

## LETTER

## Apparent climatically induced increase of tree mortality rates in a temperate forest

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### Abstract

We provide a first detailed analysis of long-term, annual-resolution demographic trends in a temperate forest. After tracking the fates of 21 338 trees in a network of old-growth forest plots in the Sierra Nevada of California, we found that mortality rate, but not the recruitment rate, increased significantly over the 22 years of measurement (1983–2004). Mortality rates increased in both of two dominant taxonomic groups (*Abies* and *Pinus*) and in different forest types (different elevational zones). The increase in overall mortality rate resulted from an increase in tree deaths attributed to stress and biotic causes, and coincided with a temperature-driven increase in an index of drought. Our findings suggest that these forests (and by implication, other water-limited forests) may be sensitive to temperature-driven drought stress, and may be poised for die-back if future climates continue to feature rising temperatures without compensating increases in precipitation.

### Keywords

Climate change, drought, forest demography, temperate forests, tree mortality.

*Ecology Letters* (2007) 10: 909–916

### INTRODUCTION

Recent observations suggest that at global scales, rapid environmental changes may be altering the structure, composition and dynamics of forests. For example, over the last several decades average global forest net primary productivity (NPP) apparently has increased, perhaps due to various combinations of increasing temperature, precipitation, cloudless days, atmospheric CO<sub>2</sub> and nutrient deposition (Boisvenue & Running 2006). However, there are notable regional exceptions to this trend, particularly in water-limited forests experiencing ongoing climatic warming without compensating precipitation increases; for example, growth of *Fagus sylvatica* L. has declined at its southern range limit in Spain (Jump *et al.* 2006). Especially in light of the central role forests play in the global carbon cycle, such observations underscore a need to improve our understanding of environmentally driven changes in forests.

Of particular importance, we need to improve our understanding of the effects of environmental changes on tree mortality rates. Model results suggest that small changes in mortality rates can profoundly affect forest structure, composition and dynamics (e.g. Kobe *et al.* 1995; Pacala *et al.* 1996; Wyckoff & Clark 2002). Yet only a handful of studies of real forests have examined long-term changes in

mortality rates, or have explored possible environmental drivers of those changes. In old-growth forests of tropical Amazonia, mortality rates have increased over the last few decades, and the increases apparently have been paralleled by increases in NPP (Laurance *et al.* 2004; Lewis *et al.* 2004b). While the authors suggest that the increasing mortality rates may be driven by enhanced competition resulting from increased resource availability (e.g. atmospheric CO<sub>2</sub> or sunny, cloudless days), the mechanisms remain unknown. To our knowledge, no comparable studies of chronic long-term changes in mortality rates have been conducted in old-growth temperate forests. However, some temperate studies have documented sudden, climatically driven forest die-back, such as in southwestern USA (e.g. Breshears *et al.* 2005).

Here, we provide a first detailed analysis of long-term, high-resolution tree demographic trends (mortality and recruitment) in old-growth temperate forests. Our study – conducted in the coniferous forests of the Sierra Nevada, California, USA – is unique in that mortality was measured annually for more than two decades, allowing us to correlate short-term variations in mortality with short-term variations in climate and other potential drivers of change. Further, because each of our 21 338 trees (living or recently dead) was examined annually, proximate causes of tree death could be assigned

with a high degree of confidence, helping us identify probable mechanisms driving changes in mortality.

We addressed three questions. First, have mortality or recruitment rates in the Sierra Nevada changed systematically over the last two decades? Second, if demographic rates have changed, are the changes consistent among different taxonomic groups and forest types? Finally, what are probable causes of the changes? We found that while recruitment rates changed little over the last two decades, mortality rates increased. The increase was not only evident for all trees combined, but also for each of two dominant genera of conifers and for most elevational zones (forest types). The increase in mortality rates resulted from increases in deaths assigned to stress and biotic causes (such as insects and pathogens), which in turn paralleled a temperature-driven increase in annual climatic water deficit (drought). Other factors, such as changes in air pollution concentrations or internal stand conditions, were not correlated with mortality rates. We conclude that these forests may be experiencing increasing deaths related to temperature-driven evaporative stress, potentially making them more vulnerable to extensive die-back during otherwise normal periods of reduced precipitation (cf. Breshears *et al.* 2005). Our results highlight a need for better information regarding ongoing, climatically driven changes in other temperate forests.

