

# Climate change vulnerability of forest biodiversity: climate and competition tracking of demographic rates

JAMES S. CLARK, DAVID M. BELL, MICHELLE H. HERSH<sup>1</sup> and LAUREN NICHOLS  
*Nicholas School of the Environment, Department of Biology, and Department of Statistical Science, Duke University,  
 Durham, NC 27708, USA*

## Abstract

Forest responses to climate change will depend on demographic impacts in the context of competition. Current models used to predict species responses, termed climate envelope models (CEMs), are controversial, because (i) calibration and prediction are based on correlations in space (CIS) between species abundance and climate, rather than responses to climate change over time (COT), and (ii) they omit competition. To determine the relative importance of COT, CIS, and competition for light, we applied a longitudinal analysis of 27 000 individual trees over 6–18 years subjected to experimental and natural variation in risk factors. Sensitivities and climate and resource tracking identify which species are vulnerable to these risk factors and in what ways. Results show that responses to COT differ from those predicted based on CIS. The most important impact is the effect of spring temperature on fecundity, rather than any input variable on growth or survival. Of secondary importance is growing season moisture. Species in the genera *Pinus*, *Ulmus*, *Magnolia*, and *Fagus* are particularly vulnerable to climate variation. However, the effect of competition on growth and mortality risk exceeds the effects of climate variation in space or time for most species. Because sensitivities to COT and competition are larger than CIS, current models miss the most important effects. By directly comparing sensitivity to climate in time and space, together with competition, the approach identifies which species are sensitive to climate change and why, including the heretofore overlooked impact on fecundity.

*Keywords:* bayesian analysis, climate change, climate tracking, competition, drought, resource tracking, tree demography

*Received 6 July 2010; revised version received 1 October 2010 and accepted 18 November 2010*

## Introduction

Efforts to anticipate biodiversity loss lead to debate on which species (or how many) are vulnerable to climate change and whether or not species interactions affect responses to climate (Pearson & Dawson, 2003; Ibáñez *et al.*, 2006; Araújo & Luoto, 2007; Beale *et al.*, 2008; Merrill *et al.*, 2008; Duncan *et al.*, 2009; Mohan *et al.*, 2009). Many modeling studies predict large species losses (Erasmus *et al.*, 2002; Thomas *et al.*, 2004; Jetz *et al.*, 2007). Some experts argue that responses will depend on competition, while others maintain that geographic ranges are not influenced by species interactions (Ibáñez *et al.*, 2006; Araújo & Luoto, 2007; Suttle *et al.*, 2007; Beale *et al.*, 2008; Merrill *et al.*, 2008; Duncan *et al.*, 2009). One important but often overlooked concern relates to the fact that many models rely on spatial correlations between climate variables and species

abundance as a basis for predicting vulnerability to changes over time. This approach can suffer from the combined problems that (i) abundance is a poor indicator of climate risk, and (ii) climate correlations in space (CIS) do not necessarily reflect vulnerability to climate changes over time (COT). High population density can indeed indicate healthy conditions for a species, but low density or absence may not result from unhealthy conditions. Population abundance is controlled by many factors, and spatial patterns in abundance provide limited insight regarding vulnerability to any one (Streng *et al.*, 1989; Elliott & Baker, 2004; Ibáñez *et al.*, 2006; Yang *et al.*, 2006; Canham & Thomas, 2010). CIS are further complicated by the fact that current abundance may depend on legacies of historical climate variation and disturbance (Foster & Boose, 1992; Clark, 1996; Barber *et al.*, 2000; Lloyd & Fastie, 2000; Bellemare *et al.*, 2002; Bush *et al.*, 2008). Credible assessment of climate vulnerability requires quantifying the contributions of changes in climate over time from those that result in spatial correlation. Moreover, climate vulnerability is substantial only if impacts from climate approach those already faced by individuals on a day-to-day basis, most notably competition with neighbors. If

<sup>1</sup>Present address: Bard College, Annandale-on-Hudson, New York, 12504 and Cary Institute of Ecosystem Studies, Millbrook, NY, 12545, USA.

Correspondence: Michelle H. Hersh, tel. +1 919 613 8036, e-mail: jimclark@duke.edu

climate variables, competition, and site variables that are unmeasured interact, then a climate relationship that holds at one location cannot necessarily be extrapolated to others.

For a southeastern US example, when temperatures increase Piedmont clay soils may not support the longleaf pine forests that now dominate the coastal plain, despite the fact that longleaf pine's calibrated climate envelope moves on to the Piedmont (Prasad *et al.*, 2007). If the distribution of longleaf pine is constrained to the northwest by factors that are correlated with soil type (e.g., disturbance and performance of competitors) and to the east and south by water bodies, the climate calibration is actually a surrogate for other variables. Including other niche variables in the model cannot remedy the problem if species abundance is not actually limited by climate in the calibration set.

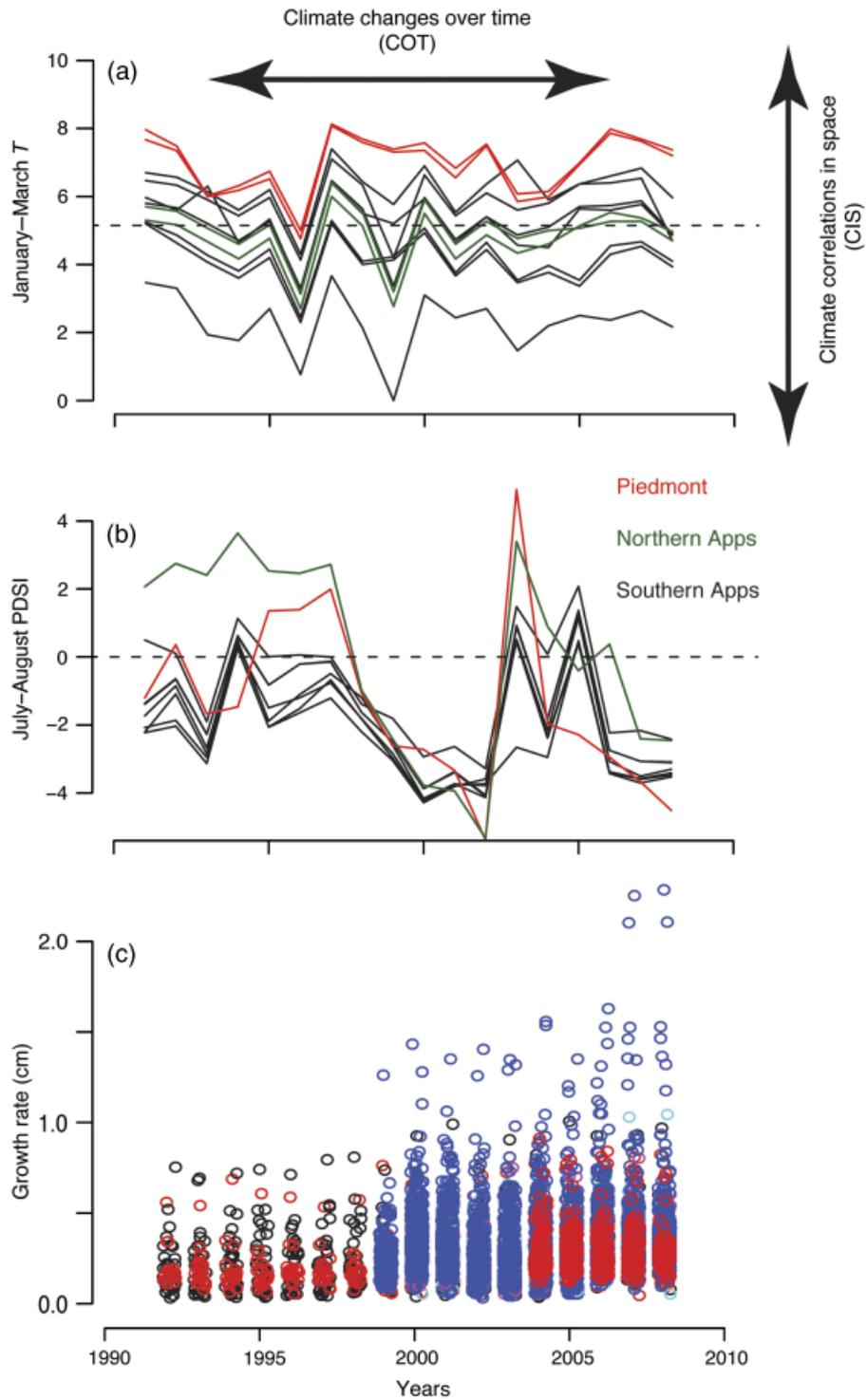
In this study, we move beyond spatial correlations of climate and species abundance to show how vulnerability to climate COT can be directly evaluated from demography, which, unlike species abundance, is closely linked to individual and population health. We present a new approach that evaluates multiple demographic responses to both climate and competition for dominant tree species in forests of the southeastern United States. A number of studies have quantified growth (McKenzie *et al.*, 2001; Lloyd & Fastie, 2002; Bunn *et al.*, 2005) or mortality (van Mantgem & Stephenson, 2007) correlations with past climate COT. Our extensive data archive of tree census data differs from previous census studies in providing annual (rather than approximately 5 years) resolution. It differs from previous historical studies by including simultaneous inference on multiple demographic states (growth, maturation, fecundity, dispersal, survival). Rather than extrapolate from spatial correlations or simulate change using parameters from the literature, we evaluate responses to risk factors on the basis of longitudinal studies of individuals that vary in their exposures to potential risk factors, individually and over time. We argue that use of spatial correlation to determine 'the equilibrium vegetation' for a hypothetical future climate (e.g.,  $2 \times \text{CO}_2$  boundary conditions in a GCM) is only a first step. The capacity to observe the impact of changing exposure to the actual risk factors, individually and in combination, addresses the scale at which the process actually occurs – the individual scale. When considering species loss, climate change is a risk factor that interacts with multiple aspects of individual health, including plant physiology and function (Breda *et al.*, 2006), vulnerability to natural enemy attack (McDowell *et al.*, 2008), competition for limited resources (Archaux & Wolters, 2006).

