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Abstract

The diverse old-growth forests in Klamath region of northern California and southern Oregon provide valuable ecosystem services (e.g., maintaining watersheds, wildlife habitat, recreation), but may be vulnerable to a wide range of stressors, including invasive species, disrupted disturbance regimes, and climatic change. Yet our understanding of how forest structure in the Klamath region relates to the current physical environment is limited. Here we provide present-day benchmarks for old-growth forest structure across a climatic gradient ranging from coastal to dry interior sites. We established 16 large (1 ha) forest plots where all stems > 5 cm in diameter were identified to species and mapped. Climate across these sites was highly variable, with estimated actual evapotranspiration correlated to several basic measures of forest structure, including plot basal area, stem size-class inequality, tree species diversity and, to a lesser extent, tree species richness. Analyses of the spatial arrangement of stems indicated a high degree of non-uniformity, with 75% of plots showing significant stem clumping at small spatial scales (0 to 10 m). Downscaled predictions of future site water balance suggest changes will be dominated by rapidly increasing climatic water deficit (D, a biologically meaningful index of drought). While these plots give a picture of current conditions, continued monitoring of these stands is needed to describe forest dynamics and to detect forest responses to ongoing and future stressors.

Keywords: Climate, forest structure, spatial pattern

Introduction

Within the landscapes of the Pacific Northwest, old-growth forests have become focal areas for conservation (Strittholt et al. 2006). Old-growth forests provide multiple ecosystem services, including the maintenance of biodiversity, watershed hydrologic integrity, and carbon storage and sequestration (Lindenmayer and Franklin 2002, Luyssaert et al. 2008). These services are in addition to the cultural, spiritual, and recreational value societies place on old-growth forests. In recognition of these features, the conservation of old-growth forests has become globally important, and large-scale projects are underway to identify and protect these resources (Asner et al. 2010). These efforts are increasingly urgent as primary forests (areas without major human disturbances) containing old-growth have been drastically reduced globally and continue to decline (FAO 2010, Mackey et al. 2014).

Old-growth forests are defined according to numerous dimensions. Forest stand age is a typical criterion (e.g., > 200 years in temperate zones), so that sufficient time elapses between major disturbances to allow the development of distinctive structural characteristics. These characteristics include trees of multiple ages and sizes, high frequency/basal area of large trees, the presence of large standing and downed dead trees, dominance of shade-tolerant species, heterogeneity in tree spatial patterns (i.e., a random to clumped spatial distribution of trees), and canopy gaps, among other measures (Oliver and Larson 1990, Franklin and Spies 1991, Franklin et al. 2002, Bauhus et al. 2009).

In comparison to more structurally uniform stands, old-growth forests are expected to have generally high resistance and resilience to disturbances such as severe wildfire and drought (Fulé et al. 2012, D'Amato et al. 2013). Consequently, old-growth structural metrics are often used to provide reference conditions to evaluate the success of forest restoration. As a result, forest restoration often attempts to promote old-growth characteristics, typically through prescribed fire and/or silvicultural treatments (Spies et al. 2006,

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Bauhus et al. 2009). Although historical forest structure may not be simple to define with certainty (Stephenson 1999), old-growth characteristics are often targets for directing restoration projects.

Forest conservation considerations therefore oblige us to describe our remaining old-growth areas and how these forests vary across diverse biophysical environments. A common attitude is that these forests, once protected, will continue to thrive. Yet evidence suggests old-growth forests can be susceptible to a wide range of stressors, including the disruption of historical disturbance regimes (often fire exclusion) (e.g., Agee 1993), invasive species (including pathogens) (McDonald and Hoff 2001, Rizzo and Garbelotto 2003), and, recently, increasing temperatures (van Mantgem et al. 2009, Allen et al. 2010, Peng et al. 2011, Williams et al. 2012).

In this paper we provide present-day benchmarks for critical elements of old-growth forest structure across a biophysically diverse array of protected areas in the Klamath region of northern California and southern Oregon. The old-growth forests of this region are of particular importance in terms of biodiversity, as the rugged mountains of this region have created climatic and disturbance refugia that have allowed high levels of endemism and diversity (Whittaker 1960, DellaSala et al. 1999, Sawyer 2007). Within the Klamath region variation in precipitation and temperature yield sharp contrasts in the water balance, which may correlate with variation in forest structure. We use a sample of 16 old-growth forest plots to examine current forest structure and how some elements of forest structure (e.g., tree species diversity) vary along a steep climatic gradient, from the Pacific Ocean to continental climates in the Klamath region.

Methods

Physical Setting

Rugged topography and proximity to the Pacific Ocean create an exceptionally strong climatic gradient across Klamath region (Sarr et al. 2007). While the region can be described as having a Mediterranean-type climate, with cool wet winters and warm dry summers, the influence of the Pacific Ocean and mountainous terrain causes a great deal of variation within the Klamath region. In particular, maritime influences decline with distance from the ocean, so that precipitation decreases and annual temperature variation increases from west to east across this region. Summer droughts, a distinguishing feature of Mediterranean climates, are modulated by summer fogs along the coast and by the slow release of snowmelt at high elevations in interior areas.

Plot Establishment

We sampled locations in old-growth forests to maximize climatic contrasts from national park units of Klamath region (Crater Lake National Park, Lava Beds National Monument, Oregon Caves National Monument, Redwood National Park, and Whiskeytown National Recreation Area) and the Cascade-Siskiyou National Monument (managed by the Bureau of Land Management) (Table 1, Figure 1). Within each of these sites we established two large (generally 1 ha) forest plots, with the exception of Redwood National Park, where we established four plots. Plots were randomly located with GIS within areas identified as old-growth by local land managers, defined as forests containing large trees and without a history of recent major disturbances. Note that plots at Lava Beds National Monument and Whiskeytown National Recreation Area had evidence of recent low-severity prescribed burning.

Plot establishment followed standard protocols (Condit 1998). Plots were surveyed with a laser range finder (Impulse, Laser Technology Inc., Centennial, CO) and compasses (MapStar II digital compass, Laser Technology Inc., and hand-held compasses). All stems > 5 cm DBH (stem diameter at breast height, 1.37 m) were individually tagged, rated as live or dead, identified to species, and mapped. Notes on individual tree condition were also taken (e.g., presence of insect or pathogen attack).

