

Forest mortality in high-elevation whitebark pine (*Pinus albicaulis*) forests of eastern California, USA; influence of environmental context, bark beetles, climatic water deficit, and warming

Constance I. Millar, Robert D. Westfall, Diane L. Delany, Matthew J. Bokach, Alan L. Flint, and Lorraine E. Flint

Abstract: Whitebark pine (*Pinus albicaulis* Engelm.) in subalpine zones of eastern California experienced significant mortality from 2007 to 2010. Dying stands were dense (mean basal area 47.5 m²/ha), young (mean 176 years), and even-age; mean stand mortality was 70%. Stands were at low elevations (mean 2993 m), on northerly aspects, and experienced warmer, drier climates relative to the regional species distribution. White pine blister rust was not observed; mountain pine beetle infestations were extensive. Ring widths were negatively correlated with climatic water deficit and positively correlated with water-year precipitation. Although trees that survived had greater growth during the 20th century than trees that died, in the 19th century trees that eventually died grew better than trees that survived, suggesting selection for genetic adaptation to current climates as a result of differential tree mortality. Air surveys (2006–2010) in the Sierra Nevada, Mt. Shasta, and Warner Mountains showed similar trends to the intensive studies. Observed mortality from air surveys was highest in the Warner Mountains (38%) and lowest in the Sierra Nevada (5%); northern aspects at lower elevations within each mountain region had the highest probabilities of mortality and dying stands had higher climatic water deficit. Scenarios for the future of whitebark pine in California are discussed.

Résumé : Une importante vague de mortalité a frappé le pin à écorce blanche (*Pinus albicaulis* Engelm.) dans les régions subalpines de l'est de la Californie de 2007 à 2010. Les peuplements touchés par la mortalité étaient denses (surface terrière moyenne de 47,5 m²/ha), jeunes (âge moyen de 176 ans) et équiennes; le taux moyen de mortalité était de 70 %. Les peuplements étaient situés à faible altitude (moyenne de 2 993 m), exposés au nord et soumis à un climat plus chaud et plus sec comparativement à la répartition régionale de l'espèce. La rouille vésiculeuse du pin blanc n'a pas été observée mais les infestations du dendroctone du pin ponderosa étaient très répandues. La largeur des cernes annuels était négativement corrélée au déficit hydrique climatique et positivement reliée à la précipitation liquide annuelle. Bien que les arbres qui ont survécu aient eu une meilleure croissance durant le 20^e siècle que les arbres qui sont morts, au 19^e siècle les arbres qui ont fini par mourir avaient une meilleure croissance que les arbres qui ont survécu, un indice de sélection pour une adaptation génétique au climat actuel due à différents taux de mortalité des arbres. Des inventaires aériens (2006–2010) dans la Sierra Nevada, le mont Shasta et les monts Warner ont révélé des tendances semblables à celles qui ont été observées dans les études intensives. La mortalité observée lors des inventaires aériens était la plus forte dans les monts Warner (38 %) et la plus faible dans la Sierra Nevada (5 %); dans chaque région montagneuse, les probabilités de mortalité étaient les plus fortes à faible altitude sur les versants nord et les peuplements touchés par la mortalité avaient un déficit hydrique climatique plus élevé. La discussion porte sur des scénarios d'avenir du pin à écorce blanche en Californie.

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Introduction

Significant tree mortality has been linked to prolonged drought in recent decades across temperate regions worldwide (Allen et al. 2010). High temperatures during droughts in many cases further stressed forest stands, increasing the

likelihood of tree mortality (Breshears et al. 2005; Raffa et al. 2008). Forests may be particularly sensitive to these “global-warming style droughts” (Breshears et al. 2005) in semi-arid regions such as California (Millar et al. 2007) as they are in the southwestern United States (Allen et al. 2010; Williams et al. 2010). Although droughts and associated im-

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C.I. Millar, R.D. Westfall, and D.L. Delany. USDA Forest Service, Pacific Southwest Research Station, 800 Buchanan Street, Albany, CA 94710, USA.

M.J. Bokach. USDA Forest Service, Pacific Southwest Region, Forest Health Protection, 1731 Research Park Drive, Davis, CA 95618, USA.

A.L. Flint and L.E. Flint. US Geological Survey, California Water Science Center, Placer Hall, 6000 J Street, Sacramento, CA 95819, USA.

Corresponding author: Constance I. Millar (e-mail: cmillar@fs.fed.us).

Fig. 1. Location of whitebark pine (*Pinus albicaulis*) study sites in eastern California. (A) Ecology plots study region in the central-eastern Sierra Nevada. Inset *i*: distribution of the species across North America. Inset *ii*: location of the intensive plot study area in central-eastern California. (B) Mountain regions included in the 2006–2010 air survey study (Warner Mountains, Mt. Shasta, and Sierra Nevada).

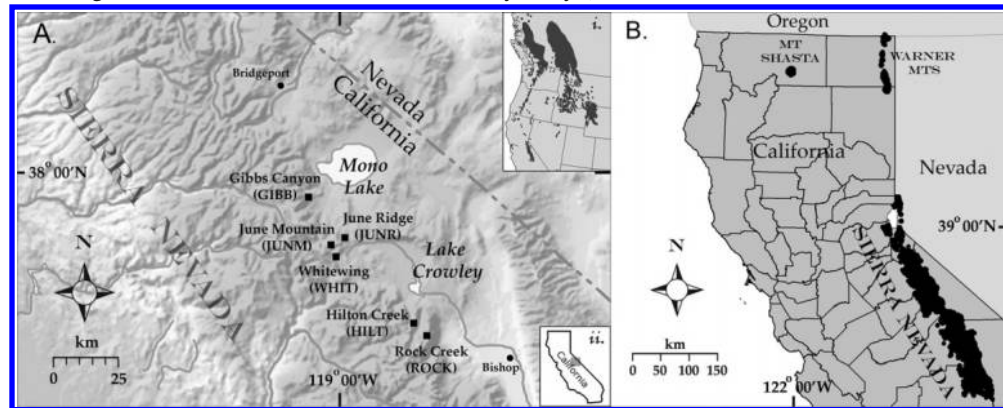


Table 1. Environmental context and sizes (area) of the six ecology plot study sites in the central-eastern Sierra Nevada.