To evaluate the importance of climate relative to competition, our approach involves sensitivity coefficients that are comparable across response variables (demographic rates), input variables (climate and competition for light), and species, and we introduce concepts of 'climate tracking' and 'resource tracking'. Sensitivity coefficients quantify the size of the effect of climate and competition on growth, fecundity, and survival. They are specific to each explanatory-variable: response-variable pair and comparable across species. Climate tracking and resource tracking are synthetic representations of tree responses that quantify how the combination of demographic rates track explanatory variables. Together, they allow us to identify demographic responses that are tracking climate relative to the resources for which trees compete. Our perspective departs from previous approaches by addressing the limitations of spatial correlations in abundance and the need to incorporate competition. It allows us to evaluate hypotheses derived from recent meta-analysis that (i) deciduous trees response to temperature exceeds that of evergreens, and (ii) that developmental trajectories could be altered by temperature change, affecting resource allocation (Way & Oren, 2010).

The long-term longitudinal study follows individuals subjected to natural variation in climate in time and space, together with natural and experimental variation in light availability, an important resource for which trees compete (Dietze & Clark, 2008; Ibáñez *et al.*, 2008). Valuable insights have come from previous long-term demographic monitoring (e.g., Goldberg & Turner, 1986; Condit *et al.*, 2006; Angert *et al.*, 2009). We build from this approach with a design that allows quantification of both temporal and spatial variation in climate at local and regional scales in the context of experimental manipulations of competition. Response variables are multivariate demographic rates, including growth, fecundity, and survival, estimated for each of >280 000 tree-years in a study that spans 6–18 years in 11 forest stands in three regions in the southeastern United States, including 40 species and >27 000 trees (Supporting Information). A hierarchical Bayes analysis was used to quantify the contributions of competition and climate change over time (COT) synthetically with climate CIS (Clark, 2010; Clark *et al.*, 2010b).

## Materials and methods

The challenge we address is illustrated by Fig. 1. Large variation in demographic rates (Fig. 1c) results from the fact that individual responses depend not only on spatial variation in hydrology and temperature, but also on moisture and temperature COT (Fig. 1a and b) along with the local competitive environment. Analysis of COT is particularly relevant,



**Fig. 1** Climate variation between sites and over time (a, b) is calibrated against demographic variation, such as growth rates of trees (c). Raw data for each of 11 stands (Table 1) in three regions, for spring temperature (above) and summer Palmer Drought Severity (PDSI, below).  $T_s$  for site  $s$  is the mean value for each time series in the upper graph.  $T_{s,t}$  is deviation from this mean value for year  $t$ . In (c) are growth rates for four species *Pinus*, including *P. rigida* (black), *P. strobus* (red), *P. taeda* (blue), and *P. echinata* (turquoise).

because it concerns the year-to-decade scale responses observed at each location, the responses of interest for greenhouse warming. CIS is also important, but it does not directly

relate to how a species responds to COT. For example, high mortality during drought years results because it is unusually dry, not because it is dry on average. Individuals at the highest

risk from climate COT are least likely to be observed in spatial studies, because they are most rapidly culled. The effect of climate variation further depends on an individual's competitive environment (McLaughlin *et al.*, 1987; Pacala & Hurtt 1993; Prentice *et al.*, 1993; Loehle & LeBlanc 1996; Uriarte *et al.*, 2005; Canham *et al.*, 2006). Our hierarchical Bayes framework quantifies how species interactions mediate climate response while allowing for the variation associated with observations, parameters, over years, between stands, and between individuals, including light available to each tree due to shading by neighbors (Clark, 2010).

Light is the most universal limiting resource for which trees compete in temperate environments (Silvertown, 2004). In this study variation in light availability for each tree  $i$  at stand location  $s$  in each year  $t$ ,  $C_{is,t}$ , comes both from natural changes in the canopies of competing trees and from large-scale canopy manipulations, implemented in an intervention design where individuals have pre- and post-treatment growth responses (Dietze & Clark, 2008; Clark *et al.*, 2010b).  $C_{is,t}$  is the exposed canopy area (ECA-m<sup>2</sup>), the fraction of the canopy exposed to direct sunlight (Wyckoff & Clark 2005).

The analysis makes use of the fact that demographic rates reflect individual and population health. Both tree growth rates and fecundities reflect nutritional status; in fact growth rate is often used as a predictor of mortality risk (Kobe *et al.*, 1995; van Mantgem *et al.*, 2003; Wyckoff & Clark, 2005; Clark *et al.*, 2007). Demographic rates further affect population success by way of competition—rapid growth enhances light capture, a limiting resource, and high fecundity increases capture of regeneration sites. This study analyzes demographic rates (growth, fecundity, survival) synthetically, as part of a single analysis (Clark *et al.*, 2010b).

Finally, if competition and COT have a large effect on demographic rates, then responses to climate change will differ from predictions of climate envelope models (CEMs). To determine the extent to which different approaches might

agree or not, we compared results from this analysis with predictions from CEMs for the same regions. The goal of hypothesis testing is not to determine which model is 'correct'. Rather, cases where demographic rates show vulnerability and CEMs predict change support one another in the same way that clinical trials and spatial epidemiology could reveal complementary evidence for disease risk. Where demographic rates show vulnerability, and other models suggest no change, there is essentially 'disagreement', suggesting need for targeted research. In the next section we summarize the analysis.

## Demographic data

We make use of the large longitudinal data set from sites detailed in Clark *et al.* (2010b). Individual trees are tracked through time at 11 sites differing in their local climate settings (Table 1). Sample sizes are provided for all field observations in the Supporting Information. Diameter measurements of trees and ring-widths on increment cores provide primary evidence for tree growth rates. Seed traps and observations of tree maturation status are the basis for fecundity estimates, the number of seeds produced by tree  $i$  in year  $t$ . Survival status informs mortality risk. Canopy status observations from the ground and remotely sensed exposed canopy area are the basis for light estimates. The synthetic model includes data models for each of the types of observations, detailed in Clark *et al.* (2010b).

## Climate variables

We focus on two aspects of climate (i) spring temperatures  $T$ , which determine growing season length and

**Table 1** Site characteristics and summary climate variables

Vegetation	Site name*	Elevation (m)	Slope (%)	Ann Prec (mm)	$T'_s$ (°C) <sup>†</sup>	Range $T'_{s,t}$ (°C) <sup>‡</sup>	Range PDSI (dimensionless)
Pitch pine/oak	C1	780	80	194	6.26	3.10	4.73
Cove hardwood	C2	820	40	194	5.20	3.17	4.70
Mixed oak/hardwood	C3	870	50	194	5.28	3.17	4.76
Mixed oak/hardwood	C4	1110	55	200	4.10	2.90	5.38
Northern hardwood	C5	1410	60	270	2.29	3.67	5.36
Cove hardwood	CL	1030	35	200	5.86	2.97	5.31
Mixed oak	CU	1140	35	245	4.25	3.02	5.47
Mixed pine/oak	DB	170	25	121	7.05	3.13	10.30
Bottomland hardwood	DH	165	4	121	6.89	2.99	10.30
Mixed hardwood	MF	720	25	102	4.73	3.30	8.96
Mixed hardwood	MP	730	35	102	5.01	3.27	8.96
Range		1240	76	168	4.76	–	–

\*Stand names indicate C, southern North Carolina Appalachian sites at Coweeta Hydrologic Lab (35°03'N, 83°27'W); M, northern North Carolina Appalachian sites at Mars Hill (35°49'N, 82°32'W); and D, North Carolina Piedmont at Duke Forest (35°58'N, 79°5'W).

<sup>†</sup>Average spring temperature at site  $s$ .

<sup>‡</sup>Range of spring temperatures at  $s$  during the study.

span the time of late winter frost events and bud, flower, and fruit set (Houle, 1999; Masaki *et al.*, 2008; Kon & Noda, 2007) and (ii) summer drought  $P$ , which can impact carbon gain for the subsequent year's growth and reproduction, and it can directly precipitate mortality (Oberhuber *et al.*, 1986; Engelbrecht *et al.*, 2005; Wright, 2005; Breda *et al.*, 2006; Nepstad *et al.*, 2007; McDowell *et al.*, 2008; Phillips *et al.*, 2009). The temporal dimensions (COT) are, for temperature,  $T_{s,t}$ , the variation in mean January to March temperatures and, for summer drought,  $P_{s,t}$ , the mean July to August Palmer Drought Severity Index (PDSI), both at  $s = 1, \dots, 11$  sites in  $t = 1, \dots, 18$  years (Fig. 1). Mean values are taken over the last 20 years. The mean values are insensitive to the precise duration. The PDSI represents a departure from mean conditions, calculated here on the basis of the last 70 years. From temperature data we calculate the site average temperature  $T'_s$ , and express COT for temperature  $T_{s,t}$  as departures from the mean for site  $s$ . PDSI uses temperature and precipitation data to evaluate soil moisture levels, as departures from the long-term average for a site. Moderate droughts have values of  $-2$ , and extreme drought, such as experienced from 2000 to 2002 and from 2006 to 2008 in the Southeastern US, have values near  $-4$  (Fig. 1b). Thus, both variables are expressed as departures from the average at each site  $s$  and isolate variation over time  $t$ .