Climate Data

We used estimates of the water balance to relate climate to vegetation (Stephenson 1990, 1998). This approach integrates the amount and timing

TABLE 1. Characteristics of forest monitoring plots. Values for mean plot DBH include ± (1 SE).

Site	Plot	Lat. (°)	Long. (°)	Elev. (m)	Tree count (ha^{-1})	Mean DBH (cm)	Basal Area (m^2 ha^{-1})	Dominant species*
Crater Lake	CRLA1	42.98	-122.08	2073	522	33.8 ± (1.2)	78.5	TSME
	CRLA2	42.81	-122.10	1568	865	28.5 ± (0.6)	79.0	ABCO
Cascade-Siskiyou	CSNM1	42.17	-122.36	1566	866	20.4 ± (0.8)	63.8	ABCO
	CSNM2	42.18	-122.37	1591	855	19.3 ± (0.7)	51.0	ABCO
Lava Beds	LABE1	41.70	-121.57	1590	115	48.2 ± (1.7)	23.8	PIPO
	LABE2	41.69	-121.47	1382	312	26.6 ± (0.7)	21.5	PIPO
Lassen Volcanic	LAVO1	40.50	-121.43	2074	1355	14.9 ± (0.4)	43.0	PICO
	LAVO2	40.48	-121.49	2522	339	36.9 ± (1.8)	64.9	TSME
Oregon Caves	ORCA1	42.09	-123.41	1290	348	40.0 ± (1.3)	60.1	PSME
	ORCA2	42.10	-123.40	1461	559	27.5 ± (1.3)	74.8	ABCO
Redwood	REDW1	41.28	-124.01	583	510	32.5 ± (2.2)	137.1	SESE
	REDW2	41.32	-124.00	203	266	73.7 ± (5.2)	265.1	SESE
	REDW3	41.20	-123.99	172	370	41.9 ± (3.3)	168.5	SESE
	REDW4	41.04	-123.80	742	675	21.9 ± (1.1)	68.2	PSME
Whiskeytown	WHIS1	40.59	-122.69	1299	287	14.9 ± (1.0)	11.1	PIPO
	WHIS2	40.59	-122.69	1299	235	24.4 ± (1.4)	19.0	PIPO

* Dominant species by basal area. Species codes are ABCO = *Abies concolor* (white fir), PICO = *Pinus contorta* (lodgepole pine), PIPO = *P. ponderosa* (ponderosa pine), PSME = *Pseudotsuga menziesii* var. *menziesii* (Douglas-fir), SESE = *Sequoia sempervirens* (coast redwood), TSME = *Tsuga mertensiana* (mountain hemlock).

of energy and water inputs, allowing biologically meaningful indices of the site's potential for plant productivity (actual evapotranspiration, AET) and drought stress (climatic water deficit, D). Deficit is calculated as PET minus AET, where PET is potential evapotranspiration. In North America, coniferous forests typically occupy areas where AET < 600 mm yr^{-1} and D < 400 mm yr^{-1} (Stephenson 1990). The distribution of vegetation types can be distinguished by AET and D from local to global scales (Stephenson 1998, Dobrowski et al. 2013). AET has also been found to be an important predictor of species diversity across plant and animal taxa (Hawkins et al. 2003) and species richness for trees in eastern North America (particularly for those areas where AET < 800 mm yr^{-1}) (Fan and Waring 2009).

Water balance parameters were derived from 30 year (1971 to 2000) averages calculated from the Basin Characterization Model (BCM) (Flint et al. 2013). BCM uses interpolated weather station data from the Parameter-elevation Regression on Independent Slopes Model (PRISM, www.prism.oregonstate.edu) (Daly et al. 2002), downscaled to a 270-m grid resolution. PRISM uses instrumental observations and a digital elevation model, making adjustments for features such as elevation, aspect, slope, and rainshadows. BCM uses the PRISM-derived monthly maximum and minimum air temperature and precipitation to drive a regional water balance model. BCM determines PET from a rigorous energy-balance calculation using topographic shading and cloudiness, while AET is calculated on the basis of changes in soil water content. As a result, deep soils provide storage of winter precipitation and maintain lower deficits during the summer dry season, while shallow soils are limited in their storage capacity, so excess winter precipitation is lost to runoff, resulting in greater annual deficits.