## METHODS

### Study sites and demographic data

Twenty-one permanent study plots ranging in size from 0.9 to 2.5 ha were established between 1982 and 1996 in old-growth stands within the coniferous forest zones of Sequoia and Yosemite national parks, Sierra Nevada, California (Stephenson & van Mantgem 2005; Table S1). Other plots in our network were excluded due to recent disturbances, such as fire or avalanche. The plots are arranged along a steep elevational gradient (*c.* 1900 m) from near lower to near upper treeline and encompass several different forest types, including ponderosa pine-mixed conifer, white fir-mixed conifer, red fir, Jeffrey pine and subalpine forests (Fites-Kaufman *et al.* 2007). The approximate horizontal distances from the lowest to the highest plots in Sequoia and Yosemite national parks are 48.5 and 57.3 km, respectively. The sites have never been logged. Frequent fires characterized the forests prior to Euro-American settlement, but the areas containing the study plots have not burned since the late 1800s (Swetnam 1993). The overall climate of this region is montane Mediterranean, with hot, dry summers and cool, wet winters, with *c.* 25–95% of the annual precipitation falling as snow, depending on elevation (Stephenson 1988). Within the forested zone, mean annual precipitation varies little with elevation (from *c.* 1100 mm at

1500 m, peaking at *c.* 1400 mm at *c.* 2000 m elevation, but declining slightly with elevations above 2000 m; Stephenson 1988). In contrast, mean annual temperature declines sharply with elevation (*c.* 5.2 °C for every 1 km increase in elevation), ranging from roughly 11 °C at the lowest plots to 1 °C at the highest. Soils are relatively young (mostly inceptisols) and derived from granitic parent material.

Within the plots all trees  $\geq 1.37$  m in height were tagged, mapped, measured for diameter and identified to species. All plots were censused annually for tree mortality. Because each tree was examined annually (and notes were taken on the presence of any damage, pathogens, etc.), proximate causes of tree death could be assigned with a high degree of confidence. At intervals of *c.* 5 years, we remeasured diameter at breast height (d.b.h., 1.37 m) of living trees. We recorded new recruitment (trees reaching 1.37 m in height) only during these diameter remeasurement years; we evenly distributed the counts of recruits in the intervening years between diameter measurement years to calculate annual recruitment rates from 1983 to 2004 (although beginning in 1999 recruitment was measured annually).

Trees that had missing data during any diameter measurement year were removed from analysis (411 trees, *c.* 2% of our data set). During the 5-year intervals for assessing recruitment prior to 1999 our censuses may have missed trees that had grown to  $\geq 1.37$  m tall, but died before being counted. Thus, to be consistent with recruitment census methods before 1999 we removed from analysis 31 trees that recruited from 1999 to 2004 but died before the next growth measurement year (*c.* 0.2% of our data set). Finally, in a single plot recruitment counts were not made consistently for *Quercus kelloggii* Newb. (black oak) because of the species' multi-stemmed growth form in the plot (Table S1). We therefore removed 123 observations of this species from this plot (*c.* 0.6% of our data set). These criteria yielded a final data set of 21 338 trees for analysis.

### Assessing demographic change

We considered trends in overall recruitment and mortality rates. We further considered trends by causes of mortality. Tree death is a complex process, often involving a lengthy chain of events that makes it impossible to assign a single ultimate cause of death (Franklin *et al.* 1987). We therefore focused on proximate causes of death – the final agents that killed trees. We divided proximate causes of mortality into two broad classes: (i) *stress and biotic* causes were assigned to standing dead trees that either showed no evidence of mechanical damage (whose deaths were likely a result of direct physiological stresses, such as from competitive suppression), or standing dead trees that clearly had been killed by insects or fungi, or rarely by mistletoes or vertebrates and (ii) *mechanical* causes were assigned to trees

killed by breaking or uprooting by wind or snow, or those crushed by another falling tree or snag.

To determine whether demographic changes were consistent among different taxonomic groups and forest types, we first checked for differences in mortality trends between two dominant genera, *Abies* and *Pinus* (together these genera comprised *c.* 76% of trees, Table S1). *Abies* is considered shade-tolerant and drought-intolerant, while *Pinus* is moderately shade-intolerant and drought-tolerant (Niinemets & Valladares 2006). We then considered differences in plot elevations, and therefore, effectively, forest type (Fites-Kaufman *et al.* 2007), which has a strong negative relationship with mortality rates (Stephenson & van Mantgem 2005). Elevation classes were as follows: low = 1500–1700 m, dominated by ponderosa pine-mixed conifer forest; mid = 2000–2300 m, dominated by white fir-mixed conifer forest; high = 2400–2600 m, dominated by red fir and Jeffrey pine forest and very high = 2900–3500 m, dominated by subalpine forest (Table S1).