Mortality region	Code	<i>N</i> plots ^a	Elevation low (m)	Elevation high (m)	Aspect(s)	Mean slope (°)	Area (ha) ^b
Gibbs Cyn	GIBB	10	2843	3005	N, NW	20	23
June Ridge	JUNR	10	2968	3052	NW, N, NE	5	15
June Mtn	JUNM	10	2868	2913	N, NE	22	181
Whitewing Mtn	WHIT	20	2825	2941	N	15	127
Hilton Cr Cyn	HILT	6	3154	3157	NW	4	93
Rock Cr Cyn	ROCK	12	3087	3114	N, NE	4	54
Sum		68					493
Mean			2958	3030		12	82

^aMain plots and outplots.

^bDefined by outer perimeter of site, which includes healthy as well as dead trees.

pacts on forest growth and mortality have occurred during previous centuries, as documented by tree-ring reconstructions for the western United States (Cook et al. 2004), the pace of current dieback, exacerbated by rapidly increasing temperatures and land-use practices, appears unprecedented historically (Allen et al. 2010; Benz et al. 2010). Projections for increasing drought in western North America in the next 20–50 years with accelerated warming suggest high probabilities for increasing forest stress and mortality in many regions.

Whereas mortality is occurring in increasingly epidemic levels at low- to mid elevations of western North America, subalpine forests have been considerably less affected. Warming at high elevations conceivably relieves stress in these otherwise climatically limited environments by improving conditions for photosynthesis (Bunn et al. 2005), and conditions such as wide spacing among trees, rocky substrates with little shrub or understory, low relative humidity, low temperatures, and persistent snowpacks have contributed to limiting insect and disease epidemics in high-elevation environments (Logan and Powell 2001, 2007). Subalpine forests in western North America nonetheless have been experiencing increased mortality as a result of interactions from climate, bark beetles, and invasive species. Drought of the late 1980s triggered mortality of high-elevation conifers in Yosemite National Park, California (Guarin and Taylor 2005), and Millar et al. (2007) attributed multiyear drought and late 20th century warming as factors contributing to beetle-mediated dieback in subalpine limber pine (*Pinus flexilis* E.

James) of the Sierra Nevada. Over the past decade, extensive high-elevation mortality has been observed in lodgepole pine (*Pinus contorta* Douglas ex Loudon) in British Columbia (Carroll et al. 2004), limber pine and bristlecone pine (*Pinus longaeva* D.K. Bailey) in Nevada (Baker 2010), limber pine in the Rocky Mountains and intermountain ranges (Kendall 1998), and limber pine, lodgepole pine, Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), white fir (*Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr.), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) in Colorado (Jahnke 2010).

The most significant ongoing mortality episode in subalpine forests of western North America, however, is in whitebark pine (*Pinus albicaulis* Engelm.) (WBP) forests. WBP is a wide-ranging species of western North America (Fig. 1). Primarily upper montane to subalpine, WBP regularly defines upper treeline and co-occurs with a diversity of conifers that varies by location. Biome-wide mortality across much of the species' range is attributed to outbreaks of white pine blister rust (WPBR) caused by the invasive exotic pathogen *Cronartium ribicola* A. Dietr. (Tomback and Achuff 2010) and of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Logan and Powell 2001; Logan et al. 2010). Extensive high-elevation mortality in WBP has been documented in many parts of the species' range (Zeglen 2002; Logan and Powell 2007), with mortality trends increasing dramatically since 1998 (Gibson et al. 2008). Climate has been directly and indirectly implicated as a cofactor in dieback of WBP forests, predisposing trees to insect and pathogen attack

Table 2. Basal areas and percent mortality for six whitebark pine (*Pinus albicaulis*) ecology plot study sites in the central-eastern Sierra Nevada.

Mortality region	<i>N</i> plots ^a	<i>N</i> trees ^b	Basal area (m ² /ha) ^c	Basal area (m ² /ha) ^b	Percent mortality ^d	Percent mortality ^e
GIBB	5	134	55.1	52.7	30	82
JUNR	5	138	40.3	35.9	32	84
JUNM	5	122	52.6	48.6	29	86
WHIT	11	272	52.5	48.0	21	58
HILT	3	53	42.9	37.4	36	90
ROCK	6	70	41.6	38.8	41	50
Sum	35	789				
Mean			47.5	43.6	28.9	70.1

^aMain plots only. Additional outplots are associated with main plots; see Table 1 and text.

^bTrees of all species greater than 12.5 cm diameter, main plots.

^cTrees of all species, all diameters, main plots.

^dWhitebark pines all diameters.

^eWhitebark pines greater than 12.5 cm diameter.

through chronic or acute stress, and enabling expansion of rust and elevational shifts by bark beetles (Logan and Powell 2001, 2007; Thomson 2009).

Mortality in California high-elevation WBP has been considerably less than in other regions of western North America. This situation appears to be changing. Gibson et al. (2008) reported very low levels of mountain pine beetle caused tree mortality on WBP in California from 1998 to 2005, with a mean of 85 ha/year. Mortality jumped to 1600 ha in 2006 and 3100 ha in 2007.

We present results from two studies that investigated the recent mortality event in WBP forests of eastern California. In the first, we investigated stand-level response in ecology plots at six areas of high mortality in the central-eastern Sierra Nevada; in the second, we analyzed data from aerial detection surveys of mortality over WBP forests of the Warner Mountains, Mt. Shasta, and Sierra Nevada. For both studies, the objective was to examine stand-level environmental factors and local- to regional-scale climatic variables that might affect tree growth and mortality.

Materials and methods

Study area and field methods

Ecology plots

The study area extended from central Mono County near Bridgeport, California, to northern Inyo County near Bishop, California, in the eastern Sierra Nevada (Fig. 1). This region lies within WBP's primary distribution in the Sierra Nevada where it is the dominant subalpine conifer throughout high elevations. At lower elevations (2400–3000 m), WBP forms a zone of upright forest, often monotypic, but occurring also with other subalpine conifers including *A. concolor*, *Abies magnifica* A. Murray, *P. contorta*, *Pinus monticola* Douglas ex D. Don, *Tsuga mertensiana* (Bong.) Carrière, and *Juniperus occidentalis* Hook. Above this is a 100–500 m zone of stunted krummholz WBP forest that extends to treeline (~3500 m in the study region). Tree species diversity in the krummholz zone is lower, with WBP most always dominant. Stand structures over the WBP range vary from dense, closed-canopy forests to sparse, open woodlands and solitary to extensive krummholz patches.