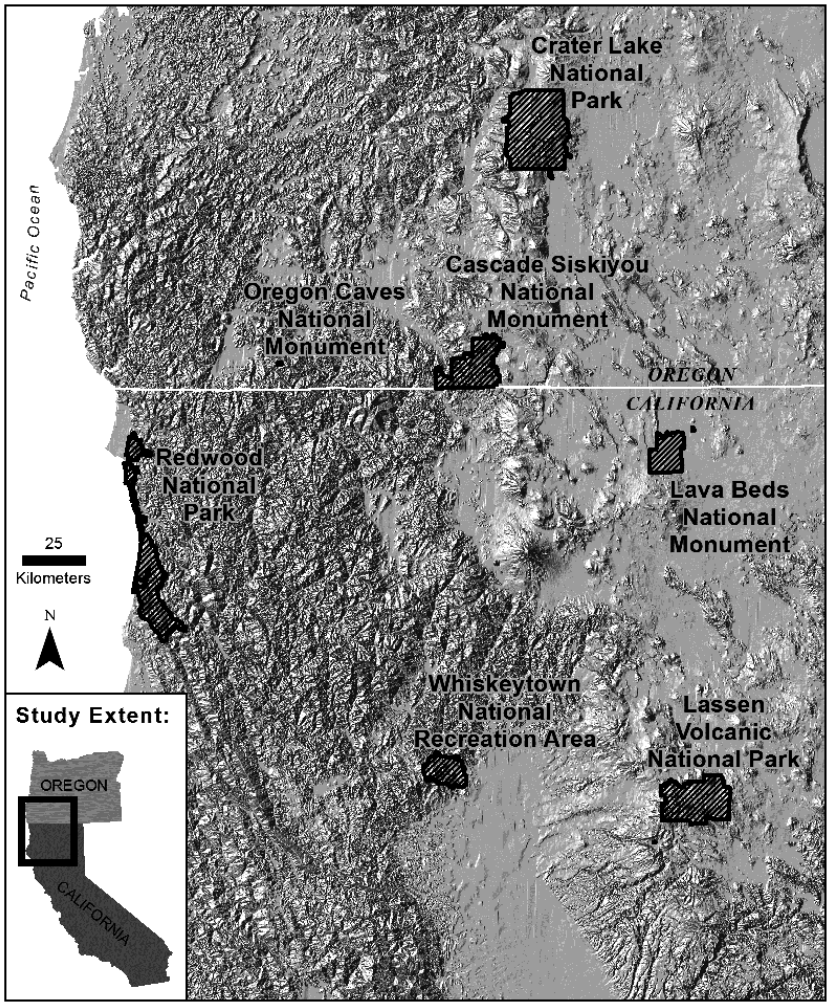

Figure 1. Location of protected areas sampled in the Klamath region.

In addition to historical climate, estimates of future climate change at our sites were derived from averaged BCM outputs run under two Global Circulation Models (GCMs) the GFDL (Geophysical Fluid Dynamics Laboratory, Stouffer et al. 2006), and PCM (Parallel Climate Model, Washington et al. 2000) for three modeled future periods (2010 to 2039, 2040 to 2069, and 2070 to 2099). The GFDL and PCM GCMs have been shown to realistically simulate recent historical climate in California, including seasonal and spatial differences in temperature and precipitation (Cayan et al. 2008). Compared to an ensemble of 16 CMIP3 GCMs, the GFDL and PCM GCMs are considered middle to low range for projections of temperature and precipitation by mid-century (Krawchuk and Moritz 2012), with the GFDL representing warmer, drier conditions, and the PCM representing warmer, wetter conditions. We present modeled differences under the high A2 emissions and the lower B1 emissions scenarios. BCM outputs for historical and future climates were obtained through the California Climate Commons (2014).

Statistical Analyses

We measured forest structure in terms of stand density (stems ha^{-1}), basal area (m^2 ha^{-1}), and size

class distributions. We determined patterns of stem size distributions for each plot using the Gini coefficient as a measure of inequality among stem diameter size classes. Linear models appeared to provide a reasonable description of the relationships between AET and plot basal area, the Gini coefficient, Shannon species diversity (H′), and species richness. Deficit is an index of drought stress and was not tested against observations of forest structure and tree species composition.

We described tree spatial distributions within each plot by considering individual trees as points, and examined nearest neighbor patterns at multiple scales using the inhomogeneous K-function, a second-moment measure that accounts for variability in the average density (also called intensity) of trees across each plot (Baddeley 2010). Intensity is the expected number of points per unit area, and may be constant (homogenous) or vary across locations (inhomogeneous). Plots of kernel estimates of intensity suggested high variations in intensity, suggesting that inhomogeneous models were more appropriate for our data. For each plot we considered spatial patterns within a search radius of up to 25% the side of the plots, or 25 m. We determined the significance of the departure from complete spatial randomness (CSR) by comparing observed values to the 95% simultaneous critical envelope (Baddeley 2010) (avoiding inflation of type I errors [Loosmore and Ford 2006]), calculated from 999 simulations of random point fields, with intensity patterns estimated using a kernel smoothing function. Results are presented in terms of the normalized K statistic, L(h) (where h represents the search radius), which is centered on zero. L(h) values within the 95% critical envelope are consistent with a random distribution of stems, while values below the critical envelope are considered significantly uniform, and values above the critical envelope are considered significantly clumped.

We used a marked point process model to directly test if large (≥ 80 cm DBH) versus small (< 80 cm DBH) stems had contrasting spatial structures using the inhomogeneous K-function normalized at zero [i.e., $L_{\text{large vs. small}}(h)$]. We used different DBH values to categorize large and small trees (e.g., 100 cm DBH), obtaining similar results. We created a 95% simultaneous critical envelope from 999 simulations using random toroidal shifts of the pattern for each size class, where observed values within the envelope indicate similar distributions, values below the envelope indicate the groups "repulse" each other in space, and values above the envelope indicate "attraction" in the groups' spatial pattern.

Results

In our study plots stem density averaged 530 trees ha^{-1} (± 1 SE = 81 trees ha^{-1}, range = 115 to 1355 trees ha^{-1}), while stand basal area averaged 76.8 m^2 ha^{-1} (± 1 SE = 16.3 m^2 ha^{-1}, range = 11.1 to 265.1 m^2 ha^{-1}). Extremely high basal areas were found in plots that contain large individual coast redwood (*Sequoia sempervirens*). Tree species richness was on average five species per plot, but variable with a range of 1 to 11 species (Table 2).

As is typical for uneven-aged forests, the average stem size class distribution followed a 'reverse-j' shaped distribution (Figure 2). The Gini coefficient among plots ranged from 0.21 to 0.60, with a mean value of 0.44 (± 0.5, 2 SE). AET was positively related to the Gini coefficient (β = 0.0004, SE = 0.0002, P = 0.03, adj. R^2 = 0.26). Plot basal area was related linearly to AET (P = 0.01), but this relationship was heavily influenced by plots dominated by coast redwood (graphs of model residuals suggested these plots were outliers and had high leverage). If the coast redwood plots were removed the relationship became non-significant (P = 0.78). Tree species composition was also positively related to AET, explaining the majority of the variance in tree species diversity (β = 0.002, SE = 0.001, P < 0.001, adj. r^2 = 0.58), but only 14% of the variance in tree species richness (P = 0.08) (Figure 3). However, the Oregon Caves plot 2 with 11 species appeared to be an outlier in terms of the linear model, and when removed AET was a better predictor of tree species richness (β = 0.008, SE = 0.001, P = 0.001, adj. r^2 = 0.53).

Water balance parameters for our forest plots spanned the entire ranges commonly associated with temperate coniferous forests (AET range = 67 to 662 mm yr^{-1}, D range = 3 to 596 mm yr^{-1})

TABLE 2. Tree species composition of forest plots.