### Indices of possible drivers of change

We sought measurements or indices of endogenous and exogenous factors potentially capable of driving long-term changes in demographic rates. The endogenous factor of greatest potential interest is changing intensity of competition within stands. As stand-level indices of competition we used stand density (stems  $\text{ha}^{-1}$ ) and aboveground living stem biomass ( $\text{Mg ha}^{-1}$ ), estimated from standard allometric equations tailored to the Sierra Nevada (Means *et al.* 1994).

Exogenous factors of interest included changing climate and air pollution. Topographic complexity and relatively sparse instrumental coverage across the Sierra Nevada meant that climatic data for our plots were best estimated by interpolation. We therefore used the Parameter-elevation Regression on Independent Slopes Model (PRISM; Daly *et al.* 2002; Daly 2006), on a 2 km grid. PRISM interpolates climate from instrumental records and a digital elevation model, making adjustments for features such as elevation, aspect, slope and rain shadows.

In the Sierra Nevada, tree deaths from stress and biotic causes are often highest in drought years (e.g. Ferrell 1996; Guarín & Taylor 2005). To provide an index of drought, we calculated climatic water deficit, which integrates temperature (energy) and precipitation inputs in a biologically meaningful way (Stephenson 1990). Water deficit can increase through increased evaporative demand, decreased water availability or both (Stephenson 1990). We used a modified Thornthwaite method (Willmot *et al.* 1985), with daylength estimated from latitude (Forsythe *et al.* 1995). We found good agreement between these estimates of climatic water deficit and those made using the coarser-resolution Variable Infiltration Capacity (VIC) hydrologic model (8 km grid; Liang *et al.*

1994); we used the finer-resolution PRISM estimates, which provided moderately better fits to the forest tree mortality data. As tree mortality resulting from stress and biotic causes often is in response to cumulative conditions over several years (Waring 1987; Manion 1991), we correlated current-year mortality with running averages of climatic water deficit for the current water year (October–September) and preceding two water years (hereafter ‘average water deficit’). In contrast, our informal observations over the last two decades suggested that tree deaths by mechanical causes were highest during years of large winter storms. To provide an index of the cumulative magnitude of large storms for each year, we summed total precipitation from the 3 months of each water year that recorded the greatest precipitation (hereafter ‘Precip<sub>max</sub>’). (Analyses based on indices using 2, 3 or 4 months all yielded similar conclusions.)

Because some species of trees in the Sierra Nevada can experience stress from ozone air pollution (Bytnerowicz *et al.* 2003), changing ozone concentrations might be an additional exogenous force affecting demographic rates. We created an index of ozone pollution (hereafter ‘O<sub>3</sub>’), using the annual average summer (June–September) daily maximum ozone concentration from the longest continually running monitoring station (Lower Kaweah) at Sequoia National Park (near the majority of plots), with the 1984 data used for the missing 1983 data.

### Statistical models

We wished to assess trends in annual demographic rates while controlling for the effects of plot identity. We therefore used generalized mixed models, with counts of demographic events (i.e. recruitment or death) modelled as a Poisson distribution with a log link function, including an offset for the total population size in the previous year, and accounting for temporal autocorrelation with a first-order autocorrelation function. Parameters were estimated using penalized quasi-likelihood methods with the plot effect modelled as random intercepts (without notable changes to fixed effect parameters when plot effects were modelled as random intercepts and slopes). Generalized linear mixed models only approximate likelihood-based model fitting, and standard methods for model selection (i.e. likelihood ratio tests, Akaike information criterion) are not valid (Venables & Ripley 2002), so parameter interpretations were based on estimation and significance testing. Parameter estimates ( $\beta$ ) of annual demographic trends were converted to percentages using the formula  $\beta (\%) = [e^{(\beta)} - 1] * 100$ . We tested the significance of the annual trend, modifiers of the annual trend (taxonomic group and elevation class) and predictors of the mortality trend (stand density, stand biomass, average water deficit, Precip<sub>max</sub> and O<sub>3</sub>). We assessed temporal trends in mortality predictors using linear

models or linear mixed models with parameters estimated using maximum likelihood. We used R for all statistical analyses (R Development Core Team 2006).

For analysis with climatic data, neighbouring plots were grouped where the 2 km PRISM grid gave identical climatic data ( $n = 14$  PRISM groups, Table S1). However, spatial autocorrelation among plots was low. The plots are arranged along a steep elevation gradient, and close geographic proximity does not necessarily translate into similar demographic rates (e.g. the association between plot distances and average recruitment and mortality rates were not significant via Mantel tests, 10 000 permutations,  $P \geq 0.31$ ). We failed to find evidence of spatial autocorrelations in the average plot residuals of our models of annual demographic trends using variogram plots.