The spatial dimensions (CIS) are the stand- $s$  mean spring temperature  $T'_s$  and hydrologic index  $P'_{s,r}$ , respectively. The latter combines the mean annual precipitation and position-on-slope at  $s$  relative to all sites included in the analysis

$$p'_s = \frac{p'_s}{p'} / \frac{z_s}{z'}$$

where  $p'_s$  is the mean precipitation and  $z_s$  is the position on slope at  $s$ , and  $(p', z')$  are the means taken over all sites, respectively. Locations with high precipitation and situated at topographic lows have high values of  $P'_{s,r}$  and vice versa. There is a large range of both precipitation and position-on-slope across sites (Table 1, Supporting Information). Values for  $T_{s,t}$  and  $P_{s,t}$  vary among sites and years, but average zero within each site; values for  $T'_s$  and  $P'_s$  vary only between sites and not over time.

We determined relative contributions of explanatory variables (tree-scale light availability  $C_{is,t,r}$ , plot-scale temporal variation in spring temperature  $T_{s,t}$  and drought  $P_{s,t}$  (COT), and stand-scale spatial variation in temperature  $T'_s$  and hydrologic conditions  $P'_s$  (CIS)) to each of the demographic variables and to their combined response. Estimates come from an integration of data from ground observations and remote sensing (Table 1) (Clark *et al.*, 2007, 2010b).

## Demographic inference

The model assimilates demographic observations to infer variation in diameter growth ( $\text{cm yr}^{-1}$ ), fecundity (seeds  $\text{yr}^{-1}$ ), and mortality risk (annual probability) for tree  $i$  at site  $s$  and year  $t$ . All parameters and latent states are estimated together (Clark *et al.*, 2010b). There is a nonlinear, multivariate state-space model for each individual, responding to its changing diameter, lagged growth rate [an AR(1) term], light availability, climate, random-individual effects, and model error. There is observation error associated with each type of observation. The multivariate state space model includes fecundity  $f_{is,t}$  (seeds per tree) and the diameter growth increment  $d_{is,t}$  (cm) which determines change in diameter

$$D_{is,t+1} = D_{is,t} + d_{is,t},$$

where  $D_{is,t}$  is the diameter of individual  $i$  at location  $s$  in year  $t$ . The model relationship between diameter growth increment, fecundity, and covariates is

$$y_{is,t} = x_{is,t-1}A + \beta_{is} + \beta_t + \varepsilon_{is,t}, \quad (1)$$

$$\beta_{is} \sim N_2(0, V)$$

$$\varepsilon_{is,t} \sim N_2(0, \Sigma).$$

The index for  $R=2$  response variables is  $r=1, 2$ , growth and fecundity, which are contained in the row vector  $y_{is,t} = [\ln d_{is,t} \ln f_{is,t}]^T$ . The first term on the right-hand side of Eqn (1) contains  $q=1, \dots, Q$  covariates. In addition to diameter and an AR(1) term covariates in the  $1 \times Q$  vector are

$$x_{is,t-1} = [1, \ln D_{is,t-1}, \ln^2 D_{is,t-1}, \ln d_{is,t-1}, \ln C_{is,t-1}, T_{s,t-1}, P_{s,t-1}, T'_s, P'_s]. \quad (2)$$

With the exception of the last four climate-related variables, all are detailed in Clark *et al.* (2010b). The  $Q \times R$  parameter matrix  $A$  contains coefficients describing how each predictor affects proportionate change in fecundity and growth in response vector  $y_{is,t}$ . Note that predictor in year  $t-1$  affect demographic rates in year  $t$ . The elements of matrix  $A$ ,  $A_{qr}$  describe how the  $q$ th covariate influences the  $r$ th response ( $r=1$  for  $\ln$  diameter growth,  $r=2$  for  $\ln$  fecundity). Together the model accounts for the fact that growth and fecundity tend to increase with tree size, but may eventually decline, fecundity can vary from year-to-year for reasons that are not tightly coupled with climate (e.g., masting)  $\beta_t$ , individuals differ in their growth and fecundity  $\beta_{is}$  for reasons not taken up by covariates in

$x_{is,t-1}$ , and, thus, are treated as random effects. In other words, shared interannual variation that is not linked to climate appears in year effects. There is error in the process model  $\varepsilon_{is,t}$  having covariance matrix

$$\Sigma = \begin{bmatrix} \sum_{11} & \sum_{12} \\ \sum_{12} & \sum_{22} \end{bmatrix}.$$

The submodel for mortality risk exploits the fact that diameter growth rate  $d_{is,t}$  provides an indication of overall vigor and a predictor of death (Kobe *et al.*, 1995; Metcalf *et al.*, 2009; Clark *et al.*, 2010b). The parameter  $\mu_d$  is the probability of mortality associated with the tree's growth rate  $d_{is,t-1}$  in the previous year  $t-1$ . We combine this growth rate effect with potential additional influence of senescence, or physiological decline that could come with increasing diameter  $\mu_D$ , where  $D_{is,t-1}$  is the previous year's diameter. The combined mortality probability is

$$\mu_{is,t} = \mu_d + \mu_D - \mu_d \mu_D. \tag{3}$$

Modeling rationale, model structure, algorithm development, and diagnostics are detailed in Clark *et al.* (2010a, b). Computation is Metropolis-within-Gibbs, a Markov Chain Monte Carlo (MCMC) technique. Extensive sensitivity analysis and testing with in- and out-of-sample prediction as applied here is the most effective basis for model evaluation (e.g., Clark *et al.*, 2010a).

### Climate and resource tracking

Two derived quantities are used to synthesize how climate and competition variables affect responses, summarized in Table 2. The total effect of a variable  $q$  in the vector  $x_{is,t-1}$  on the multivariate response vector  $y_{is,t}$  can be summarized by how well the model predicts that variable  $x_{is,t-1(q)}$ . This 'tracking' of a variable  $q$  differs from standard indices (e.g., parameters  $A_{qr}$  or sensitivity coefficients discussed below), which describe only the effect of  $q$  on a single response variable. The tracking coefficients are synthetic and come from the model, to determine how well the model predicts an explanatory variable. Inversion of Eqn (1) involves

algebra and some general distribution theory, yielding

$$x_{is,t(q)} \sim N(\hat{x}_{is,t(q)}, Q_q^T \Sigma Q_q), \tag{4}$$

where the predictive mean is

$$\hat{x}_{is,t(q)} = (y_{is,t+1} - x_{is,t(-q)} A_{(-q)} \beta_{is} - \beta_t) Q_q,$$

$$Q_q = A_q^T (A_q A_q^T)^{-1},$$

$A_q$  is the  $q$ th row of  $A$ ,  $A_{(-q)}$  is  $A$  lacking row  $q$ , and  $x_{is,t(-q)}$  is the covariate vector lacking covariate  $q$ . This is the prediction of an input variable  $q$  for a specific tree year. There is a prediction for each individual and each year. We predict tracking coefficients for each individual and year from the integral

$$p(x_{is,t(q)} | y, x) = \int N(x_{is,t(q)} | \hat{x}_{is,t(q)}, Q_q^T \Sigma Q_q) p(\theta | y, x) d\theta,$$

where  $\theta$  is the posterior distribution for all parameters estimated in the model, and  $(y, x)$  is the set of all observations. The integral is evaluated numerically from MCMC output.

An index of climate tracking that takes account of both predictive mean and variance derives from model selection techniques, here used to determine how well the model predicts the explanatory rather than response variables. Predictive loss is a model selection criterion that rewards goodness of fit and small predictive variance (Gelfand & Ghosh, 1998). By direct analogy with predictive loss, we can combine goodness of fit and small predictive variance with the deviance criterion

$$D_q = G_q + P_q, \tag{5}$$

where the first term is goodness of fit is given by

$$G_q = \frac{1}{n} \sum_{i,s} \sum_t \sum_q (x_{is,t(q)} - \hat{x}_{is,t(q)})^2$$

for a total of  $n$  observations, and the second-term constitutes the predictive variance

$$P_q = Q_q^T \Sigma Q_q.$$

Close tracking of a covariate results in small  $G_q$ , small  $P_q$ , and thus, small  $D_q$ .

**Table 2** Variable and parameter summary

Inputs $x_{is,t}$	Responses $y_{is,t}$	Parameters	Derived parameters
Spring temperature, spatial $T_s$ Moisture, spatial $P_s$	Diameter growth $\ln d_{is,t}$	$A, \Sigma$	$\frac{dy_r}{dx'_q}$
Spring temperature, temporal $T_{s,t}$ Moisture, temporal (summer PDSI) $P_{s,t}$	Fecundity $\ln f_{is,t}$		
Light competition, spatio-temporal (exposed canopy area) $C_{is,t}$	$\mu_{is,t}$	$\mu_d, \mu_D$	$x'_q$

### Sensitivity analysis

Because growth, fecundity, and predictor variables have different dimensions and scales we place them on a common scale of proportionate responses to a dimensionless predictor variable

$$x'_q = \frac{x_q - x_q^{(\min)}}{x_q^{(\max)} - x_q^{(\min)}}$$

i.e., standardized for the range of variation for the species  $(x_q^{(\max)} - x_q^{(\min)})$ . The sensitivity index of response  $r$  (diameter growth or log fecundity) to covariate  $x'_q$  is

$$\frac{dy_r}{dx'_q} = \frac{dy_r}{dx_q} \frac{dx_q}{dx'_q} = \frac{A_{qr} - \sum_{r'} \Sigma_{r'r'}^{-1} A_{qr'}}{x_q^{(\max)} - x_q^{(\min)}}, \quad (6)$$

i.e., element  $(q, r)$  of parameter matrix  $A$ , modified by the contribution from the covariance between response  $r$  and the other response  $r'$  and standardized for the range of the predictor. Mortality risk is on a common (probability) scale for all species, so we evaluate sensitivities on this scale, again, standardized for predictor variables,

$$\frac{\partial \mu}{\partial x'_q} = (1 - \mu_D) \frac{\partial \mu}{\partial \ln d_{is,t-1}} \times \frac{\partial \ln d_{is,t-1}}{\partial x_q} \times \frac{\partial x_q}{\partial x'_q}, \quad (7)$$

$$= \frac{\partial \mu}{\partial \ln d_{is,t-1}} \times \frac{(1 - \mu_D)(A_{q1} - \Sigma_{12} \Sigma_{22}^{-1} A_{q2})}{x_q^{(\max)} - x_q^{(\min)}}.$$

The uncertainties in sensitivity estimates are represented by one standard deviation (boxes) and 95% credible intervals (whiskers) in Figs 2 and 3. The model uncertainty is contained in covariance matrix  $\Sigma$ . This matrix describes error in the state-space model of growth and fecundity over time [Eqn (1)]. The uncertainty contributed by parameter estimates is characterized by the joint posterior for the model, which is obtained by integrating over the posterior, described in detail in Clark (2010). To include both types of uncertainty we drew random parameter vectors from the joint posterior and evaluated Eqns (6) and (7).