Site	Plot	Species*
Crater Lake	CRLA1	TSME 91%, ABPR 8%
	CRLA2	ABCO 48%, ABMA 43%, PICO 3%, PIPO 3%, PIMO 1%, TSME 1%
Cascade-Siskiyou	CSNM1	ABCO 50%, PSME 32%, PILA 10%, CADE 8%
	CSNM2	ABCO 52%, PILA 25%, PSME 21%, CADE 3%
Lava Beds	LABE1	PIPO 100%
	LABE2	PIPO 98%, JUOC 2%
Lassen Volcanic	LAVO1	PICO 50%, ABMA 43%, TSME 7%
	LAVO2	TSME 100%
Oregon Caves	ORCA1	PSME 56%, ABCO 39%, CADE 3%, ACMA 2%
	ORCA2	ABCO 53%, PSME 36%, CHLA 4%, CHCH 3%, PILA 3%
Redwood	REDW1	SESE 51%, PSME 38%, TSHE 9%, LIDE 2%
	REDW2	SESE 87%, PSME 13%
	REDW3	SESE 62%, PSME 30%, LIDE 5%, TSHE 3%
	REDW4	PSME 74%, LIDE 18%, ACMA 3%, ARME 2%, QUCH 2%
Whiskey-town	WHIS1	PIPO 51%, PILA 48%, ABCO 1%
	WHIS2	PIPO 54%, PILA 39%, ABCO 3%, PSME 3%

*Species composition of live stems ≥ 5 cm DBH at time of plot establishment. ABCO = *Abies concolor*, ABMA= *A. magnifica*, ABPR = *A. procera.* ACMA = *Acer macrophyllum*, ARME = *Arbutus menziesii*, CADE = *Calocedrus decurrens*, CHCH = *Chrysolepis chrysophylla*, CHLA = *Chamaecyparis lawsoniana*, CONU = *Cornus nuttallii*, JUOC = *Juniperus occidentalis*, LIDE = *Notholithocarpus densiflorus* syn. *Lithocarpus densiflorus,* PICO = *Pinus contorta*, PILA = *P. lambertiana*, PIMO= *P. monticola*, PIPO = *P. ponderosa*, PSME = *Pseudotsuga menziesii* var. *menziesii*, QUCH = *Quercus chrysolepis*, SESE = *S. sempervirens,* TABR = *Taxus brevifolia*, TSHE = *Tsuga heterophylla,* TSME = *T. mertensiana*. Percentages may not add to 100 due to rounding.

(Figure 4). One plot (Lassen Volcanic 2) had unusually low AET for a coniferous forest, but it is a high elevation forest dominated by *Tsuga mertensiana* (mountain hemlock). Over the coming century some forests that currently have low AET (plots Crater Lake 1 and Lassen Volcanic 2) are expected to see large increases in AET (changes

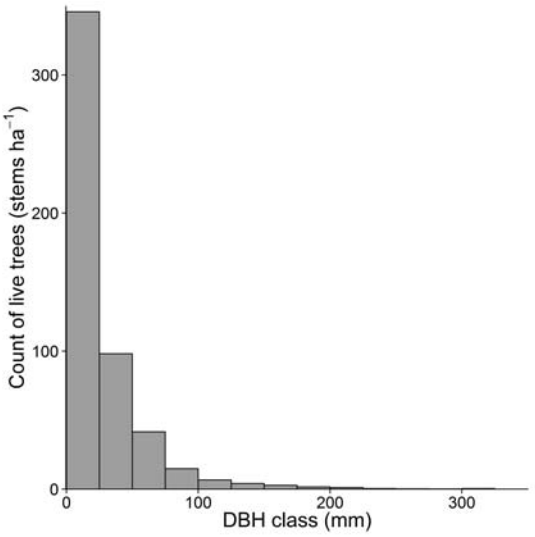

Figure 2. Histogram of total live tree stem size classes across all 16 forest plots.

relative to the 1971 to 2000 period averaged over both GCMs and emissions scenarios; ΔAET_{2039} = 49, ΔAET_{2069} = 68, ΔAET_{2099} = 70 mm yr^{-1}). However, expected changes at our plots appear to be dominated by increases in D (changes relative to the 1971 to 2000 period averaged over all plots, both GCMs and emissions scenarios; ΔD_{2039} = 29, ΔD_{2069} = 58, ΔD_{2099} = 108 mm yr^{-1}) (Figure 4). These changes represent a 17% average increase in AET and a 39% average increase in average D by the end of the century. Sites near the coast (forests at Redwood National Park, AET > 500 mm yr^{-1}) are expected to see relatively smaller changes compared to more interior sites.

Contour plots of the spatial intensity showed that the density of stems was highly variable across each plot (not shown), indicating the need to use inhomogeneous measures of spatial pattern. The inhomogeneous L(h) statistic showed that 12 plots (75%) had significant stem clumping at small spatial scales (0 to 10 m), while 6 plots (38%) had uniform arrangements of stems at distances generally > 10 m (Figure 5). The marked point process model comparing large (≥ 80 cm DBH) versus small (< 80 cm DBH) stems suggested that these groups are strongly segregated for 10 of 16 plots (63%) at spatial scales greater than 10 m.