## RESULTS

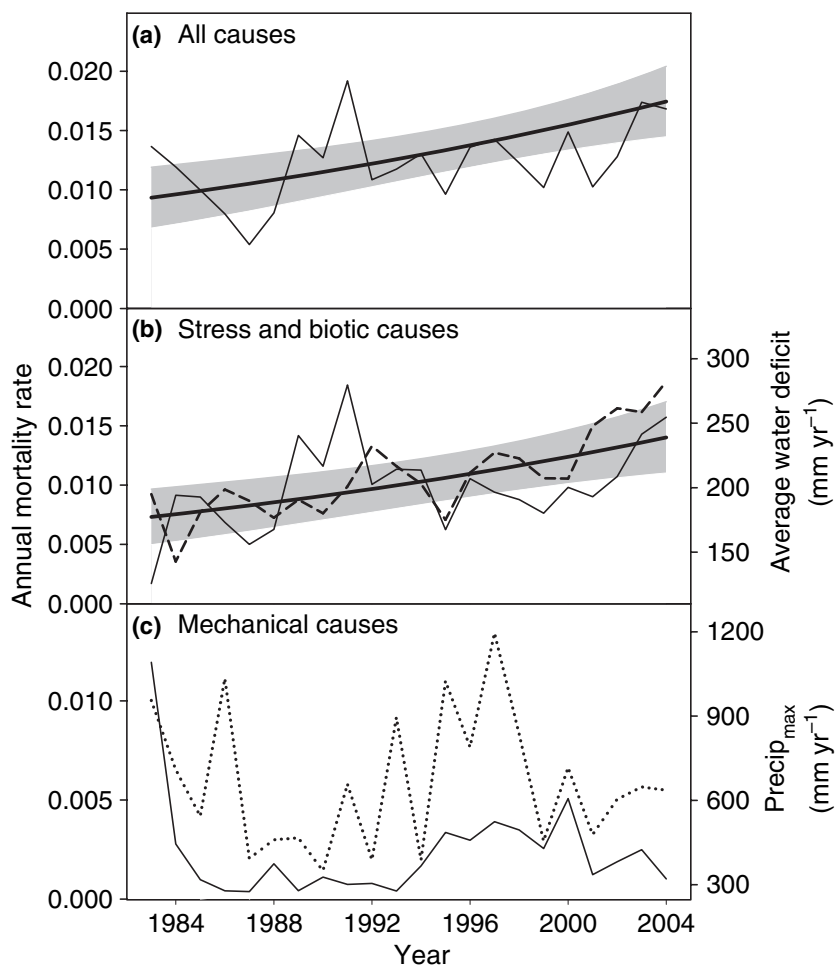
### Changes in demographic rates

Over the two decades of measurement, the average mortality rate increased at 3% per year, meaning that

mortality rate nearly doubled over the study period ( $P = 0.0004$ ; Fig. 1a, Table 1). In contrast, we found no evidence for changes in the recruitment rate ( $P = 0.91$ , Fig. S1).

The increase in mortality rate was not related to adding new plots to the monitoring network over time; mortality rate also increased when we considered only those plots established before or on 1985, 1990 or 1995 ( $P \leq 0.002$ ). Additionally, mortality rate increased when we considered only data reported from 1985 to 2004, 1990 to 2004 and 1995 to 2004 ( $P \leq 0.03$ ). Finally, mortality rate still increased significantly if we calculated it in the same manner that we calculated recruitment rate – i.e. the cumulative count of dead trees during the  $\approx 5$  years between diameter measurements were distributed evenly among those years ( $\beta_{\text{Year}} = 0.03$ , SE = 0.01,  $P < 0.0001$ ).

Mortality rate attributed to stress and biotic causes was much higher than mortality rate attributed to mechanical causes (Fig. 1b,c). We found an average 3% per year increase in mortality rate from stress and biotic causes (Table 1), but did not find evidence for changing mortality rate from mechanical causes (Table 1).