We selected the largest patches of tree mortality in the study region for analysis. From north to south, this included stands at Gibbs Canyon (GIBB), June Ridge (JUNR), June Mountain (JUNM), Whitewing Mountain (WHIT), Hilton Creek (HILT), and Rock Creek (ROCK) (Fig. 1). Six-metre circular plots (Table 1), separated by at least 60 m, were distributed randomly throughout the mortality zones at all study regions except WHIT. At WHIT, we used plot locations from a previous study of forest structure, which were at the corners of a rectangular grid across the ridge slope. We excluded plots at WHIT that contained no WBP or were outside the perimeter of highest tree mortality. Within plots, we extracted increment cores from all WBP with stems greater than 12.5 cm diameter at 0.5 m above ground level. For basal area analysis, we counted live trees including seedlings of all sizes and species and measured diameters at 1.5 m above ground. We did not core the occasional stems of trees that died long ago (e.g., downed, rotted stems).

Because the number of live trees was often few or none in the main plots, we established outplots adjacent to main plots to achieve sufficient sample sizes of living and dead tree-ring series to develop chronologies. Outplots were within 25 m of the plot centers and had no standard size or shape. For outplots, we cored an additional five live and five dead trees. Outplot trees were approximately the same size classes as trees in the main plots. For both main plots and outplots, we measured stem diameters of sampled WBP at coring height, noted signs of insect activity, presence-absence of blue-stain fungus, and relative health of the tree.

Air surveys

The Pacific Southwest Region of the USDA Forest Service conducts annual air surveys of forest mortality over federal and state lands in California. Current-year tree mortality is sketch-mapped by aerial observers. Map labels are categorized by damage type, number of trees affected, and affected tree species. Surveyors also note the probable damage-causing agent (fire, bark beetles, etc.). We used data from 2006–2010 air surveys of mid- to upper elevations from the Warner Mountains (Modoc Plateau), southern Cascade Mountains (Mt. Shasta), and Sierra Nevada, extending from Nevada County to the southern extent of the Golden Trout Wilderness, central Tulare County (Fig. 1).

Table 3. Correlations between detrended tree-ring series and the master chronology (r) and number of trees (series) per chronology (n) by site and composites of live and dead tree sets.

Class	Site	n	r
Live	GIBB	24	0.456
	JUNR	22	0.377
	JUNM	22	0.467
	WHIT	40	0.399
	HILT	17	0.508
	ROCK	47	0.431
	Composite	163	0.394
Dead	GIBB	60	0.516
	JUNR	48	0.411
	JUNM	52	0.471
	WHIT	66	0.466
	HILT	35	0.517
	ROCK	50	0.478
	Composite	304	0.419

Note: Only series with more than 100 years of measurable rings and intercorrelations >0.2 were used.

Analyses of field data

Ecology plots

Air-dried increment cores were prepared for ring width measurement, dating, and analysis using standard tree-ring techniques (Cook and Kairiukstis 1990). Pith and bark dates were obtained for all ring width time series that could be dated. Cross-dating was done with reference to live and dead tree chronologies developed for each site by the standard program COFECHA-OSX2007 (Holmes et al. 1986; Krusic and Cook 2007) using live trees to establish calendar dates. Series that had correlations with the master chronology less than 0.2 were excluded as being unlikely to represent regional influences such as climate.

Chronologies were highly correlated among sites, so we combined time series to make composite live and dead chronologies, further eliminating series with low correlations with the master. The combined (live and dead) raw ring width data, prescreened by COFECHA, were imported into ARSTAN vs. 40c (Krusic and Cook 2006) for detrending and standardization of ring widths by biweight robust averaging to remove exogenous factors such as density and to maximize correlations with climate (Cook 1985). Rather than standard methods, we used the RCS detrending algorithm (Esper et al. 2002) for its skill in preserving low-frequency trends in long tree-ring chronologies despite short segment lengths. For detrending, we used a stiff n -year spline in a wavelength of $0.67n$ years, where n is the length of the chronology, with a 50% cutoff of the frequency response. No end-of-series biases were apparent.

Air surveys

Sketch maps from 2006 to 2010 air surveys were digitized and converted to GIS layers in ArcGIS 9.1.3 (Environmental Systems Resource Institute 2009) for analysis. Total distribution of WBP was delineated for California using three data sources: (i) the WBP species distribution layer created by the

