiliency to the exceedance of a climate variable threshold. A persistent growth response indicates study stands were sensitive to a climate variable threshold exceedance for several years following the year of exceedance. There were only three persistent growth responses observed during the study period despite ten periods where study stands exhibited sensitivity to the exceedance of a climate variable threshold (Fig. 4, Table 3). Specifically, there were persistent growth responses to two large summer deficits (1910, 1936) and to lagged summer deficit in 1937. The low proportion of forest growth responses to climate variable threshold exceedances that led to a persistent response indicates that study stands are relatively resilient to climate extremes.

Forest disturbance.—Contemporary eco-physiological studies note forest growth responses to large climatic water deficits, as experienced during a drought, may be modified by biotic disturbance such as forest tent caterpillar defoliation (McDowell et al. 2008, Anderegg et al. 2015). In the northeastern Minnesota study stands, 20% of forest growth responses coincided with forest tent caterpillar defoliation within the study region (Table 3). Only one period of forest tent caterpillar defoliation coincided with a period of forest growth sensitivity to a climatic threshold exceedance: response to spring deficit from 1951 to 1954 (Fig. 4, Table 3). Instead, periods of forest growth sensitivity to one or more climate variables that coincided with forest tent caterpillar defoliation of host species in the study region occurred when climate variable values were below set thresholds suggesting defoliation within study stands increased growth sensitivity to water availability (Fig. 5).

As noted in Anderegg et al. (2015), there can be complex interactive effects of water stress and insect defoliation on forest productivity. There were two instances in which a forest growth response to a climate variable occurred in the opposite direction than expected (i.e., positive effect of climatic water deficit, negative effect of mean snow pack) during periods of forest tent caterpillar defoliation of host species: a positive response to lagged summer deficit from 1953 to 1954, and a negative response to snow pack from 1992 to 1993. The positive response to lagged summer deficit in 1953 and 1954 may have been caused by the presence of drought-weakened trees, which were subsequently killed or further weakened by caterpillar defoliation creating improved growing conditions for study

trees by reducing competition levels. The snow pack variable is indicative of spring soil water recharge; large snow pack values, however, may cause shortened growing seasons by delaying leaf flush. The negative response to snow pack in 1992 and 1993, therefore, may have been due to delayed leaf flush reducing carbon assimilation prior to forest tent caterpillar defoliation leading to poor growth years. Mean annual snow pack was particularly high in 1992 exceeding the set threshold value (Fig. 5). We categorize the growth response to snow pack in 1992 as a disturbance response, rather than a threshold response given the response coincided with forest tent caterpillar defoliation of host species in the study region and was in the opposite direction than expected.

Forest dynamics.—Stand characteristics driven by forest dynamics including age and size structure, stem density, and species composition are likely to impact forest growth responses to climate extremes. Stem density, in particular, provides a measure of inter-tree competition for light, water, nutrients, and growing space. A number of studies have demonstrated the resistance and resilience of forest growth to drought are sensitive to inter-tree competition levels as measured through stand-level basal area (a measure of stand density). Specifically, there is evidence that reducing basal area via thinning increases forest growth resistance and resilience to drought Aussenac and Granier 1988, Laurent et al. 2003, Klos et al. 2009, Martínez-Vilalta et al. 2012, D'Amato et al. 2013, Sohn et al. 2016, Bottero et al. 2017, but see Floyd et al. 2009 for counter example). The benefit of thinning, however, may last only a few years and, in some cases, can cause stands to become more sensitive to drought as they mature given an increased presence of large trees with high water demand due to large leaf area to sapwood area ratios (McDowell et al. 2006, D'Amato et al. 2013).