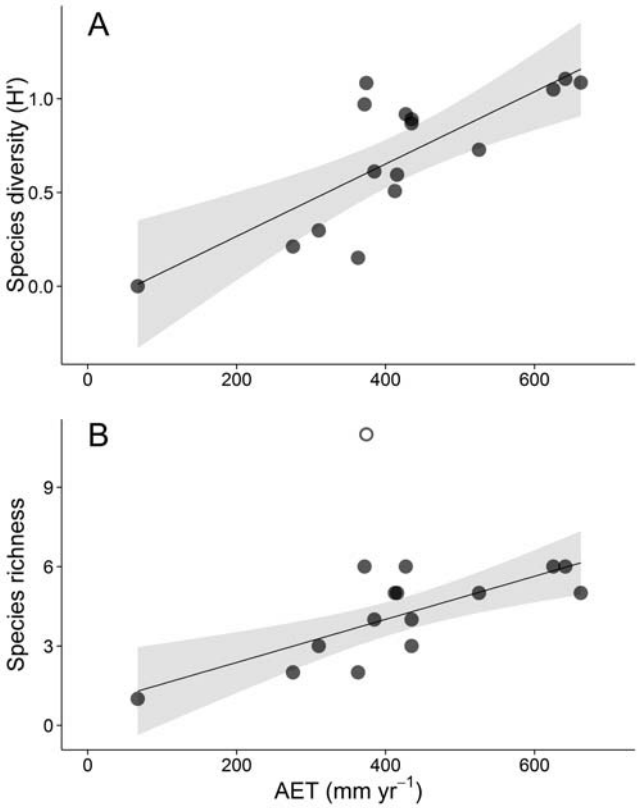

Figure 3. Linear models of actual evapotranspiration (AET) as a predictor of (A) species diversity and (B) richness. The black line is the predicted relationship using a linear model, with shaded areas representing one SE. For the species richness model a single observation (Oregon Caves plot 2) with unusually high richness was removed (open symbol).

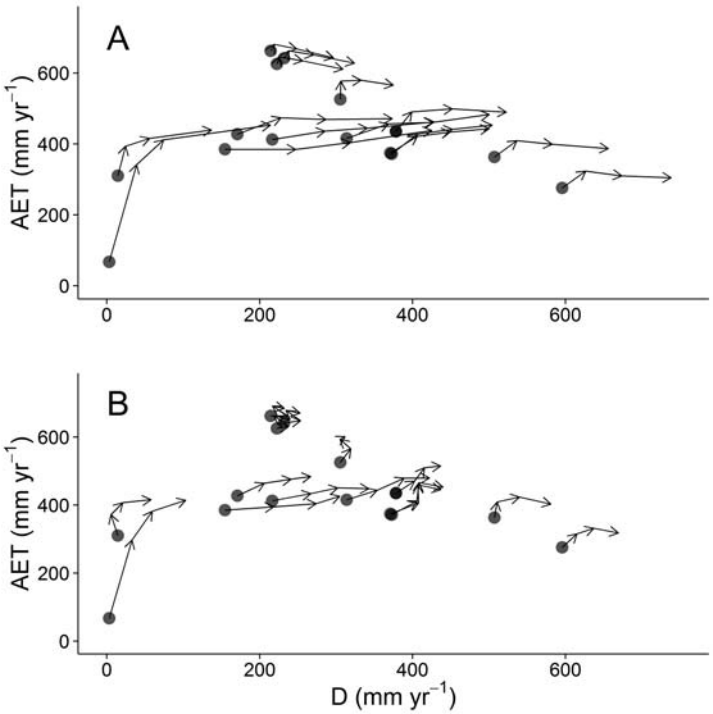

Figure 4. Average actual evapotranspiration (AET) and climatic water deficit (D) for all plots and modeled changes estimated from BCM over the coming century (A) for a high A2 emissions scenario and (B) the lower emissions B2 scenario. Points represent historical 30-year normals (1971-2000), with line segments representing conditions expected at 2010-2039, 2040-2069, and 2070-209 averaged from two general circulation models (GFDL and PCM).

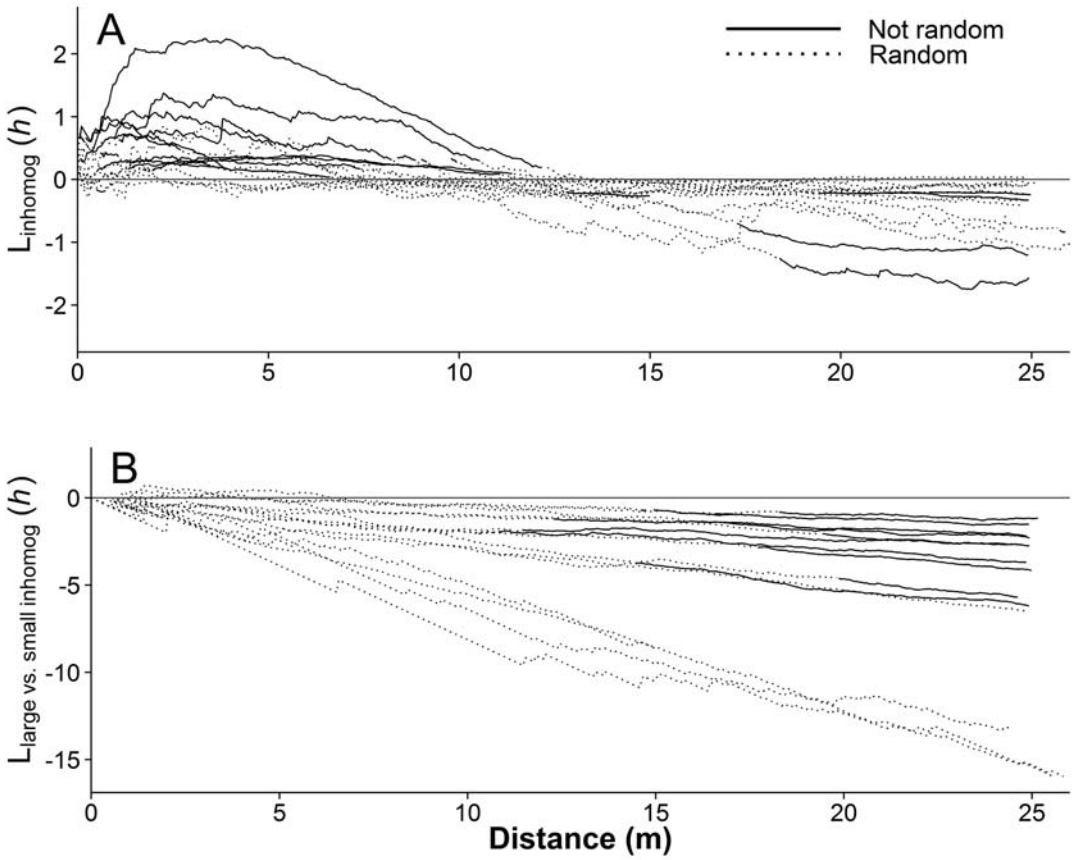

Figure 5. Tree spatial pattern for all species at sixteen old-growth plots (A), and for large (≥ 80 cm DBH) versus small (< 80 cm DBH) trees at all plots. Lines are the observed normalized K-function [L(*h*)] for individual plots. Dashed intervals represent random distributions and solid intervals above and below the zero control line indicate statistically significant ($\alpha = 0.05$) clumping or repulsion, respectively. Significance was determined by departures from 95 percent simultaneous critical envelopes (Baddeley 2010).