### Distribution of data

Although rarely evaluated in calibration-prediction studies, the distribution of explanatory variables is critical (Iverson *et al.*, 2008). There must be adequate range to insure that effects can be identified, and predictor variables cannot be redundant—correlations between them cannot be excessively large. Both criteria are fulfilled here. The range of temperature both within (3.0–3.7 °C) and between (4.8 °C) stands (Supporting Information) is

relevant for scenarios of change under mid-21st Century climate change (IPCC, 2007). Owing to droughts in the 1990s and the 2000s, summer PDSI varies widely within sites, approaching the maximum range for PDSI (approximately –5 to 5, Fig. 1b). The hydrological index is calculated from sites that range over 168 cm in annual precipitation and from 4% to 80% slopes.

Correlations in predictor variables  $x$  affect the estimates of parameters  $A$ . All correlations between predictor covariates are <0.2 in absolute value (Table 3), which explains why posterior densities of  $A$  also show low correlation (detailed in Clark *et al.*, 2010b). Because sensitivity coefficients are derived from  $A$ , they too show low posterior correlation. There is AR(1) structure in Eqn (4) to accommodate serial dependence in  $y_t$ . However, the predictions of tracking variables  $x_{t(q)}$  are only weakly dependent on design structure. From Eqn (4) note that the effect of autocorrelation in  $x_q$ , for any lag  $k$  is zero

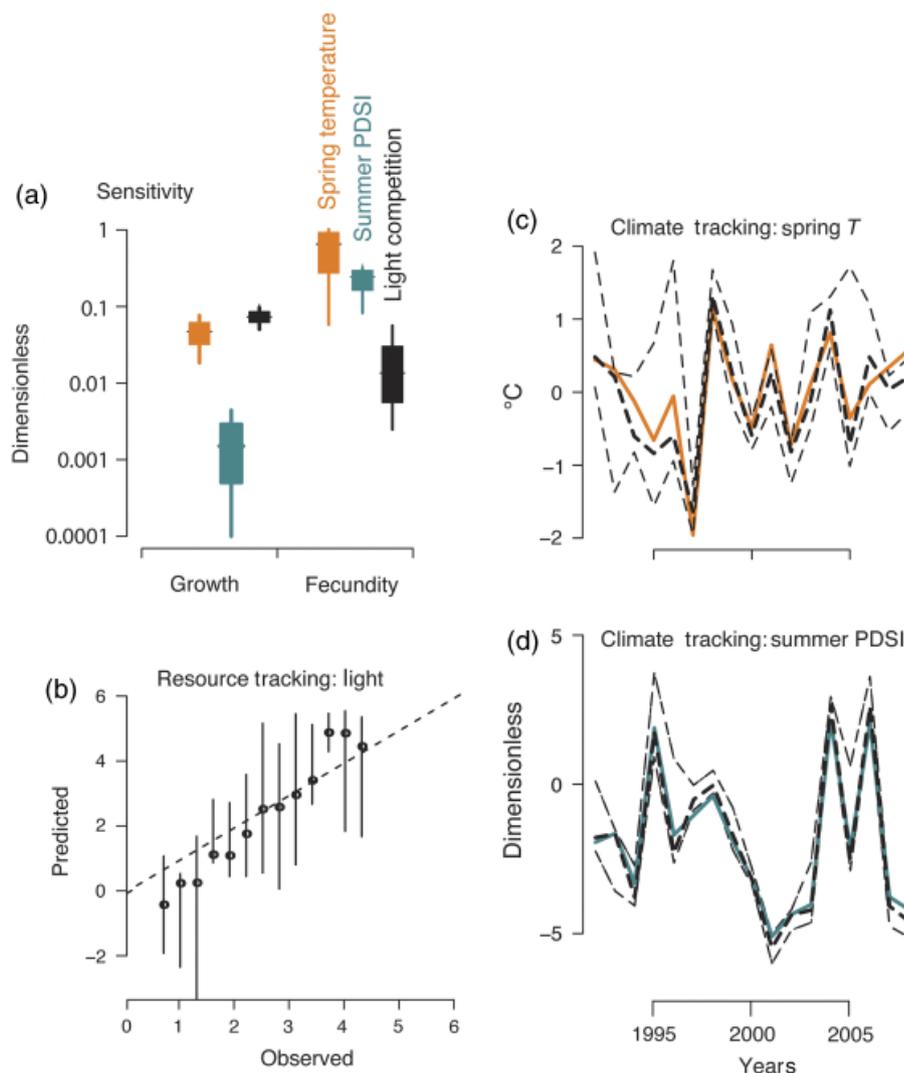
$$\frac{\partial \hat{x}_{t(q)}}{\partial x_{t-k(q)}} = 0.$$

### Comparison with CEM

To determine the extent to which approaches differ in their predictions for response to climate change, we compared results from this analysis with predictions from CEMs. Based on the USDA Forest Service's Forest Inventory and Analysis Program, CEM predictions have been developed for two emissions scenarios and three climate models: the Parallel Climate Model, the Hadley CM3 model, and the Geophysical Fluid Dynamics Laboratory model ([http://www.nrs.fs.fed.us/atlas/tree/tree\\_atlas.html](http://www.nrs.fs.fed.us/atlas/tree/tree_atlas.html)) (Iverson *et al.*, 2008). We compared the average changes for each species predicted by the three models with sensitivities determined in this study. We completed comparisons for the two National Forests closest and most similar in elevation to our study regions, one in the Piedmont (Uwharrie National Forest) and another in the Appalachian Mountains (Nantahala National Forest). These comparisons involve different assumptions and thus are complementary in their implications.

### Results

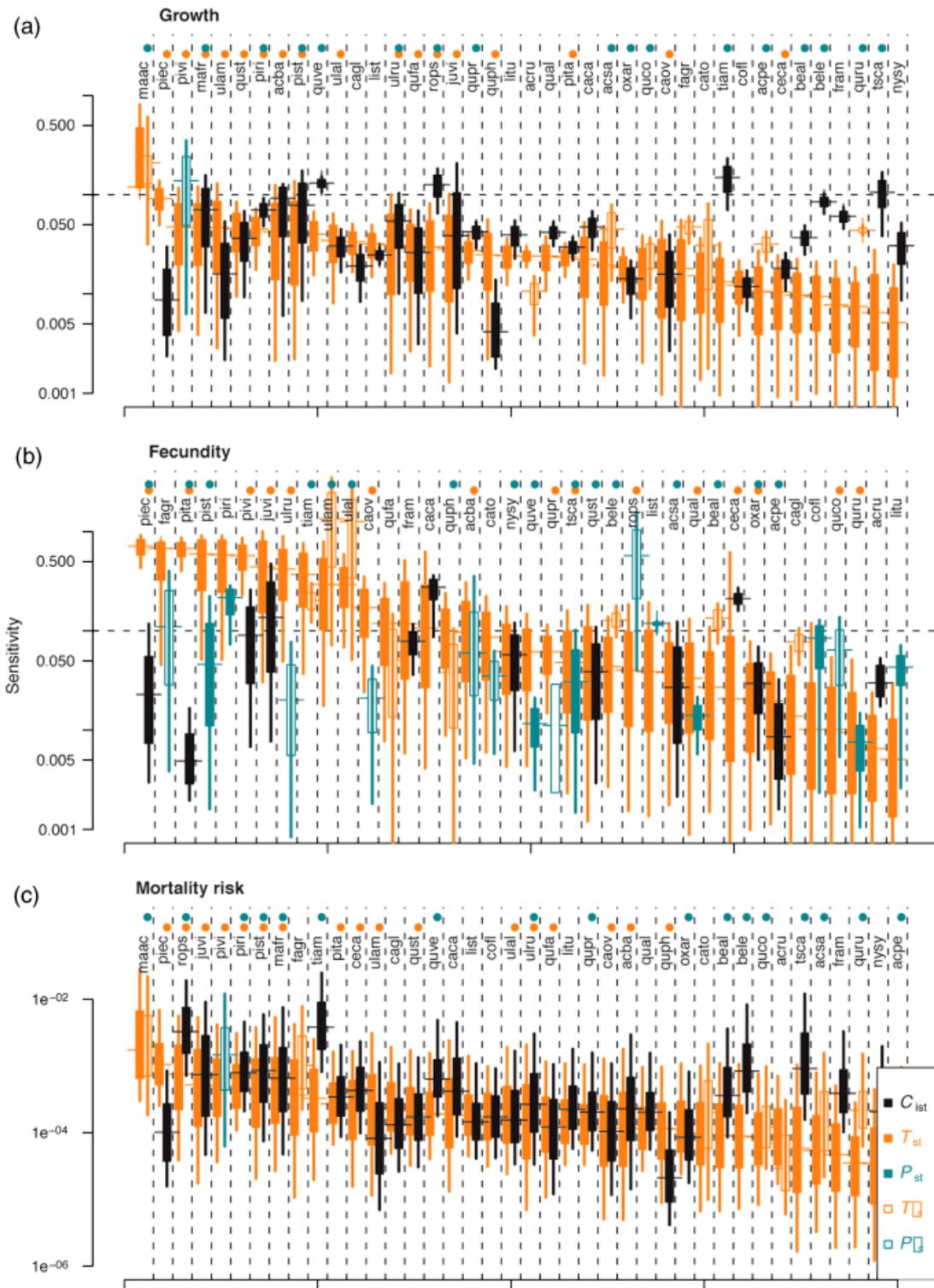
Incorporating competition with responses to variation in both time and space (COT and CIS) leads to new insights that differ from CEM predictions. Sensitivity coefficients to spring temperature, summer PDSI, and light competition can be directly compared, as shown by the example for *Pinus rigida* in Fig. 2a. Spring