**Figure 1** Annual tree mortality rates from 1983 to 2004 for 21 permanent forest plots in the Sierra Nevada, California. The thin solid line represents the annual mortality rate averaged among plots, with the thick solid line showing the expected mortality rate ( $\pm 2$  SE, shaded area) from significant ( $P < 0.05$ ) models of the annual trend (Table 1). (a) Mean annual mortality rate for all causes of death increased at 3% per year (Table 1). (b) Mean annual mortality rate for stress and biotic causes increased at 3% per year (Table 1). Average water deficit (dashed line), an index of drought (see text for definition), predicted changes in the stress and biotic mortality rate (Table 2). (c) Mean annual mortality rate for mechanical causes did not show a significant trend (Table 1), although  $\text{Precip}_{\text{max}}$  (dotted line), an index of storm intensity (see text for definition), predicted annual variability in the mechanical mortality rate (Table 2).

**Table 1** Fixed effects of the generalized linear mixed models describing annual changes in mortality rates

Model	Fixed effect	$\beta$	SE	d.f.	<i>P</i> -value
Annual trend	Year	0.0298	0.0084	307	0.0004
Stress and biotic deaths annual trend	Year	0.0309	0.0092	307	0.0009
Mechanical deaths annual trend	Year	0.0233	0.0166	307	0.1610
<i>Abies</i> annual trend	Year	0.0320	0.0079	276	0.0001
<i>Pinus</i> annual trend	Year	0.0927	0.0122	307	< 0.0001
Annual trend and elevation class	Year	0.0301	0.0083	307	0.0004
	Elevation class – mid	–0.2198	0.0999	17	0.0419
	Elevation class – high	–0.3314	0.1265	17	0.0180
	Elevation class – very high	–1.1740	0.3041	17	0.0013
Annual trend and stand density	Year	0.0286	0.0081	306	0.0005
	Elevation	–0.0004	0.0001	19	0.0073
	Stand density	0.0001	0.0001	306	0.4460
Annual trend and stand biomass	Year	0.0299	0.0080	306	0.0002
	Elevation	–0.0005	0.0001	19	0.0001
	Stand biomass	0.0000	0.0001	306	0.9808

Models show the results of including all observations, and subdividing the data into proximate causes of death and taxonomic groups. When taxonomic groups were modelled together there was weak support for including an interaction term ( $\beta_{\text{Year} * \text{Pinus group}} = 0.0325$ , SE = 0.0168,  $P = 0.0536$ ) signifying that, compared to the *Abies* group, the *Pinus* group may have had a greater rate of increase in mortality over time. Additional models include terms for elevation classes (based on comparisons against the low elevation class), stem density (stems ha<sup>-1</sup>) and stand biomass (Mg ha<sup>-1</sup>). There was little support for interactions among fixed effects for the models that included terms for elevation classes, stem density or stand biomass.

The increase in overall mortality rate was not limited to a particular taxonomic group; both *Abies* and *Pinus* showed increases over the measurement period (average rates of increase of 3% and 10% per year, respectively, Table 1). The magnitude of temporal changes in mortality rate declined with increasing elevation (Table 1). Consistent with that, all individual elevation classes showed increasing mortality rate trends except the subalpine (very high) plots. Demographic rates decline with increasing elevation in the Sierra Nevada (Stephenson & van Mantgem 2005), so longer observations and larger samples might be needed to definitively detect changes at very high elevation sites.

### Correlates of changes in demographic rates

Indices related to competition were not correlated with changes in mortality rate. There was a small, but statistically significant, decrease in stand density as mortality rate increased through time ( $\beta_{\text{Year}} = -1.17$ , SE = 0.67,  $P = 0.01$ , linear mixed model, Fig. S2), but stand density was not a predictor of the mortality trend, so long as plot elevation was factored out (Table 1). Stand biomass did not change significantly ( $\beta_{\text{Year}} = 0.03$ , SE = 0.24,  $P = 0.91$ , linear mixed model, Fig. S2), nor was it a predictor of mortality rate trend (Table 1). As suggested by these results, the

increase in mortality rate has been predominately in small trees (e.g. d.b.h. < 40 cm,  $n = 18\,832$  trees,  $P = 0.0003$ ; d.b.h.  $\geq 40$  cm,  $n = 2506$  trees,  $P = 0.23$ ; we obtained similar results for different definitions of small and large trees).

Linear mixed models of the climatic data indicated increasing average temperatures over the study period ( $\beta_{\text{Year}} = 0.13$ , SE = 0.01,  $P < 0.0001$ ), but no trend in precipitation ( $\beta_{\text{Year}} = -5.61$ , SE = 4.63,  $P = 0.23$ ), collectively resulting in a significant increase in climatic water deficits ( $\beta_{\text{Year}} = 5.95$ , SE = 0.63,  $P < 0.0001$ ). The increase in the overall mortality rate was explained by increasing average water deficit, as was the increase in the stress and biotic mortality rate (Fig. 1b, Table 2). Deaths resulting from mechanical causes were predicted by Precip<sub>max</sub>, the annual greatest three monthly values for precipitation (Fig. 1c, Table 2). There was no trend in O<sub>3</sub> over the study period ( $P = 0.54$ ), nor was O<sub>3</sub> correlated with changes in mortality rate ( $P = 0.21$ ).