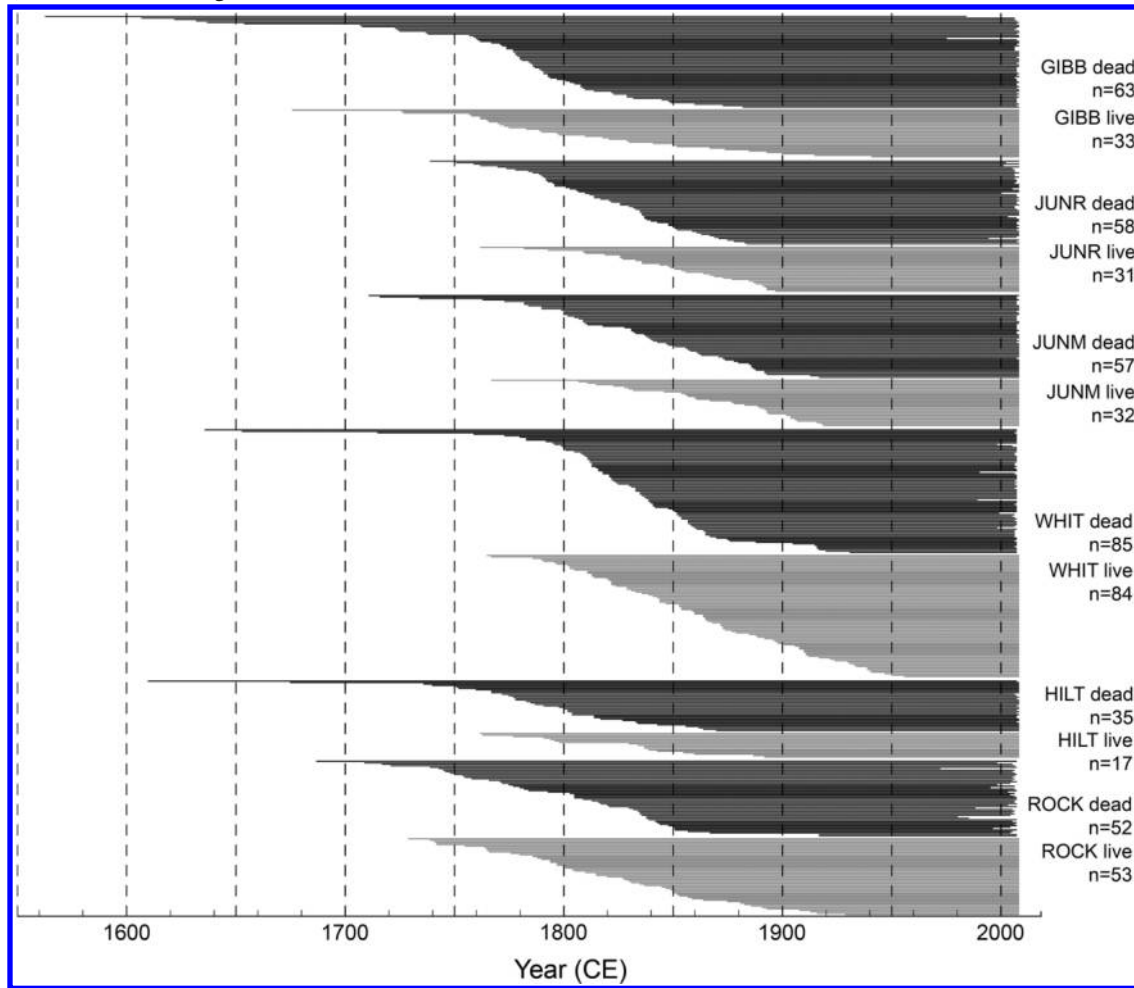
US Forest Service Forest Health Technology Enterprise Team (FHTET) for use in the 2012 National Insect and Disease Risk Model (US Forest Service 2011a), (ii) the US Forest Service Region 5 Remote Sensing Lab existing vegetation (“eveg”) layers (US Forest Service 2011b), selecting for all polygons where WBP was the only or the dominant species, and (iii) aerial survey polygons from 2006 to 2010 where WBP was indicated to be the dominant host species (US Forest Service 2011c). Selected polygons from the latter two of these sources were converted into raster data sets and snapped to the FHTET layer at a spatial resolution of 30 m (900 m² pixels), which roughly corresponded to the area of the smallest mortality polygons. The area of analysis was constrained to include only those areas that had been flown in all 5 years. Pixels were coded for the presence of WBP as indicated by any of the three source layers and for the presence of WBP mortality in any of the 5 years of aerial survey data. Mortality was coded as a binary variable and thus did not indicate which or how many years mortality had been mapped or the quantitative amount of mortality within the pixel (which potentially ranged from a single stem to all trees within the pixel). Three regions of relatively large and contiguous WBP forests were selected from the overall data set, excluding small disjunct and isolated stands; these were the Warner Mountains, Mt. Shasta (Southern Cascade Mountains), and the Sierra Nevada. WBP pixels in these regions were converted to a centroid point layer and elevation and aspect values transferred to each point from their respective rasters. The resulting table of WBP pixels showing presence-absence of mortality, region, elevation, and aspect was exported to Excel for analysis.

Nominal logistic regression analyses were performed in JMP (SAS Institute Inc. 2011) using elevation as a continuous covariate and aspect classed into nine groups including flat. Pixel mortality class (live, dead) was the dependent variable weighted by bin counts. In the logistic regressions, frequency of mortality was assessed from 0% to 100% against a linear model of aspect, elevation, and aspect \times elevation interaction for each mountain region (Warner Mountains, Mt. Shasta, and Sierra Nevada) for the combined 5 year (2006–2010) data set.

Because the Warner Mountains WBP stands clustered into distinct subregions with high variance among them, we subdivided the Warner Mountains data sets into north, central, and south groups. Further, to compare air survey results with those from ecology plot monitoring in the Sierra Nevada, we extracted all air survey pixels (277 837 total) and their associated survival and mortality data for a central-eastern Sierra Nevada subset of the Sierra Nevada region using polygons of dominant vegetation from the California Gap Analysis (Davis et al. 1998). This subregion included pixel records east of the Sierra crest and included approximately the same north to south latitudinal extent as the six ecology plot sites.

Models with the best fit as identified by the lowest Akaike information criterion (a measure of relative goodness of fit) values were chosen; in cases where two models had identical Akaike information criterion values, the simpler model (fewer terms) was chosen. Significance of difference in frequency of mortality was evaluated by χ^2 tests on log-likelihood ratios. For the central-eastern Sierran subset, we classed elevation into 100 m intervals and latitude and longitude into 200 m

Fig. 2. Individual tree-ring series ages for six whitebark pine (*Pinus albicaulis*) stands in the central-eastern Sierra Nevada. Dark lines are dead trees and light lines are live trees. Birth (pith) dates (common era) are shown at the left and death dates (for dead trees) and bark dates (for live trees) are shown at the right. Overall $N = 600$ trees.



intervals to get sufficient numbers of pixel counts per bin. We then applied a model of all factors, including main effects and all interactions, with aspect as a nominal effect and elevation, latitude, and longitude as continuous effects. Again, the pixel mortality class was the dependent variable, weighted by bin counts. In this case, we did not select effects but merely evaluated the model with respect to the log-likelihood χ^2 values of the effects. Rather than graphing raw mortality data as a function of elevation and aspect, we created smoothed curves by fitting the predicted probabilities of mortality with a third-order polynomial of elevation by aspect using separate fits for each aspect.