**Fig. 2** Sensitivity coefficients for *Pinus rigida* (a) describe the proportionate response of a specific demographic rate to a specific variable, such as spring temperature (orange), summer drought (green), or competition for light (black). Predictive distributions are plotted over time for climate variables (dashed lines) together with the true values (solid lines) in (c) and (d). For light availability (b), predictions are plotted against true values with a line of agreement (dashed). Predictive intervals (95%) are bounded by dashed lines in (c) and (d) and by vertical lines in (b).

temperature (orange) has the largest impact overall and most strongly affects fecundity. It is followed by the effect of summer drought (turquoise) on fecundity. However, next in importance are effects of light competition (black) and spring temperatures on growth rate. Lowest impacts come from light competition on fecundity and summer drought on growth. Although growth rate is the only variable typically analyzed in longitudinal studies of climate variation, this analysis shows that it responds more to competition than to either climate variable. The ability to directly compare effects of different sources of variation across different demographic rates can be extended to all species (Fig. 3).

Sensitivities to competition and climate variables span two orders of magnitude for growth and fecundity and four orders of magnitude for mortality risk. Because warming is the most consistent change predicted for the southeastern United States, species are ordered in Fig. 3 from most to least sensitive to  $T_{s,t}$ . The first obvious departure from previous studies is the demonstration that fecundity, not tree growth and mortality, is the most responsive to climate change. Whereas only *Magnolia acuminata* has growth sensitivity to temperature greater than 10% (Fig. 3a), many species have sensitivities this large for fecundity (Fig. 3b). Spring temperature variation has a much larger effect on



**Fig. 3** Sensitivity (mean, 1 and 2 standard deviations) for each of three demographic responses to light ( $C_{is,t}$ ), spring temperature variation over time ( $T_{s,t}$ ), summer drought variation over time ( $P_{s,t}$ ), spring temperature variation in space ( $T'_s$ ) and hydrological variation in space ( $P'_s$ ). Species are ranked according to sensitivity to temperature variation in time  $T_{ij,t}$  (orange). Also shown for each species is the variable accounting for most of the variation together with  $T_{ij,t}$ . Sensitivities are shown for (a) growth (Eqn 6), (b) fecundity (eqn 6), and (c) survival (Eqn 7). In (a) and (b) the horizontal line is drawn at 10% for reference.

fecundity than does any variable on growth. Thus, the capacity to compete for regeneration sites locally and migrate in response to climate change, which both depend heavily on fecundity (Clark *et al.*, 2001), represent one of the most critical consequences of climate change. Examples of species highly sensitive for all three demographic responses are in the genus *Pinus* and *Ulmus* [*Magnolia* spp. are also sensitive in growth (Fig. 3a) and survival (Fig. 3c), but fecundity is not estimated due to inadequate data on seed production].

Competition accounts for most of the variation in growth and mortality risk (black bars in Fig. 3a and c), in all but a few cases exceeding that from temperature variation in time  $T_t$  or any other climate variable. Although temperature variation in time is the dominant control on fecundity for a large number of species (Fig. 3b), unlike growth, the secondary sensitivity often includes temperature and moisture variation in time and competition for light.

Results confirm the need to complement traditional predictive modeling of climate CIS, which accounts for little demographic variation, with longitudinal studies of impacts of climate COT. In a minority of cases  $T'_s$  or  $P'_s$  (based on CIS) emerge as the dominant source of variation in demographic rates (Fig. 3). Coming from an analysis that spans the climate space of southern mixed pine and oak to northern hardwoods (Table 1), this lack of importance suggests that spatial correlation in climate and abundance provides limited insight for responses over time.

Figure 4 shows demographic sensitivities from our longitudinal analysis compared with predictions of CEMs from nearby national forests. 'Agreement' between the two methods would mean that species having low sensitivity (horizontal axis) are also predicted to have small changes in abundance (vertical axis). For all three demographic rates, many of the species showing the highest sensitivity to spring temperature variation and summer drought over time were predicted to have the lowest predicted response to climate change in CEMs (Fig. 4). The two approaches appear to 'agree' only that the fecundity response of *Pinus taeda* is large (the highest bar in Fig. 4c). For growth and mortality risk the responses contrast for all species except *Pinus taeda*, for both spring temperature and summer drought.

Given the large difference in sensitivity to COT vs. CIS, it is not surprising that demographic sensitivities contrast with predictions from CEMs (Fig. 4). To better illustrate why the two methods should produce different results we turn to synthetic estimates of climate tracking and resource tracking (Materials and methods). The large variation in demographic rates of Fig. 1c is typical, because many factors contribute (Clark,

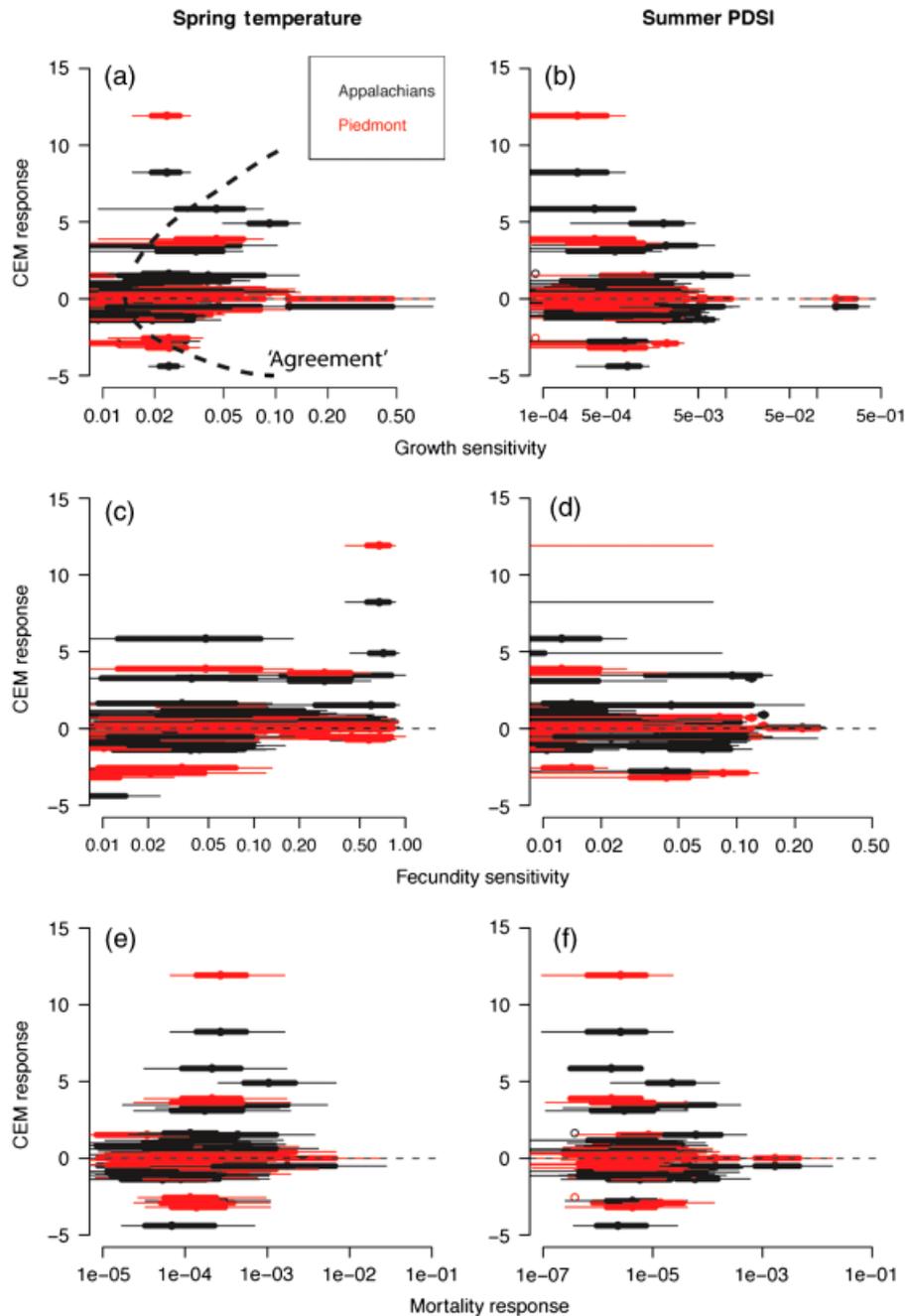
2010). If a species is sensitive to climate or resources, the fitted model should 'predict' that variable, whether or not there is evidence for its effects in a response variable like Fig. 1c. For example, although growth rates of *P. rigida* are not obviously related to summer PDSI or spring temperature effects in Fig. 1c, the fitted model predicts both variables with a high degree of precision (Fig. 2c and d); *P. rigida* closely 'tracks' both spring temperatures and summer drought. The relatively low importance of competition for light (large predictive intervals in Fig. 2b) comes from the fact that, in this region, this species occurs on xeric ridgelines, where crowns are relatively unaffected by competing trees. Taken together, the sensitivity coefficients show the effect size on a specific demographic variable (Fig. 2a), whereas predictive distributions show the importance of a variable for the synthetic response (Fig. 2b).