### DISCUSSION

In response to our three original questions, we found the following. First, tree mortality rate has increased over the past two decades in temperate old-growth forests of the

**Table 2** Fixed effects of the generalized linear mixed models for annual changes in mortality rates as predicted by climatic data, with neighbouring plots grouped where estimated climate was identical ( $n = 14$  groups, Table S1)

Model	Fixed effect	$\beta$	SE	d.f.	$P$ -value
Annual trend	Year	0.0115	0.0108	189	0.2900
	Average water deficit	0.0033	0.0010	189	0.0008
	Precip <sub>max</sub>	0.0002	0.0001	189	0.1745
Stress and biotic deaths annual trend	Year	0.0047	0.0117	190	0.5168
	Average water deficit	0.0046	0.0012	190	0.0001
Mechanical deaths annual trend	Year	0.0214	0.0244	190	0.3814
	Precip <sub>max</sub>	0.0008	0.0003	190	0.0027

The trend in the overall mortality rate was explained by an index of drought (average water deficit, see text for definition), as was the trend in stress and biotic mortality rate. Mechanical mortality rates were related to an index of storm intensity (Precip<sub>max</sub>, see text for definition). Interaction terms among the fixed effects were not significant.

Sierra Nevada of California, and the increase is a consequence of increasing tree deaths attributed to stress and biotic causes. In contrast, recruitment rate has not changed. Second, the increase in mortality rate apparently has been pervasive, rather than being limited to a given taxonomic group or forest type (elevational zone). Finally, the increase in mortality rate has coincided with a temperature-driven increase in estimated climatic water deficit (drought). While this correlation does not prove causation, we suggest that the biologically most plausible interpretation of our results is that a temperature-driven increase in water deficits is contributing to increasing mortality rates.

Other possible causes of the increase in mortality rate do not stand up to scrutiny. Specifically, change in mortality rate was uncorrelated with an index of ground-level ozone pollution and stand-level indices of competition (stand density and biomass). Related to the latter, it is unlikely that increased mortality rate simply reflects a response to crowded understory conditions that have developed in the absence of fire in these historically fire-prone forests (Parsons & DeBenedetti 1979). If understory trees were undergoing self-thinning, we would expect both increasing stand biomass and gradually decreasing mortality rates (Peet & Christensen 1987) instead of unchanging stand biomass and increasing mortality rates. Additionally, many of our forest plots are in higher elevation forests that are currently close to their historic fire return intervals (Pitcher 1987), while lower elevation forests have had 100–140 years since the cessation of burning to attain quasi-equilibrium (Swetnam 1993; Roy & Vankat 1999). Finally, mortality rates are increasing for both the shade-tolerant *Abies* and generally shade-intolerant *Pinus*, and canopy closure – as reflected in cumulative tree size (i.e. stand biomass) – almost certainly has not increased during our observations. However, the effects of an exotic pathogen on *Pinus lambertiana* Dougl. likely contributed to the greater increase in mortality of *Pinus* compared to *Abies* (van

Mantgem *et al.* 2004), though members of the genus *Pinus* that are not currently affected by the pathogen still showed an increasing mortality rate ( $P = 0.037$ ).

The apparent increase in mortality rate in response to increasing water deficit so far has been gradual and subtle, and is concentrated in small trees. The concentration of mortality in small trees has meant that stand densities have decreased without a detectable decrease in stand biomass. (For example, if all trees 0–10 cm d.b.h. were to die in our plots, stand density would decrease by 55%, but stand biomass would decrease by only 0.2%.) Climatic conditions so far have remained below thresholds that might lead to large-scale forest die-back. However, if forests in the Sierra Nevada are as sensitive to increasing evaporative demand as our findings imply, they may now be poised for die-back during otherwise normal periods of reduced precipitation, similar to the recently documented die-back in the piñon-juniper woodlands of south-western North America (Breshears *et al.* 2005). But even in the absence of periods of significantly reduced precipitation, continued temperature-driven changes in mortality rate have the potential to dramatically alter forests (Pacala *et al.* 1996).