Discussion

The old-growth forests we sampled in the Klamath region contain a broad range of climates, with a corresponding variation in structural and compositional attributes. The positive associations we found with basal area, diversity, and richness and AET gradient are in agreement with past studies that have demonstrated that forest structure and diversity is highly correlated with climate (Whittaker 1960, Stephenson 1990, Hawkins et al. 2003, Fan and Waring 2009).

The current relationships between climate and forest structure may change over the next 100 years. Current warming trends across the western United States have already resulted in substantial changes to mountain snowpacks and forest hydrology (Mote et al. 2005, Stewart et al. 2005), fire activity in some areas (Littell et al. 2009, Miller et al. 2012, Williams et al. 2012), reductions in forest biodiversity (Damschen et al. 2010, Harrison et al. 2010), rapidly increasing forest tree mortality rates (van Mantgem and Stephenson 2007, van Mantgem et al. 2009), and increased risks of forest die-back (Allen et al. 2010). We might expect similar trends at our forest sites within Klamath region (Olson et al. 2012). Indeed, projected conditions estimated from downscaled GCMs suggest that by the close of this century many of our forest sites will experience changing climatic conditions.

Another important consideration is heterogeneity in the magnitude and direction of projected environmental change across our sites (Figure 4). Whereas moisture-limited forests (fir and pine in our study area) at low- to mid-elevations will possibly be most strongly affected by increases in D, higher elevation forests, where moisture is less limiting, may show increasing AET, due to increases in temperature and longer growing seasons, with modestly increasing D. The Basin Characterization Model also suggests muted changes for AET and D in our coastal redwood forest plots, likely due to continuing marine influences on temperatures.

Yet predictions of future forest conditions in the Klamath region are highly uncertain. For example, our poor understanding of fog patterns makes it difficult to confidently predict changes for coastal forests (Johnstone and Dawson 2010). We are also unsure of the mechanisms whereby increased drought stress leads to tree mortality so that predictions of forest demographic responses to climatic change is highly uncertain (Das et al. 2013). Tree seedlings are also likely to be highly sensitive to climate (van Mantgem et al. 2006), and seedlings of some species may already be responding to observed climate change (Bell et al. 2014). The potential for greater forest pest activity is also unknown (Weed et al. 2013). This might be particularly important for exotic pathogens, such as white pine blister rust (*Cronartium ribicola*) (McDonald and Hoff 2001, Sarr et al. 2007) and sudden oak death (*Phytophthora ramorum*) (Maloney et al. 2005), which may show increased virulence under warmer conditions. It is also likely that many stressors will work in combination, so that their interactions may lead to more pronounced impacts (e.g., van Mantgem et al. 2013). In contrast, physiological research has suggested that some tree species may show growth enhancement with elevated CO_2, through increases in water use efficiency (Norby et al. 1999), yet the implications for the full suite of species and age classes in old-growth forests in the Klamath region is scarcely understood.

While predicting exact future conditions in the Klamath region may not be possible, managers can still act (Millar et al. 2007). There are likely to be areas, even in interior sites, that resist change (e.g., north facing slopes or areas with deep, well-watered soils). The identification of these potential refugia may help to prioritize management actions (Olson et al. 2012). Conversely, sites that are already near the climatic edge for supporting forests may not be worth large management investments. Managers can also act to help buffer the effects of climate changes by reducing current threats via removing/suppressing exotic species or restoring historical fire regimes. However, given the magnitude of expected changes, historical conditions may not automatically provide the most resistant and resilient ecosystem states (sensu Walker et al. 2004).

If managers are seeking to recreate historical forest structures we found little support for restoration treatments that create uniform stem spatial patterns (Bauhus et al. 2009). We identified strong evidence of clumping at small spatial scales (from approximately < 10 m) and generally random spatial arrangement of stems at larger spatial scales. Moreover, there appeared to be segregation between large and small stems at large (approximately > 10 m) spatial scales. These results are in agreement with findings from other coniferous forests (Larson and Churchill 2008, van Mantgem and Stuart 2012). How well current old-growth conditions reflect stand structure prior to European settlement is difficult to determine precisely (Stephenson 1999). The disruption of historical disturbance regimes, exotic species (including pathogens), fragmentation, and other changes have likely altered old-growth forests. But until a better model for restoration targets is identified, these old-growth stands provide our best model of reference conditions in the Klamath region.

These results represent an initial effort to quantify current old-growth forest conditions in the Klamath region. Future surveys will allow us to measure forest dynamics, particularly changes in forest demographic rates (growth, recruitment and mortality). These plots may also serve to provide a setting to study a wider suite of measures of biodiversity, such as insects or land-birds. Our plot data could be combined with other forest monitoring efforts to get a broader understanding of old-growth forest in the Klamath region (e.g.,

the national-scale Forest Inventory and Analysis program, Bechtold and Patterson 2005). Ideally, plot-based measurements could be combined with remotely sensed imagery to provide large scale assessments of forest condition (Gonzalez et al. 2010). The continued measurement and monitoring of these old-growth stands is needed to ensure we are able detect any subtle, pervasive trends that may be occurring (van Mantgem et al. 2009).

Acknowledgments

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Literature Cited

Agee, J. K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC.

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J.H. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660-684.

Asner, G. P., G. V. N. Powell, J. Mascaro, D. E. Knapp, J. K. Clark, J. Jacobson, T. Kennedy-Bowdoin, A. Balaji, G. Paez-Acosta, E. Victoria, L. Secada, M. Valqui, and R. F. Hughes. 2010. High-resolution forest carbon stocks and emissions in the Amazon. Proceedings of the National Academy of Sciences 107:16738-16742.