If demographic rates of a species are not tracking a climate variable now, then data do not support the interpretation that it will respond to near-term changes in that variable in the future. In contrast to *P. rigida*, *Liriodendron tulipifera* populations of the southern Appalachians are not 'tracking' current climate, as demonstrated by the wide predictive intervals in the middle panels of Fig. 5. The inability to 'predict' climate variation indicates that these variables are not influencing current growth and reproduction. Overall, *Liriodendron* demography 'tracks' summer drought more closely than it does spring temperature, but not with the precision of *P. rigida* (Fig. 5). *Liquidambar* populations on the Piedmont sites track summer drought, but not spring temperature (Fig. 5).

Combining sensitivity and concepts of climate tracking allows identification of species at risk of climate change. The predictive loss associated with tracking highlights species of the genera *Pinus*, *Ulmus*, *Magnolia*, and *Fagus* as sensitive to both spring temperature and summer PDSI (Fig 6). These genera are sensitive in terms of individual demographic rates (Fig. 3) and they are tracking climate closely (Supporting Information). In addition to these species, spring temperatures are closely tracked by *Tilia*, and summer drought is closely tracked by *Cercis* and *Liquidambar*.

## Discussion

Demographic tracking studies complement CEMs by determining the vulnerability of individual trees to exposure to risk factors, including COT, CIS, and competition. CEMs afford valuable insight (Thomas *et al.*, 2004; Iverson *et al.*, 2008), showing how the abundance of a species is correlated with spatial variation in climate. The maps that are generated from regression models give a sense of differences between species in

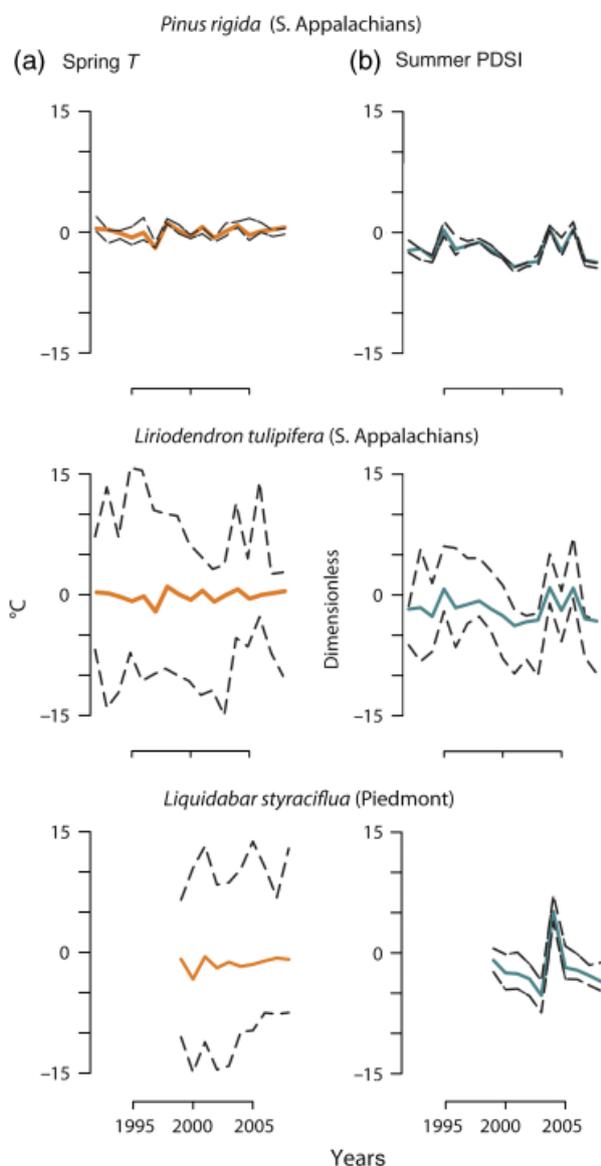


**Fig. 4** Comparisons of demographic sensitivities (mean, 1 and 2 standard deviations) from Fig. 3 with predicted change in importance from climate envelop models (CEMs). The dashed line in (a) indicates a pattern expected if the two methods agreed. The six panels are for all combinations of growth (a, b), fecundity (c, d), and survival (e, f) for spring temperature (a, c, e) and summer drought (b, d, f).

how extreme climate impacts could become. Especially careful studies by Iverson *et al.*, (2008) combine climate with other variables that correlate with abundance.

Despite their utility, CEMs can only provide limited insight on vulnerability, for the same reasons that public health scientists do not rely heavily on spatial correlations to determine the types of individuals that are

vulnerable to risk factors. First, in any spatial analysis of demography, the individuals at highest risk are least likely to be observed. This biased representation of risk affects inference – the individuals available for study are those that are healthy in a given setting, and estimates depend on the distribution of data (e.g., Lavine, 1991) lacking calibration for the risky environ-



**Fig. 5** Examples of species closely tracking climate (*Pinus rigida* above) and not (*Liriodendron* center). In the bottom panel *Liquidambar* is closely tracking summer drought, but not spring temperature. Colored lines are the climate variable, dashed lines the 95% predictive intervals of it based on the fitted model. For all three species, predictions are shown for spring temperature (a) and summer drought (b).

ment. Spatial correlations between climate and abundance miss the fact that low rainfall on average has different effects than low rainfall as an extreme event – for this reason PDSI is calculated as a departure from the local mean climate. Moreover, CEMs do not resolve the individual scale, i.e., the scale where competition and climate interact. Finally, the response variable, species abundance, is only weakly related to risk – species rarity or absence does not necessarily mean that the climate is unsuitable.

Results from these methods (Fig. 4) can contrast not only because CEMs do not include competition, but also because they use different dimensions for calibration (space) and prediction (time), and the response variable in CEMs (species abundance) is a weak diagnostic of climate risk. Spatial correlations between species abundance and climate depend on variables other than climate, such as soils and hydrology (Breda *et al.*, 2006; Ibáñez *et al.*, 2006; Iverson *et al.*, 2008; McDowell *et al.* 2008) and legacies of land use and exploitation (Ellis & Ramankutt, 2008; Chazdon *et al.*, 2009). Including large numbers of niche variables in CEMs does resolve the limitations of spatial correlation. The ranges of many species are determined by water bodies, geographic variation in parent material, distributions of other species with which they interact, political boundaries, and the sampling variation that attends all of these factors. Regression coefficients from geographic comparisons can have negligible connection to climate effects at any given location, partly because species abundance does not respond to annual to decadal scale climate variation, unless large changes occur. Even in cases where population frontiers may respond rapidly to climate variation, such areas can represent the minority of observations in many data sets and have little impact on the estimates for regression models. Finally, the fine spatial scales relevant for competition are not resolved in CEMs. Increasing the spatial resolution of CEMs finds habitats that are missed at coarse resolution (Luoto & Heikkinen, 2008; Randin *et al.*, 2009), but the meter scale at which competition operates is not accommodated by the highest resolution CEMs. For many species we find that the consequences of climate change for growth and mortality are overwhelmed by competition (Fig. 3). On the other hand, climate emerges as a dominant driver of reproductive effort.

The FIA database provides substantial spatial information on species abundance, in the form of several repeated samples from small plots spanning environmental gradients. This valuable resource was implemented to provide a periodic inventory of forest resources. Individual stems have been measured from one to three times at intervals of up to 5 years. Growth and survival over an interval can be compared with spatial variation in climate and environmental gradients and between size classes (Canham *et al.*, 2006; Iverson *et al.*, 2008; Purves, 2009; Woodall *et al.*, 2010). An ordinal crown variable provides some indication of competition for the census year (Lichstein *et al.*, 2010). Its demographic value is limited because individuals are difficult to track between censuses, which are few (typically two censuses), uneven in duration (several years), and cannot be matched with interannual climate variability. Few demographic variables are recorded on