Though we detected no change in recruitment rates during our study, it is possible that recruitment and mortality are responding with differing lags or response strengths to climatic changes (Brubaker 1986; Lloyd 1997). Tree seedling dynamics are strongly influenced by climate (van Mantgem *et al.* 2006; Ibáñez *et al.* 2007). However, our ability to detect these climatic influences may be attenuated or lost by the time we measure recruitment of stems that are reaching breast height.

We have provided the first demonstration of long-term, chronic changes in demographic rates in otherwise undisturbed old-growth temperate forests, and have linked those changes to a possible climatic driver. Our work highlights the value of annual-resolution demographic data, which allowed

us to correlate both short-term variations in demographic rates with short-term variations in climate and other potential drivers of change, and (because each tree was examined annually) to assign causes of tree mortality and thereby identify probable mechanisms driving the changes in mortality rate. Our work contributes to a growing body of evidence indicating that ongoing environmental changes may be driving both chronic and acute changes in forests worldwide (e.g. Lewis *et al.* 2004a; Breshears *et al.* 2005; Lapenis *et al.* 2005; Boisvenue & Running 2006).

## ACKNOWLEDGEMENTS

We thank the many people involved in establishing and maintaining the permanent forest plots for the first 22 years. We also thank Sequoia and Yosemite National Parks for their invaluable cooperation and assistance. Julie Yee provided essential statistical advice. Mike Dettinger, Dan Cayan and Hugo Hidalgo shared water deficit estimates from the VIC model. The comments of Dylan Schwilk and four anonymous referees improved earlier drafts of this manuscript. The use of trade, product or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government. This work is a contribution of the Western Mountain Initiative, a USGS global change research project.

## REFERENCES

- Boisvenue, C. & Running, S.W. (2006). Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. *Glob. Change Biol.*, 12, 1–21.
- Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G. *et al.* (2005). Regional vegetation die-off in response to global-change-type drought. *Proc. Natl Acad. Sci. USA*, 102, 15144–15148.
- Brubaker, L.B. (1986). Responses of tree populations to climatic change. *Vegetatio*, 67, 119–130.
- Bytnerowicz, A., Arbaugh, M.J. & Alonso, R. (2003). *Ozone Air Pollution in the Sierra Nevada: Distribution and Effects on Forests*. Elsevier, Oxford, UK.
- Daly, C. (2006). Guidelines for assessing the suitability of spatial climate data sets. *Int. J. Climatol.*, 26, 707–721.
- Daly, C., Gibson, W.P., Taylor, G.H., Johnson, G.L. & Pasteris, P. (2002). A knowledge-based approach to the statistical mapping of climate. *Clim. Res.*, 22, 99–113.
- Ferrell, G.T. (1996). The influence of insect pests and pathogens on Sierra forests. In: *Sierra Nevada Ecosystem Project: Final Report to Congress* (ed. Erman, D.C.). University of California, Centers for Water and Wildland Resources, Davis, pp. 1177–1192.
- Fites-Kaufman, J.A., Rundel, P., Stephenson, N. & Weixelman, D.A. (2007). Montane and subalpine vegetation of the Sierra Nevada and Cascade ranges. In: *Terrestrial Vegetation of California*, 3rd edn (eds Barbour, M.G., Keeler-Wolf, T. & Schoenherr, A.A.), University of California Press, Berkeley, CA, pp. 456–501.
- Forsythe, W.C., Rykiel, E.J. Jr, Stahl, R.S., Wu, H. & Schoolfield, R.M. (1995). A model comparison for daylength as a function of latitude and day of year. *Ecol. Modell.*, 80, 87–95.
- Franklin, J.F., Shugart, H.H. & Harmon, M.E. (1987). Tree death as an ecological process. *Bioscience*, 37, 550–556.
- Guarín, A. & Taylor, A.H. (2005). Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. *For. Ecol. Manage.*, 218, 229–244.
- Ibáñez, I., Clark, J.S., LaDeau, S. & Hille Ris Lambers, J. (2007). Exploiting temporal variability to understand tree recruitment response to climate change. *Ecol. Monogr.*, 77, 163–177.
- Jump, A.S., Hunt, J.M. & Peñuelas, J. (2006). Rapid climate change-related growth decline at the southern range-edge of *Fagus sylvatica*. *Glob. Change Biol.*, 12, 2163–2174.
- Kobe, R.K., Pacala, S.W., Silander, J.A. & Canham, C.D. (1995). Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.*, 5, 517–532.
- Lapenis, A., Shivdenko, A., Shepaschenko, D., Nilsson, S. & Aiyer, A. (2005). Acclimation of Russian forests to recent changes in climate. *Glob. Change Biol.*, 11, 2090–2102.
- Laurance, W.F., Oliveira, A.A., Laurance, S.G., Condit, R., Nascimento, H.E.M., Sanchez-Thorin, A.C. *et al.* (2004). Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature*, 428, 171–175.
- Lewis, S.L., Malhi, Y. & Phillips, O.L. (2004a). Fingerprinting the impacts of global change on tropical forests. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 359, 437–462.
- Lewis, S.L., Phillips, O.L., Baker, T.R., Lloyd, J., Malhi, Y., Almeida, S. *et al.* (2004b). Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 359, 421–436.
- Liang, X., Lettenmaier, D.P., Wood, E.F. & Burges, S.J. (1994). A simple hydrologically based model of land surface water and energy fluxes for general circulation models. *J. Geophys. Res.*, 99, 14415–14428.
- Lloyd, A.H. (1997). Response of tree-line populations of foxtail pine (*Pinus balfouriana*) to climate variation over the last 1000 years. *Can. J. For. Res.*, 27, 936–942.
- Manion, P.D. (1991). *Tree Disease Concepts*, 2nd edn. Prentice-Hall, Englewood Cliffs, New Jersey.
- Means, J.E., Hansen, H.A., Koerper, G.J., Alaback, P.B. & Klopsch, M.W. (1994). Software for computing plant biomass – BIOPAK users guide. General Technical Report PNW-GTR-340. USDA Forest Service, Portland, OR, p. 184.
- Niinemets, Ü. & Valladares, F. (2006). Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecol. Monogr.*, 76, 521–547.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A. Jr, Kobe, R.K. & Ribbens, E. (1996). Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.*, 66, 1–43.
- Parsons, D.J. & De Benedetti, S.H. (1979). Impact of fire suppression on a mixed-conifer forest. *For. Ecol. Manage.*, 2, 21–33.
- Peet, R.K. & Christensen, N.L. (1987). Competition and tree death. *Bioscience*, 37, 586–595.
- Pitcher, D.C. (1987). Fire history and age structure in red fir forests of Sequoia National Park, California. *Can. J. For. Res.*, 17, 582–587.