Climate and tree response analysis

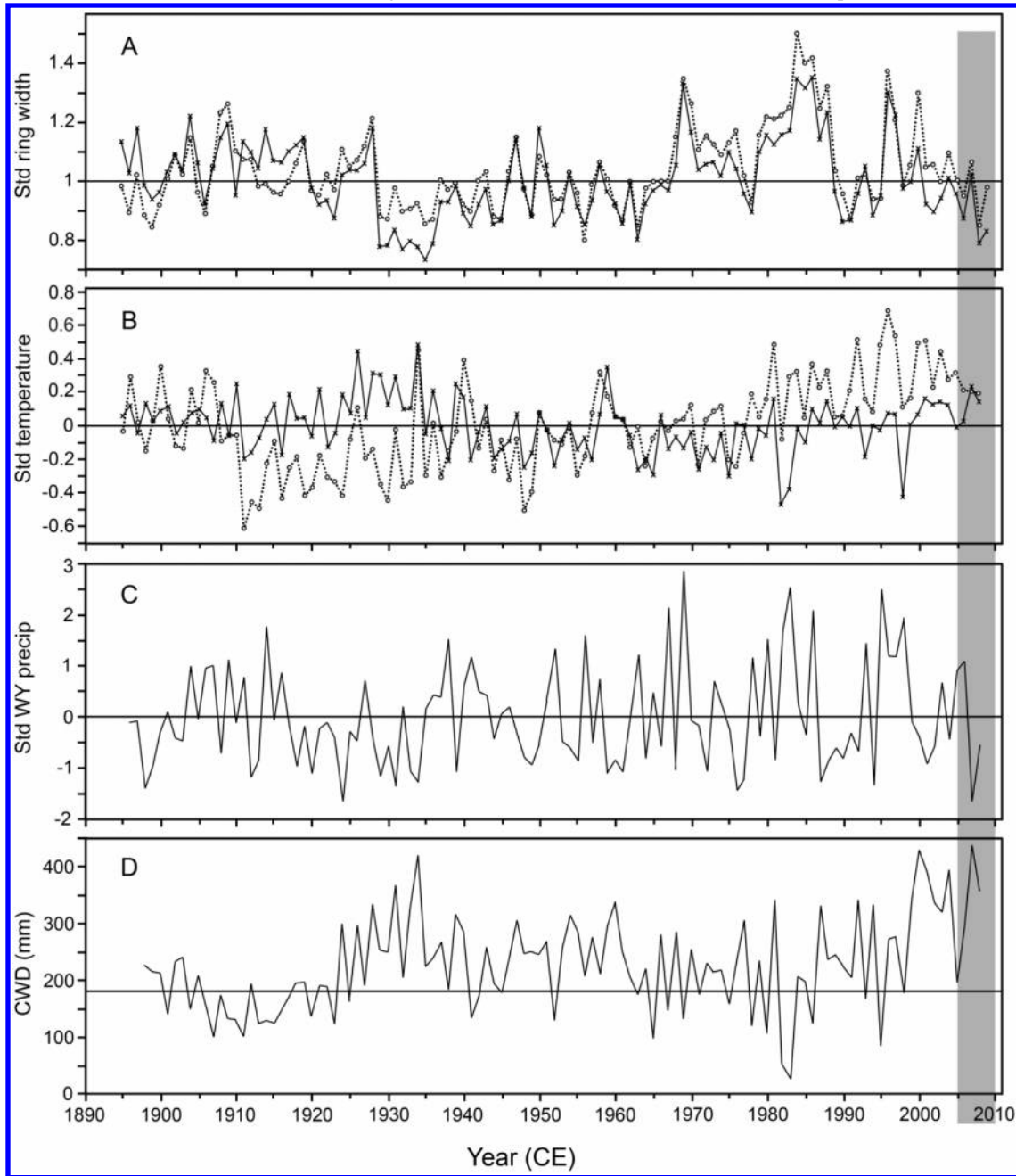
Long-term instrumental climate records were compiled from four Historical Climate Network weather stations with a period of record of 1895 to present: Davis, Lake Tahoe, Yosemite, and Independence (Easterling et al. 1999). The data sets were selected for having long records, bias adjusted, and missing data estimated. Following the approach of Millar et al. (2007), we statistically combined the data from the individual stations into composite records (1895–2009), taking the first principal component for mean monthly minimum and maximum temperature, respectively, and annual, winter

(October–March), and water-year (WY) (July–June) precipitation, respectively. Higher correlations of tree growth with winter and WY precipitation led us to use those variables rather than annual climate values. To assess moisture availability for plant growth, we also used annual climatic water deficit (CWD) for the same time period. CWD is a measure of evaporative demand that exceeds available water and is computed as potential evapotranspiration minus actual evapotranspiration. CWD ranges from zero, when soils are fully saturated, to positive values with no upper limit. Higher values indicate soils depleted of water and water increasingly unavailable to meet transpiration demand. CWD values were modeled for each of the six mortality sites and the central-eastern Sierra Nevada subsample of air survey pixels from PRISM regional climate projections, downscaled to 270 m (L.E. Flint and A.L. Flint, unpublished) and applied to a regional water balance model (Flint and Flint 2007a, 2007b).

As no high-elevation, long-term instrumental weather stations exist near our sites in the central-eastern Sierra Nevada, we evaluated recent (1971–2000) climate conditions with the 30 arc-sec (~800 m grid) PRISM climate model (Daly et al. 1994). We extracted data for annual, January, and July temperature, respectively, and annual, January, and July minimum and maximum temperature, respectively. We

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Fig. 3. Whitebark pine (*Pinus albicaulis*) mortality (interval shown as a band of grey from 2004 to 2010 common era), growth in six ecology plot stands of the central-eastern Sierra Nevada, and climatic trends for 1895–2010. (A) Whitebark pine growth, composite of six ecology plot sites: solid line, dead trees; broken line, live trees. (B) Standardized minimum monthly temperature (broken line) and maximum monthly temperature (solid line) in the composite record derived from four regional weather stations. (C) Standardized water-year (WY) precipitation derived from the same composite climate record. (D) Climatic water deficit (CWD) modeled from regional downscaled climate projections (Flint and Flint 2007a, 2007b). Positive values indicate greater demand for moisture than available for transpiration (i.e., water stress).