Baddeley, A. 2010. Analysing spatial point patterns in R, version 4.1. CSIRO. Available online at http://www.csiro.au/resources/pf16h (accessed 19 May 2014).

Bauhus, J., K. Puettmann, and C. Messier. 2009. Silviculture for old-growth attributes. Forest Ecology and Management 258:525-537.

Bechtold, W. A., and P. L. Patterson. 2005. The Enhanced Forest Inventory and Analysis Program—National Sampling Design and Estimation Procedures. General Technical Report SRS-80, USDA Forest Service, Asheville, NC.

Bell, D. M., J. B. Bradford, and W. K. Lauenroth. 2014. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. Global Ecology and Biogeography 23:168-180.

California Climate Commons. 2014. The basin characterization model downscaled climate and hydrology datasets. Available online at http://climate.calcommons.org/article/featured-dataset-california-basin-characterization-model (accessed March 25, 2014).

Cayan, D. R., E. P. Maurer, M. D. Dettinger, M. Tyree, and K. Hayhoe. 2008. Climate change scenarios for the California region. Climatic Change 87:S21-S42.

Condit, R. 1998. Tropical Forest Census Plots. Springer Verlag, New York.

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

Daly, C., W. P. Gibson, G. H. Taylor, G. L. Johnson, and P. Pasteris. 2002. A knowledge-based approach to the statistical mapping of climate. Climate Research 22:99-113.

Damschen, E. I., S. Harrison, and J. B. Grace. 2010. Climate change effects on an endemic-rich edaphic flora: resurveying Robert H. Whittaker's Siskiyou sites (Oregon, USA). Ecology 91:3609-3619.

Das, A. J., N. L. Stephenson, A. Flint, T. Das, and P. J. van Mantgem. 2013. Climatic correlates of tree mortality in water-and energy-limited forests. PLOS ONE 8:e69917.

DellaSala, D. A., S. B. Reid, T. J. Frest, J. Strittholt, and D. Olson. 1999. A global perspective on the biodiversity of the Klamath-Siskiyou ecoregion. Natural Areas Journal 19:300-319.

Dobrowski, S. Z., J. Abatzoglou, A. K. Swanson, J. A. Greenberg, A. R. Mynsberge, Z. A. Holden, and M. K. Schwartz. 2013. The climate velocity of the contiguous United States during the 20th century. Global Change Biology 19:241-251.

Fan, W., and R. H. Waring 2009. Actual Evapotranspiration (AET) and tree species richness in the eastern USA. *In* W. McWilliams, G. Moisen, and R. Czaplewski (editors), Forest Inventory and Analysis (FIA) Symposium 2008. USDA Forest Service, Rocky Mountain Research Station, Park City, UT. Pp. 1-13.

FAO. 2010. Global Forest Resources Assessment 2010. Food and Agriculture Organization of the United Nations, Rome, Italy. Available online at http://www.fao.org/forestry/fra/fra2010/en/ (accessed 19 May 2014).

Flint, L. E., A. L. Flint, J. H. Thorne, and R. Boynton. 2013. Fine-scale hydrologic modeling for regional landscape applications: the California Basin Characterization Model development and performance. Ecological Processes 2:1-21.

Franklin, J. F., and T. A. Spies. 1991. Ecological definitions of old-growth Douglas-fir forests. *In* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff (editors). Wildlife and Vegetation of Unmanaged Douglas-Fir

Forests USDA Forest Service General Technical Report, PNW-GTR-285, Portland, OR. Pp. 61-69.

Franklin, J. F., T. A. Spies, R. V. Pelt, A. B. Carey, D. A. Thornburgh, D. R. Berg, D. B. Lindenmayer, M. E. Harmon, W. S. Keeton, D. C. Shaw, K. Bible, and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155:399-423.

Fulé, P. Z., J. E. Crouse, J. P. Roccaforte, and E. L. Kalies. 2012. Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? Forest Ecology and Management 269:68-81.

Gonzalez, P., G. P. Asner, J. J. Battles, M. A. Lefsky, K. M. Waring, and M. Palace. 2010. Forest carbon densities and uncertainties from Lidar, QuickBird, and field measurements in California. Remote Sensing of Environment 114:1561-1575.

Harrison, S., E. I. Damschen, and J. B. Grace. 2010. Ecological contingency in the effects of climatic warming on forest herb communities. Proceedings of the National Academy of Sciences 107:19362-19367.

Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J.-F. Guégan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, and E. M. O'Brien. 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105-3117.

Johnstone, J. A., and T. E. Dawson. 2010. Climatic context and ecological implications of summer fog decline in the coast redwood region. Proceedings of the National Academy of Sciences 107:4533-4538.

Krawchuk, M., and M. Moritz. 2012. Fire and Climate Change in California. California Energy Commission. Publication number: CEC-500-2012-026.

Larson, A. J., and D. Churchill. 2008. Spatial patterns of overstory trees in late-successional conifer forests. Canadian Journal of Forest Research 38:2814-2825.

Lindenmayer, D. B., and J. F. Franklin. 2002. Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach. Island Press, Washington, DC.

Littell, J. S., D. McKenzie, D. L. A Peterson, and A. L. A Westerling. 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916-2003. Ecological Applications 19:1003-1021.

Loosmore, N., and E. Ford. 2006. Statistical inference using the G or K point pattern spatial statistics. Ecology 87:1925-1931.

Luyssaert, S., E. D. Schulze, A. Borner, A. Knohl, D. Hessenmoller, B. E. Law, P. Ciais, and J. Grace. 2008. Old-growth forests as global carbon sinks. Nature 455:213-215.

Mackey, B., D. A. DellaSala, C. Kormos, D. Lindenmayer, N. Kumpel, B. Zimmerman, S. Hugh, V. Young, S. Foley, and K. Arsenis. 2014. Policy options for the world's primary forests in multilateral environmental agreements. Conservation Letters 8:139-147.