One goal of the current analysis was to understand the role of stand characteristics, such as density, in shaping forest growth responses to climate extremes. Unfortunately, past stand density cannot be inferred from tree rings alone, as no growth records exist from previously deceased trees (Foster et al. 2014). In the current study, we apply knowledge of the fundamental processes occurring following initiation of a new cohort of trees within a stand based on general models of stand development (Oliver and Larson 1996) to analyze the role of past dynamics on forest growth responses to climate extremes. Specifically, we considered the cumulative growth response across all climate variables for the threshold/persistent and unknown response categories as a function of mean years since initiation excluding the initial study period (1897–1929) when growth data from less than 20 study stands were available (Fig. 7). Initiation here defines a large recruitment event leading to the formation of a new cohort of trees within a study stand. There is evidence of a large increase in the number of threshold/persistent and unknown growth responses 20–45 yr following initiation, on average (Fig. 7). Study
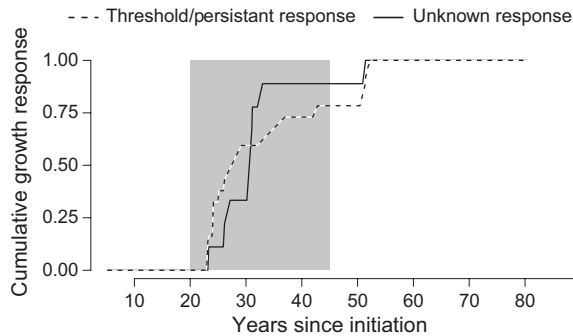
Fig. 7. Cumulative distribution of forest growth responses to all climate variables under the variable climate effects model as a function of years since initiation (initiation marks establishment a new cohort of trees within a study stand) for the threshold/persistent and unknown response categories. Note, the cumulative growth response functions exclude growth responses that occurred early in the study period when growth data from less than 20 study stands were available (1987–1929). Gray shading highlights responses 20–45 yr following initiation when understory stem density and inter-tree competition are high.

stands 20–45 yr after initiation are likely to have high stem densities corresponding to high levels of inter-tree competition and density-dependent mortality. The cumulative threshold/persistent growth response function suggests study stands are more sensitive to climate extremes (as represented by climate variable threshold exceedances) during periods of high stem density following large regeneration events when individual trees experience higher levels of competition, on average, than in older, mature stands. Over 85% of all unknown forest growth responses (i.e., responses that did not coincide with a climate variable threshold exceedance or forest tent caterpillar defoliation event) occurred within 33 yr of initiation, on average (excluding the first 33 yr of the study period), providing evidence that study stands are more sensitive to water availability when they are young (Fig. 7).

Management applications.—The results of the VCE model combined with previous studies of forest resistance and resilience to drought following thinning suggest that forest managers may be able to reduce forest sensitivity to climatic water deficit by thinning stands during periods of peak density and inter-tree competition (i.e., during the stem exclusion phase of development in even-aged stands). This period corresponds to the stage at which thinning treatments are traditionally applied to increase resource levels for residual trees and mimic density-dependent mortality. Thinning from below (removing only trees in intermediate or suppressed canopy positions) may limit the formation of large canopy crowns with high leaf area to sapwood area ratios reducing sensitivity to climatic water deficit as stands mature; further, thinning from below may minimize levels of evaporative demand at the forest floor due to the high levels of canopy cover it maintains relative to other thinning approaches. In uneven-aged stands where intermediate thinning

treatments may not be applicable, forest managers may be able to increase forest growth resistance and resilience to water deficit by minimizing forest gap sizes through individual tree or small group selection harvests that limit the amount of forest in the stem exclusion phase of development at a given time and increase the range of tree sizes and spatial diversity present in a given stand (Churchill et al. 2013). Moreover, the pronounced influence of forest tent caterpillar outbreaks and their interaction with climatic water deficit on productivity underscores the importance of maintaining mixed-species stands with a diversity of host and non-host species to minimize the impact of insect defoliation on future productivity.

The modeling approach developed here relies on the dynamic nature of forests to advance understanding of the effects of past disturbance and forest dynamics on forest growth responses to climate extremes. The model results demonstrate the importance of considering the effects of disturbance and forest dynamics on forest growth responses to climate extremes if the goal is to maintain forest productivity under changing climatic conditions. In its current form, the state space framework applies a random walk to model changes in climate variable coefficients over time, rather than modeling changes as a function of past disturbance and forest dynamics. Future work will apply the framework to data sets that provide more specific information on disturbance history and past forest dynamics allowing climate coefficients to be modeled explicitly as a function of disturbance and stand characteristics including density and stand age. In particular, the framework will be applied to data sets with sufficient sample sizes of individuals from forest tent caterpillar host vs. non-host species to explicitly model the effects of insect defoliation on forest growth responses to climate. Despite the data limitations in the current analysis, the hierarchical state space framework we have developed provides a novel method to analyze dynamic forest responses to climate extremes driven by forest disturbance and dynamics.

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