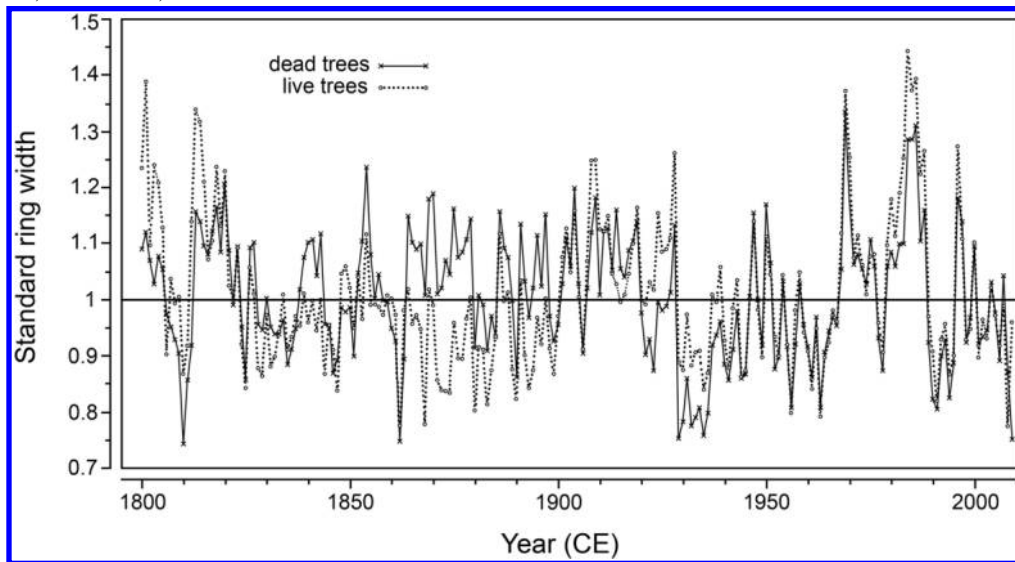


downscaled these values using methods described in Millar et al. (2006) to estimate observed climate on a grid size of ~400 m. We also extracted PRISM data for the tiles overlying the six ecology plot sites and for the central-eastern Sierra Nevada subsample of the air survey pixels.

To test relationships of climate and ecological responses, we analyzed simple linear correlations (SAS Institute Inc. 2011) as well as nonlinear relationships. For the latter, we conducted a second-order least squares response-surface model (JMP) (SAS Institute Inc. 2011) of standardized ring

widths versus minimum and maximum annual temperature, respectively, winter and WY precipitation, and annual CWD as well as standard indices of the Palmer Drought Severity Index (California Division 5; indices from the National Oceanic and Atmospheric Administration (2006) for 1900–2006), Pacific Decadal Oscillation (Mantua et al. 1997), Arctic Oscillation (Thompson and Wallace 1998), and North Atlantic Oscillation (Hurrell 1995). We evaluated the behavior of these variables in second-order response-surface models of the form $(x + y + \dots) + (x + y + \dots)^2$, where redundant inter-

Fig. 4. Whitebark pine (*Pinus albicaulis*) growth from six ecology plot sites in central-eastern Sierra Nevada for 1800–2010 common era. Solid line, dead trees; broken line, live trees.



action terms were omitted. Living and dead classes were included in a mixed-effect, least-squares model with interactions between class effects and surface model terms to test heterogeneity of slopes between the effects.

Minimum and maximum temperatures, 2-year-lagged winter precipitation, and 2-year-lagged CWD were the final variables used in the model. We graphed predicted growth using the response-surface model of variables screened where contour intervals represent standardized growth response and axes are units of standardized deviations from the mean for each climate variable, and in each case, calculations were run under mean, low, and high values of the remaining variables. Climate space for the models is contained within the envelope of the composite 20th century instrumental weather record.

Results

Environmental context and stand demographics

Ecology plots

Environmental contexts of the mortality stands were highly consistent across the six sites (Table 1). Stands were located at the far eastern edges of the Sierran escarpment and in relatively low-elevation portions of WBP's distribution in this region. The mean elevation (center of stands) was 2993 m (range 2825–3157 m). Aspects were dominantly north, including northwest and northeast; slopes averaged 12°. Soils were diverse and included granitic, metamorphic, and volcanic (tephra). The study stands ranged in size from 15 to 181 ha (mean 82 ha) (Table 1).

From the six mortality regions, we sampled 68 plots (including main and outplots) and cored 730 WBP stems in total (Tables 1 and 2). Stands comprised dominantly WBP of the conifer class, with very limited admixture of other species (primarily lodgepole pine). Mean stem diameter over all sites for WBPs cored was 25.9 cm (SD 8.1 cm). Mean diameters were not significantly different between dead and live tree classes. Stands were relatively dense, with mean basal area

for standing live, dying, and recently dead trees of 47.5 m²/ha (range 40.3–55.1 m²/ha) for all species and a mean of 43.6 m²/ha (range 35.9–52.7 m²/ha) for WBP stems. Mean site mortality for WBP with diameters greater than 12.5 cm at coring height was 70% and ranged from 50% at ROCK, where plot locations included areas of low mortality, to 90% at HILT. Mortality in trees smaller than 12.5 cm stem diameter was very low and trace in the seedling and sapling classes. Live trees of similar size and stature were mixed with dead trees in each stand, although there were patches of nearly total stem death. Rare lodgepole pines occurring within plots also were dying. Evidence of mountain pine beetle was prominent as the likely ultimate cause of tree death, with diagnostic galleries, exit holes, and dead adult insects encased in pitch. Blue-stain fungus (*Ophiostoma* spp.) was evident on increment cores of all dead trees and on cores of many trees scored in the field as fading (dying). Except legacy deadwood, trees appeared to have died within the past several years, as indicated by foliage color and foliage still on the branches, intact bark, and upright trees.

Of WBP stems cored in the field, we were able to measure ring widths and accurately cross-date a total of 250 live trees and 350 dead trees. Individual tree-ring series from dead and live trees at each site cross-dated strongly against each other; mean series correlations ranged from 0.377 to 0.517 (Table 3). High correlations of series among stands (except JUNM, which was omitted) enabled us to build a composite chronology.

Tree ages of both live and dead stems at all stands were relatively young compared with expected longevity of WBP, clustering between 130 and 220 years, with an overall mean age of 176 ± 52.3 years (mean ± SD) (Fig. 2). Dead trees were significantly older (χ^2 tests, $p < 0.05$) than live trees within stands, with a dead group mean age of 198 ± 46.3 years and a live group mean age of 167 ± 48.4 years. Mean year of death over all stands was 2007, and mean stand death years ranged from 2004 to 2009 (Figs. 2 and 3). Of the 350 dead trees that we cored, the earliest death date was 1972; only 16 trees died before 2000.

Table 4. Percent mortality and aspects of whitebark pine (*Pinus albicaulis*) stands from air surveys of eastern California including the Warner Mountains, Mt. Shasta, and Sierra Nevada, 2006–2010 data combined.