- R Development Core Team (2006). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Roy, D.G. & Vankat, J.L. (1999). Reversal of human-induced vegetation changes in Sequoia National Park, California. *Can. J. For. Res.*, 29, 399–412.
- Stephenson, N.L. (1988). *Climatic control of vegetation distribution: the role of the water-balance with examples from North America and Sequoia National Park, California*. Dissertation, Cornell University, Ithaca, New York.
- Stephenson, N.L. (1990). Climatic control of vegetation distribution: the role of the water balance. *Am. Nat.*, 135, 649–670.
- Stephenson, N.L. & van Mantgem, P.J. (2005). Forest turnover rates follow global and regional patterns of productivity. *Ecol. Lett.*, 8, 524–531.
- Swetnam, T.W. (1993). Fire history and climate change in giant sequoia groves. *Science*, 262, 885–889.
- van Mantgem, P.J., Stephenson, N.L., Keifer, M.B. & Keeley, J. (2004). Effects of an introduced pathogen and fire exclusion on the demography of sugar pine. *Ecol. Appl.*, 14, 1590–1602.
- van Mantgem, P.J., Stephenson, N.L. & Keeley, J.E. (2006). Forest reproduction along a climatic gradient in the Sierra Nevada, California. *For. Ecol. Manage.*, 225, 391–399.
- Venables, W.N. & Ripley, B.D. (2002). *Modern Applied Statistics with S*, 4th edn. Springer, New York.
- Waring, R.H. (1987). Characteristics of trees predisposed to die. *Bioscience*, 37, 569–574.
- Willmot, C.J., Rowe, C.M. & Mintz, Y. (1985). Climatology of the terrestrial seasonal water cycle. *J. Clim.*, 5, 589–606.
- Wyckoff, P.H. & Clark, J.S. (2002). The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. *J. Ecol.*, 90, 604–615.

## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Word doc.** A word-file consisting of the following:

- **Table S1** Characteristics of the 21 forest plots.
- **Figure S1** Average annual recruitment rate from 1983–2004 for the 21 forest plots.
- **Figure S2** Stand density and biomass trends from 1982–2004 for the 21 forest plots.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2007.01080.x>

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Editor, Josep Penuelas

Manuscript received 30 April 2007

First decision made 5 June 2007

Manuscript accepted 12 June 2007