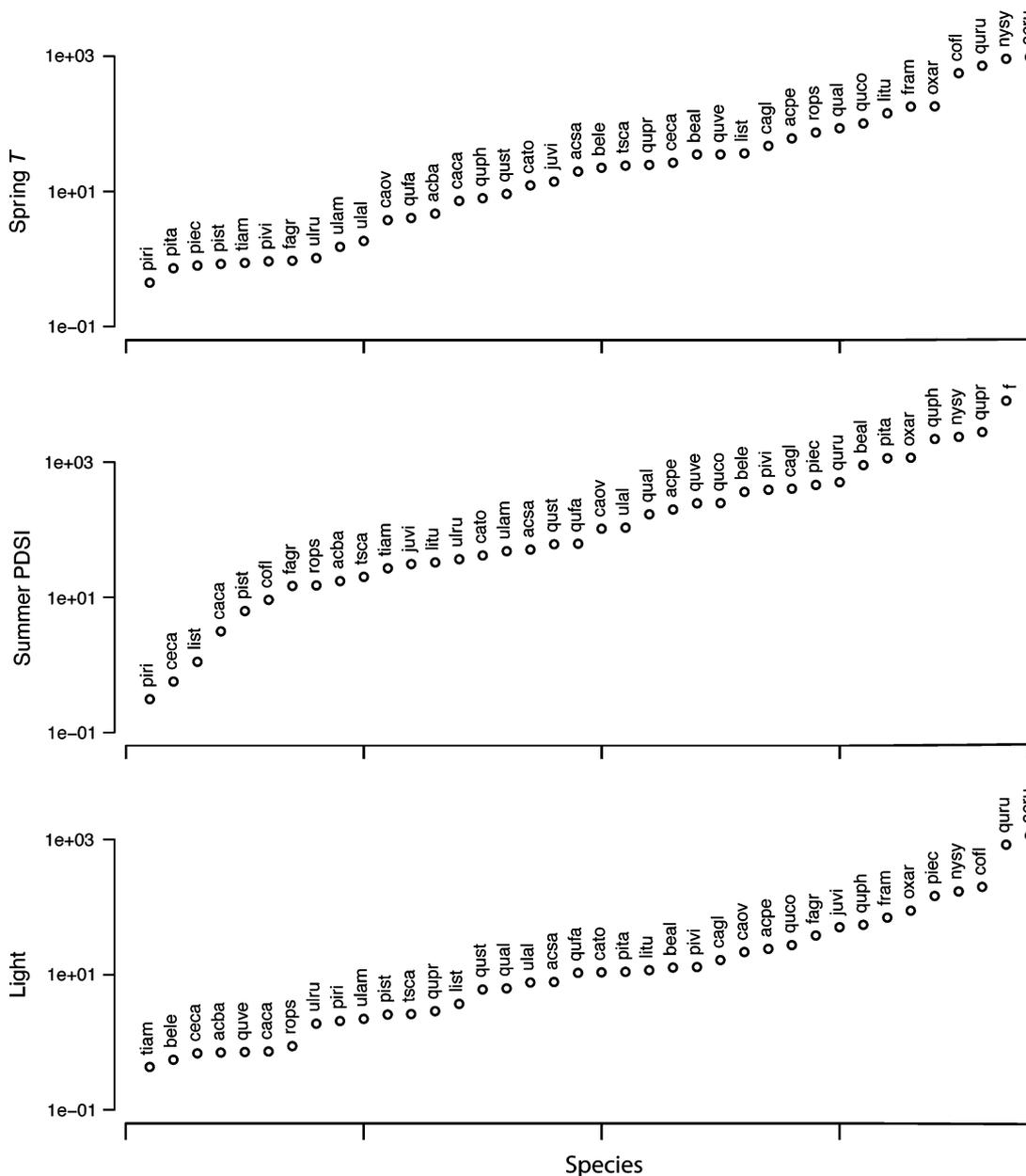


Fig. 6 Predictive loss values for climate tracking (upper two panels) and resource tracking (lower panel), ordered by increasing values of  $D_q$  (Eqn 5). Those with the lowest values most closely track climate variation over time and are most sensitive to change.

individuals (e.g., there is no information related to fecundity). Longitudinal methods bring the advantages of the full demographic response to climate and competition at the scale of individual responses and inter-annual climate variation, but lack the extensive geographic coverage of FIA. Clearly, these different methods complement one another.

Demographic approaches can complement studies of past changes in distribution and abundance (Hodkinson, 2005; Beckage, 2008). By themselves, historical changes are difficult to attribute. Species changes occur

for reasons that include atmospheric CO<sub>2</sub>, land use, and a changing biotic environment – they typically cannot be attributed to climate alone, but instead to a combination of factors. Studies of past growth bring additional insight (Salzer *et al.*, 2009; McMahon *et al.*, 2010), but represent only part of the demographic response, fecundity being the most sensitive. By combining sensitivity and climate tracking in an analysis that synthesizes climate and competition effects on all demographic rates we can sharpen the interpretation. We can rank species in terms of their tracking of climate

**Table 3** Correlation matrix for predictors in the model

	Canopy	Spring temperature	Summer PDSI	Mean spring temperature
	$C_{is,t}$	$T_{s,t}$	$P_{s,t}$	$T'_s$
$T_{s,t}$	0.056			
$P_{s,t}$	-0.0097	-0.15		
$T'_s$	0.16	0.023	-0.021	
$P'_s$	-0.11	-0.0061	0.014	-0.096

and resources (Fig. 6) and identify how each demographic rate responds to each explanatory variable individually (Fig. 3). Differences among species in the extent to which they track climate change help to explain differences from a CEM approach. Climate tracking inverts the model to determine whether or not a specific risk factor  $x$  is being tracked by the synthetic (multivariate) response vector  $y$ . Ability to predict  $x$  identifies it as a variable of importance for the full response  $y$ . If a species is not tracking a climate variable now, there is not yet any indication of actual risk. *Liriodendron* and *Acer rubrum* are predicted to be among the species most strongly affected by climate change in the CEM analysis of these same species and regions (Fig. 4), but they are not even tracking contemporary climate variation according to this analysis (Figs 5 and 6). Conversely *Pinus rigida* is closely tracking contemporary climate, yet is predicted to experience no change in CEM models.

Our results did not support the hypothesis that responses follow simple functional-type classes. We did not find that deciduous species were more responsive to temperature than evergreens (Way & Oren, 2010), with both groups being represented in the most and least sensitive extremes (Fig. 3a). However, the hypothesis that temperature can change developmental trajectories is consistent with our finding that fecundity responded disproportionately to temperature (Fig. 3b). More comparisons with the detailed studies synthesized by Way & Oren, (2010) hold promise for linking multiyear longitudinal responses back to physiological responses to temperature and moisture.

## Conclusions

By quantifying the direct effect of climate variation on demographic rates over time (COT), as well as spatial correlations in abundance (CIS), we estimate sensitivity to climate change, the most relevant issue for future biodiversity. This longitudinal demographic analysis of individual responses to climate, in the form of growth, fecundity, and survival complements the interpretation that has come from CEMs and historical analysis of

species abundance. Although the problems of dimension, scale, and attribution have long been recognized as potential sources of confusion (Pearson & Dawson, 2003; Ibáñez *et al.*, 2006; Araújo & Luoto, 2007; Beale *et al.*, 2008; Merrill *et al.*, 2008; Duncan *et al.*, 2009), this analysis confirms that climate COT could differ substantially from predictions based on spatial climate correlations. Unlike previous studies of forests that have focused almost entirely on growth and survival, we find that the most dramatic changes in time are expected from fecundity responses to both spring warming and summer drought. For fecundity, climate variation in time represents a stronger control for most species than does competition. Because fecundity affects not only capacity to compete for new sites but also migration, this result has significance both locally and regionally. When dispersal includes rare long-distance dispersal events, as is common for trees, small increases in fecundity translate to large changes in migration potential (Clark *et al.*, 2001) that interact with land cover transformation. Thus, the high sensitivities we report might be amplified.

Although the highest proportionate sensitivities involve temperature changes on fecundity, the role of light competition exceeds climate sensitivities for both growth and mortality risk. Fecundity will track climate change for many species, but growth and survival will continue to respond most strongly to their local competitive environment. The resulting response may not bear much resemblance to the predictions that come from spatial climate correlations.

By sharpening inference on climate risk, our approach can more directly guide policy and planning. Species in the genera *Pinus*, *Ulmus*, *Fagus*, and *Magnolia* appear strongly influenced by climate variation, with their current demographic responses being dominated by fluctuations in at least two climate variables. As climate continues to change, these species will respond. Warming springs will benefit, whereas drought will harm. By identifying the species at risk and why, future research can focus on the physiological (as opposed to demographic) basis for vulnerability, and how spatial variation in resources, at both landscape and geo-

graphic scales, should be exploited to assure availability of suitable habitat with climate change.

## Acknowledgements

For comments on the manuscript we thank Emily Moran, Carl Salk, Denis Valle, and three anonymous reviewers. The study was supported by NSF grants DEB9981392, BDEI0131905, IDEAO308498, SEII0430693, DDDAS0540347, and the Coweeta LTER.