Region/subregion	Aspect	<i>N</i> pixels mortality	<i>N</i> pixels no mortality	<i>N</i> pixels total	% of aspect pixels scored as mortality	% of total pixels scored as mortality	% of north aspects scored as mortality	% of south aspects scored as mortality
Main mountain regions								
Warner Mountains	North	13 413	17 979	31 391	42.7	12.0		
	East	10 879	14 608	25 487	42.7	9.8		
	South	4 255	7 938	12 192	34.7	3.8		
	West	13 535	28 820	42 354	32.0	12.1		
							32	11
Total ^a		42 088	69 361	111 449		37.8		
Mt. Shasta	North	2 606	5 266	7 872	33.1	12.1		
	East	235	4 547	4 782	4.9	1.1		
	South	71	2 573	2 645	2.7	0.3		
	West	1 006	5 169	6 174	16.3	4.7		
							67	2
Total		3 918	17 555	21 473		18.2		
Sierra Nevada	North	11 953	216 560	228 513	5.2	1.5		
	East	7 397	174 027	181 424	4.1	0.9		
	South	4 920	141 743	146 663	3.3	0.6		
	West	11 882	235 394	247 276	4.8	1.5		
							33	14
Total ^a		36 163	767 798	803 961		4.5		
Grand total		82 169	854 714	936 883		8.8	34	11
Subregions within the Sierra Nevada								
Central-eastern Sierra Nevada	North	6 457	88 001	94 458	6.8	2.4		
	East	2 594	54 954	57 548	4.5	0.9		
	South	3 027	42 397	45 424	6.6	1.1		
	West	8 648	71 645	80 293	10.7	3.1		
							31	15
Total ^a		20 726	257 111	277 837		7.5		
Western Sierra Nevada	North	4 411	137 174	141 585	3.1	0.8		
	East	3 092	92 578	95 670	3.2	0.6		
	South	3 197	105 452	108 649	2.9	0.6		
	West	5 321	175 111	180 432	2.9	1.0		
							28	20
Total		16 021	510 315	526 336		3.0		

^aData for pixels on flat ground are not shown; this accounts for differences between totals and sums of values for cardinal directions.

Fig. 5. Effect of latitude and longitude on probability of whitebark pine (*Pinus albicaulis*) mortality in central-eastern Sierra Nevada populations as delineated by air surveys. (A) North aspects; (B) south aspects. Six ecology plot study sites are also indicated.

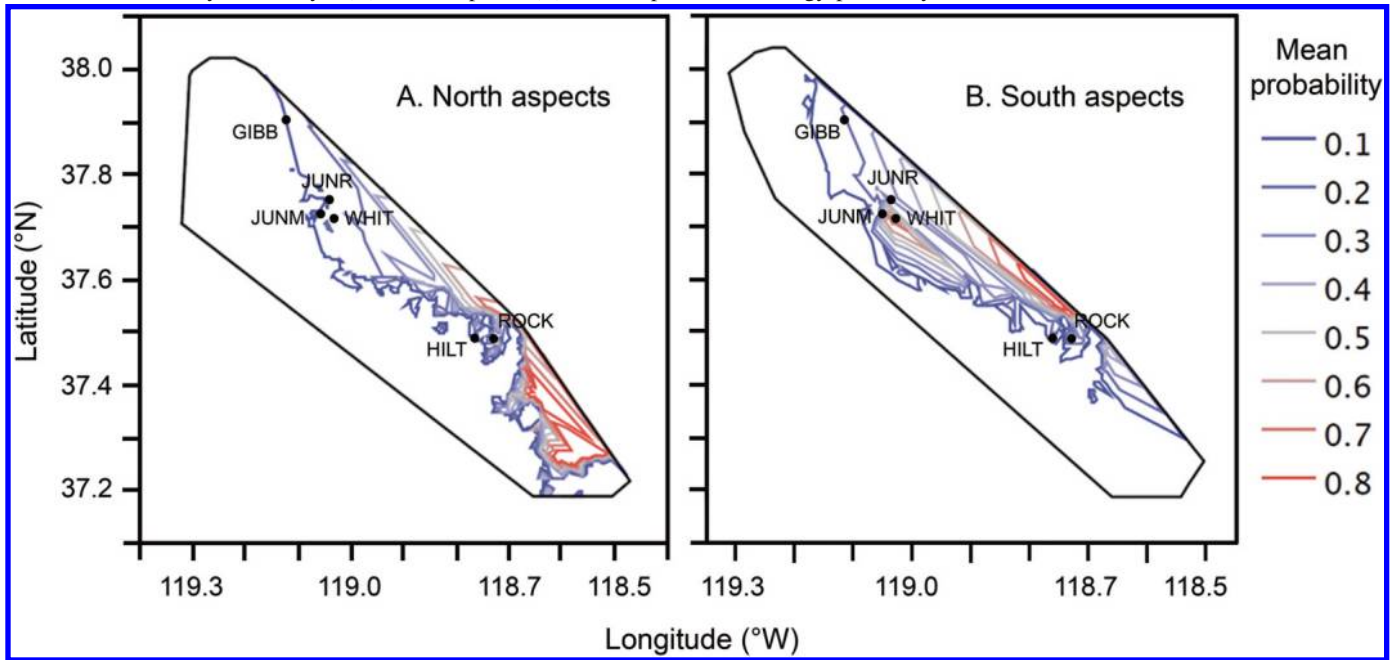


Table 5. Air surveys of whitebark pine (*Pinus albicaulis*) mortality pixels relative to elevation and aspect in the Warner Mountains, Southern Cascade Mountains (Mt. Shasta), and Sierra Nevada, 2006–2010 data combined.

Region	Aspect	Mean elevation of pixels scored as mortality (m)	Mean elevation of pixels scored as no mortality (m)
Warner Mountains	North	2414	2430
	East	2394	2418
	South	2457	2485
	West	2498	2499
Regional mean		2443	2466
Mt. Shasta	North	2418	2515
	East	2394	2487
	South	2396	2541
	West	2436	2552
Regional mean		2406	2526
Sierra Nevada	North	2925	3070
	East	2956	3130
	South	3044	3136
	West	3025	3099
Regional mean		2988	3109
Overall mean		2677	3040

Relative growth of live and dead WBP, as indicated by standardized ring widths in the composite chronology (Fig. 3A), fluctuated at interannual and multiyear scales over the past 115 years, with no significant positive or negative trend over the century. Although live and dead tree growth had similar patterns in interannual growth variability over this period, dead trees grew consistently and significantly ($p < 0.0001$) less than live trees on an annual basis and had greater extremes of minimal growth.