Maloney, P. E., S. C. Lynch, S. F. Kane, C. E. Jensen, and D. M. Rizzo. 2005. Establishment of an emerging generalist pathogen in redwood forest communities. Journal of Ecology 93:899-905.

McDonald, G. I., and R. J. Hoff. 2001. Blister rust: An introduced plague. *In* D. F. Tomback, S. F. Arno, and R. E. Keane (editors). Whitebark Pine Communities. Island Press, Washington, DC. Pp. 193-220.

Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17:2145-2151.

Miller, J., C. Skinner, H. Safford, E. E. Knapp, and C. Ramirez. 2012. Trends and causes of severity, size, and number of fires in northwestern California, USA. Ecological Applications 22:184-203.

Mote, P. W., A. F. Hamlet, M. P. Clark, and D. P. Lettenmaier. 2005. Declining mountain snowpack in western north America. Bulletin of the American Meteorological Society 86:39-49.

Norby, R. J., S. D. Wullschleger, C. A. Gunderson, D. W. Johnson, and R. Ceulemans. 1999. Tree responses to rising CO_2 in field experiments: implications for the future forest. Plant, Cell & Environment 22:683-714.

Oliver, C. D., and B. C. Larson. 1990. Forest Stand Dynamics. McGraw-Hill, Inc., New York.

Olson, D., D. A. DellaSala, R. F. Noss, J. R. Strittholt, J. Kass, M. E. Koopman, and T. F. Allnutt. 2012. Climate change refugia for biodiversity in the Klamath-Siskiyou ecoregion. Natural Areas Journal 32:65-74.

Peng, C., Z. Ma, X. Lei, Q. Zhu, H. Chen, W. Wang, S. Liu, W. Li, X. Fang, and X. Zhou. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. Nature Climate Change 1:467-471.

Rizzo, D. M., and M. Garbelotto. 2003. Sudden oak death: endangering California and Oregon forest ecosystems. Frontiers in Ecology and the Environment 1:197-204.

Sarr, D. A., D. C. Odion, S. R. Mohren, E. E. Perry, R. L. Hoffman, L. K. Bridy, and A. A. Merton. 2007. Klamath Network: Vital Signs Monitoring Plan. National Park Service. Natural Resource Report NPS/KLMN/NRR-2007/016, Ashland, OR.

Sawyer, J. O. 2007. Forests of northwestern California. *In* M. B. Barbour, T. Keeler-Wolf, and A. A. Schoeherr (editors). Terrestrial Vegetation of California. University of California Press, Berkeley. Pp. 253-295.

Spies, T. A., M. A. Hemstrom, A. Youngblood, and S. Hummel. 2006. Conserving old-growth forest diversity in disturbance-prone landscapes. Conservation Biology 20:351-362.

Stephenson, N. L. 1990. Climatic control of vegetation distribution: the role of the water balance. American Naturalist 135:649-670.

Stephenson, N. L. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of veg-

etation distribution across spatial scales. Journal of Biogeography 25:855-870.

Stephenson, N. L. 1999. Reference conditions for giant sequoia forest restoration: structure, process, and precision. Ecological Applications 9:1253-1265.

Stewart, I. T., D. R. Cayan, and M. D. Dettinger. 2005. Changes toward earlier streamflow timing across Western North America. Journal of Climate 18:1136-1155.

Stouffer, R., A. Broccoli, T. Delworth, K. Dixon, R. Gudgel, I. Held, R. Hemler, T. Knutson, H.-C. Lee, and M. Schwarzkopf. 2006. GFDL's CM2 global coupled climate models. Part IV: Idealized climate response. Journal of Climate 19:723-740.

Strittholt, J. R., D. A. Dellasala, and H. Jiang. 2006. Status of mature and old growth forests in the Pacific Northwest. Conservation Biology 20:363-374.

van Mantgem, P., J. C. B. Nesmith, M. Keifer, E. Knapp, A. L. Flint, and L. E. Flint. 2013. Climatic stress increases forest fire severity across the western United States. Ecology Letters 16:1151-1156.

van Mantgem, P. J., and N. L. Stephenson. 2007. Apparent climatically-induced increase of mortality rates in a temperate forest. Ecology Letters 10:909-916.

van Mantgem, P. J., N. L. Stephenson, J. C. Byrne, L. D. Daniels, J. F. Franklin, P. Z. Fulé, M. E. Harmon, A. J. Larson, J. M. Smith, A. H. Taylor, and T. T. Veblen. 2009. Widespread increase of tree mortality rates in the western United States. Science 323:521-524.

van Mantgem, P. J., N. L. Stephenson, and J. E. Keeley. 2006. Forest reproduction along a climatic gradient in the Sierra Nevada, California. Forest Ecology and Management 225:391-399.

van Mantgem, P. J., and J. D. Stuart 2012. Structure and dynamics of an upland old-growth forest at Redwood National Park, California. *In* R. B. Standiford, T. J. Weller, D. D. Piirto, and J. D. Stuart (editors), Proceedings of Coast Redwood Forests in a Changing California: A Symposium for Scientists and Managers. USDA Forest Service General Technical Report PSW-GTR-238, Albany, CA. Pp. 323-333.

Walker, B., C. S. Holling, S. R. Carpenter, and A. Kinzig. 2004. Resilience, adaptability and transformability in social-ecological systems. Ecology and Society 9:5.

Washington, W., J. Weatherly, G. Meehl, A. Semtner Jr, T. Bettge, A. Craig, W. Strand Jr, J. Arblaster, V. Wayland, and R. James. 2000. Parallel climate model (PCM) control and transient simulations. Climate Dynamics 16:755-774.

Weed, A. S., M. P. Ayres, and J. A. Hicke. 2013. Consequences of climate change for biotic disturbances in North American forests. Ecological Monographs 83:441-470.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30:279-338.

Williams, A. P., C. D. Allen, A. K. Macalady, D. Griffin, C. A. Woodhouse, D. M. Meko, T. W. Swetnam, S. A. Rauscher, R. Seager, H. D. Grissino-Mayer, J. S. Dean, E. R. Cook, C. Gangodagamage, M. Cai, and N. G. McDowell. 2012. Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change 3:292-297.