## References

- Angerter AL, Huxman TE, Chesson P, Venable DL (2009) Functional tradeoffs determine species coexistence via the storage effect. *Proceedings of the National Academy of Science USA*, **106**, 11641–11645.
- Ararijo MB, Luoto M (2007) The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, **16**, 743–753.
- Archaux F, Wolters V (2006) Impact of summer drought on forest biodiversity: what do we know? *Annals of Forest Science*, **63**, 645–652.
- Barber VA, Juday GP, Finney BP (2000) Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature*, **405**, 668–673.
- Beale CM, Lennon JJ, Gimona A (2008) Opening the climate envelope reveals no macroscale associations with climate in European birds. *Proceedings of the National Academy of Science USA*, **105**, 14908–14912.
- Beckage B, Osborne B, Pucko C, Gavin DG, Siccama T, Perkins T (2008) An upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont, USA. *Proceedings of the National Academy of Science USA*, **105**, 4197–4202.
- Bellemare J, Motzkin G, Foster DR (2002) Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. *Journal of Biogeography*, **29**, 1401–1420.
- Breda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, **63**, 625–644.
- Bunn AG, Graumlich LJ, Urban DL (2005) Trends in twentieth-century tree growth at high elevations in the Sierra Nevada and White Mountains, USA. *Holocene*, **15**, 481–488.
- Bush MB, Silman MR, McMichael C, Saatchi S (2008) Fire, climate change and biodiversity in Amazonia: a late-holocene perspective. *Philosophical Transactions of the Royal Society of London, Series B*, **363**, 1795–1802.
- Canham C, Thomas R (2010) Local frequency but not relative abundance of temperate tree species varies along climate gradients in eastern North America. *Ecology*, in press.
- Canham CD, Papaik M, Uriarte M, McWilliams W, Jenkins JC, Twery MJ (2006) Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. *Ecological Applications*, **16**, 540–554.
- Chazdon RL, Harvey CA, Komar O *et al.* (2009) Beyond reserves: a research agenda for conserving biodiversity in human-modified tropical landscapes. *Biotropica*, **41**, 142–153.
- Clark JS (1996) Testing disturbance theory with long-term data: alternative life history solutions to the distribution of events. *American Naturalist*, **148**, 976–996.
- Clark JS (2010) Individuals and the variation required for high species diversity. *Science*, **327**, 1129–1132.
- Clark JS, Lewis M, Horvath L (2001) Invasion by extremes: variation in dispersal and reproduction retards population spread. *The American Naturalist*, **157**, 537–554.
- Clark JS, Dietze M, Agarwal P, Chakraborty S, Ibanez I, LaDeau S, Wolosin M (2007) Resolving the biodiversity debate. *Ecology Letters*, **10**, 647–662.
- Clark JS, Agarwal P, Bell DM *et al.* (2010a) Inferential ecosystem models, from network data to prediction. *Ecological Applications*, in press.
- Clark JS, Bell D, Chu C *et al.* (2010b) High dimensional coexistence based on individual variation: a synthesis of evidence. *Ecological Monographs*, **80**, 569–608.
- Condit R, Ashton P, Bunyavechewin S *et al.* (2006) The importance of demographic niches to tree diversity. *Science*, **313**, 98–101.
- Dietze M, Clark JS (2008) Rethinking gap dynamics: the impact of damaged trees and sprouts. *Ecological Monographs*, **78**, 331–347.
- Duncan RP, Cassey P, Blackburn TM (2009) Do climate envelope models transfer? A manipulative test using dung beetle introductions. *Proceedings of the National Academy of Science USA*, **267**, 1449–1457.
- Elliott GP, Baker WL (2004) Quaking aspen at treeline: a century of change in the San Juan Mountains, Colorado, USA. *Journal of Biogeography*, **31**, 733–745.
- Ellis EC, Ramankutt N (2008) Putting people in the map: anthropogenic biomes of the world. *Frontiers in Ecology and the Environment*, **6**, 439–447.
- Engelbrecht BMJ, Kursar TA, Tyree MT (2005) Drought effects on seedling survival in a tropical moist forest. *Trees*, **19**, 312–321.
- Erasmus BFN, Van Jaarsveld AS, Chown SL, Kshatriya M, Wessels KJ (2002) Vulnerability of South African animal taxa to climate change. *Global Change Biology*, **8**, 679–693.
- Foster DR, Boose ER (1992) Patterns of forest damage resulting from catastrophic wind in central New England, USA. *Journal of Ecology*, **80**, 79–99.
- Gelfand AE, Ghosh S (1998) Model choice: a minimum posterior predictive loss approach. *Biometrika*, **85**, 1–11.
- Goldberg DE, Turner RM (1986) Vegetation change and plant demography in permanent plots in the Sonoran desert. *Ecology*, **7**, 695–712.
- Hodkinson ID (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews Cambridge Philosophical Society*, **80**, 489–513.
- Houle G (1999) Mast seeding in *Abies balsamea*, *Acer saccharum*, and *Betula alleghaniensis* in an old growth, cold temperate forest of north-eastern North America. *Journal of Ecology*, **87**, 413–422.
- Ibáñez I, Clark JS, Dietze MC *et al.* (2006) Predicting biodiversity change: outside the climate envelope, beyond the species-area curve. *Ecology*, **87**, 1896–1906.
- Ibáñez I, Clark JS, Dietze M (2008) Evaluating the sources of potential migrant species: implications under climate change. *Ecological Applications*, **18**, 1664–1678.
- IPCC (2007) *Climate Change 2007: Impacts, Adaptation and Vulnerability*. Cambridge University Press, Cambridge, UK.
- Iverson LR, Prasad AM, Matthews SN, Peters M (2008) Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest and Ecology Management*, **254**, 390–406.
- Jetz W, Wilcove DS, Dobson AP (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, **5**, 1211–1219.
- Kobe RK, Pacala SW, Silander JA Jr, Canham CD (1995) Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications*, **5**, 517–532.
- Kon H, Noda T (2007) Experimental investigation on weather cues for mast seeding of *Fagus crenata*. *Ecology Research*, **22**, 802–806.
- Lavine M (1991) Problems in extrapolation illustrated with shuttle O-ring data. *Journal of the American Statistical Association*, **86**, 919–921.
- Lichstein JW, Dushoff J, Ogle K, Chen A, Purves DW, Caspersen JP, Pacala SW (2010) Unlocking the forest inventory data: relating individual-tree performance to unmeasured environmental factors. *Ecology Applications*, **20**, 684–699.
- Lloyd AH, Fastie CL (2002) Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change*, **52**, 481–509.
- Loehle C, LeBlanc D (1996) Model-based assessments of climate change effects on forests: a critical review. *Ecological Modeling*, **90**, 1–31.
- Luoto M, Heikkinen RK (2008) Disregarding topographical heterogeneity biases species turnover assessments based on bioclimatic models. *Global Change Biology*, **14**, 483–494.
- Masaki T, Oka T, Osumi K, Suzuki W (2008) Geographical variation in climatic cues for mast seeding of *Fagus crenata*. *Population Ecology*, **50**, 357–366.
- McDowell N, Pockman WT, Allen CD *et al.* (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*, **178**, 719–739.
- McKenzie D, Hessl AE, Peterson DL (2001) Recent growth of conifer species of western North America: assessing spatial patterns of radial growth trends. *Canadian Journal of Forest Research*, **31**, 526–538.
- McLaughlin SB, Downing DJ, Blasing TJ *et al.* (1987) An analysis of climate and competition as contributors to decline of red spruce in high elevation Appalachian forests of the eastern United States. *Oecologia*, **72**, 487–501.
- McMahon SM, Parker GG, Miller DR (2010) Evidence for a recent increase in forest growth. *Proceedings of the National Academy of Sciences USA*, doi: 10.1073/pnas.0912376107.
- Merrill RM, Gutierrez D, Lewis OT, Gutierrez J, Diez SB, Wilson RJ (2008) Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. *Journal of Animal Ecology*, **77**, 145–155.
- Mohan JE, Cox R, Iverson L (2009) Northeastern forest composition and carbon dynamics in a future, warmer world. *Canadian Journal of Forest Research*, **39**, 213–230.

- Nepstad DC, Tohver IM, Ray D, Moutinho P, Cardinot G (2007) Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology*, **88**, 2259–2269.
- Oberhuber W, Stumböck M, Kofler W (1986) Climate-tree-growth relationships of Scots pine stands (*Pinus sylvestris* L.) exposed to soil dryness. *Trees – Structure and Function*, **1**, 19–27.
- Pacala SW, Hurtt GC (1993) Terrestrial vegetation and climate change: integrating models and experiments. In: *Biotic Interactions and Global Change* (eds Kareiva PM, Kingsolver JG, Huey RB), pp. 57–74. Sinauer Associates Inc., Sunderland, MA.
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimatic envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.
- Phillips OL, Aragão LE, Lewis SL *et al.* (2009) Drought sensitivity of the Amazon rainforest. *Science*, **323**, 1344–1347.
- Prasad AM, Iverson LR, Matthews S, Peters M 2007–ongoing. A Climate Change Atlas for 134 Forest Tree Species of the Eastern United States [database]. Northern Research Station, USDA Forest Service, Delaware, Ohio. Available at: <http://www.nrs.fs.fed.us/atlas/tree> (accessed 2007).
- Prentice IC, Sykes MT, Cramer W (1993) A simulation model for the transient effects of climate change on forest landscapes. *Ecological Modelling*, **65**, 51–70.
- Purves D (2009) The demography of range boundaries vs range cores in Eastern US tree species. *Proceedings of the Royal Society Series B*, **276**, 1477–1484.
- Randin CF, Engler R, Normand S *et al.* (2009) Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology*, **15**, 1557–1569.
- Salzer M, Hughes M, Bunn A, Kipfmüller K (2009) Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *Proceedings of the National Academy of Science USA*, **106**, 20346–20353.
- Silvertown J (2004) Plant coexistence and the niche. *Tree*, **19**, 605–611.
- Streng DR, Glitzenstein JS, Harcombe PA (1989) Woody seedling dynamics in an East Texas floodplain forest. *Ecological Monographs*, **59**, 177–204.
- Suttle KB, Thomsen M, Power M (2007) Species interactions reverse grassland responses to changing climate. *Science*, **315**, 640–642.
- Thomas CD *et al.* (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Uriarte M *et al.* (2005) Seedling recruitment in a hurricane-driven tropical forest: light limitation, density dependence and the spatial distribution of parent trees. *Journal of Ecology*, **93**, 291–304.
- van Mantgem PJ, Stephenson NL (2007) Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecological Letters*, **10**, 909–916.
- van Mantgem PJ, Stephenson NL, Mutch LS, Johnston VG, Esperanza AM, Parsons DJ (2003) Growth rate predicts mortality of *Abies concolor* in both burned and unburned stands. *Canadian Journal of Forest Research*, **33**, 1029–1038.
- Way DA, Oren R (2010) Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiology*, **30**, 669–688.
- Woodall CW, Oswald CM, Westfall JA *et al.* (2010) Selecting tree species for testing climate change migration hypotheses using forest inventory data. *Forest Ecology Management*, **259**, 778–785.
- Wright SJ (2005) The El Niño Southern Oscillation influences tree performance in tropical rainforests. In: *Tropical Rainforests: Past, Present, and Future* (eds Bermingham E, Dick CW, Moritz C), pp. 295–310. University of Chicago Press, Chicago.
- Wyckoff P, Clark JS (2005) Comparing predictors of tree growth: the case for exposed canopy area. *Canadian Journal of Forest Research*, **35**, 13–20.
- Yang Y, Watanabe M, Li F, Zhang J, Zhang W, Zhai J (2006) Factors affecting forest growth and possible effects of climate change in the Taihang Mountains, northern China. *Forestry*, **79**, 135–147.

### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Number of seed collections from a total of 481 seed traps and 4661 seed trap-years.

**Table S2.** Numbers of observations, listed by species.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.