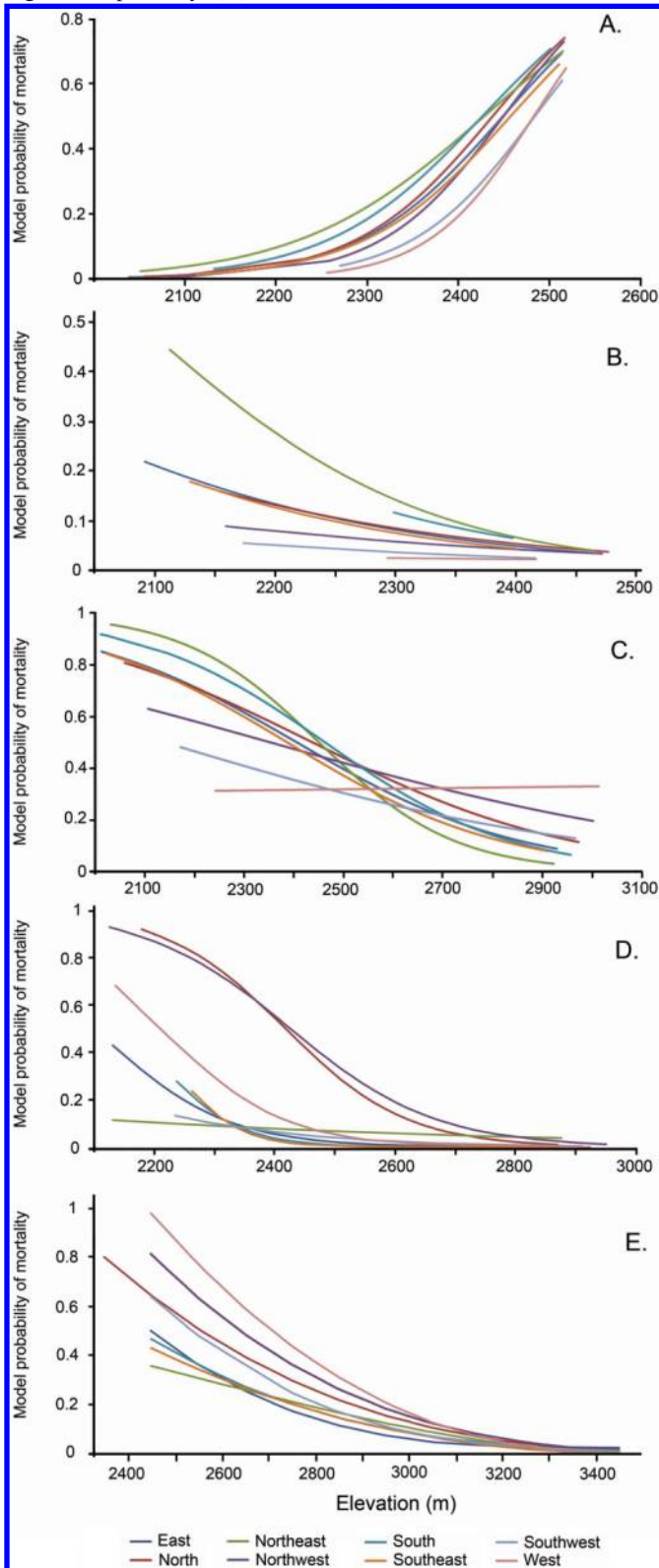
Relative growth of live versus dead trees over 200 years, however, varied by century (Fig. 4). By contrast with the 20th century trend, dead trees grew significantly greater in a

paired t test ($p < 0.0004$) than live trees in the 19th century. Not until the early 1920s did the rank switch, and live tree growth began consistently to exceed dead trees; after 1920, live tree-ring width significantly exceeded annual growth of trees that eventually died.

Air surveys

Overall, 936 883 WBP forest pixels were assessed from the Warner Mountains, Mt. Shasta, and Sierra Nevada, representing a total of 84 319 ha of forest surveyed for WBP mortality by air (Fig. 1; Table 4) (US Forest Service 2011c). Of the total area, 12% was in the Warner Mountains, 2% at Mt.

Fig. 6. Effect of elevation and aspect on probability of whitebark pine (*Pinus albicaulis*) mortality. Populations detected by air surveys. (A, B, and C) Warner Mountains, north, central, and southern regions, respectively; (D) Mt. Shasta; (E) Sierra Nevada.



Shasta, and 86% in the Sierra Nevada. Percent mortality differed significantly ($p < 0.001$) among ranges, with the highest levels in the north and decreasing southward: 37.8% of pixels were scored as mortality in the Warner Mountains, 18.2% in the Mt. Shasta area, and 4.5% in the Sierra Nevada. The mean over all regions was 8.8%.

Environmental context differed significantly across aspects within regions ($p < 0.0001$). Considering only mortality pixels, 34% were on north slopes and 11% on south slopes (Table 4). This pattern was strongest at Mt. Shasta; in the Warner Mountains and Sierra Nevada, mortality on west aspects was also high. The pattern of greater mortality on north and west slopes was similar when analyzed more intensively for pixels within western and eastern Sierran subregions (Table 4). Within the set of air survey pixels extracted for the central-eastern Sierra Nevada WBP subregion, probabilities of mortality by aspect varied across latitude in this subregion (Table 4; Fig. 5). Southern aspects had higher probabilities at higher latitudes of this subregion whereas northern aspects had higher probabilities at lower latitudes and eastern longitudes.

In addition to aspect, mortality pixels were significantly lower in elevation ($p < 0.0001$) than no-mortality pixels in the southern Warner Mountains, Mt. Shasta, and Sierra Nevada regions and nonsignificantly lower in the central and northern Warner Mountains (Table 5; Fig. 6). In the northern subregion of the Warner Mountains, an opposite trend occurred (Fig. 6A) where probability of mortality increased with elevation on all aspects. In the central and southern Warner Mountains, the negative relationships with elevation were strongest for populations on northerly aspects (Figs. 6B and 6C).

Climate

Composite regional weather records showed significant increases in minimum temperature ($p < 0.001$) but not maximum temperature ($p > 0.05$) over the 20th century, with an average warming of 1 °C from 1910 to 2010 (Fig. 3B). Century-long trends were not observed in maximum temperature, although multiyear variability existed throughout the record. Similarly, WY precipitation was characterized by high inter-annual and multiyear variability rather than directional change in mean (Fig. 3C). Multiyear droughts persisted 6–8 years, in some cases with a wet year intervening (see Millar et al. (2007) for details). Precipitation in 2007 was the lowest annual WY value on record. Mean CWD mirrored patterns of WY precipitation (Fig. 3D), with high values of CWD reflecting periods of low precipitation. A strong positive linear trend ($p < 0.0001$) of CWD occurred from 1982 to 2010, and the highest values of CWD in the past 115 years occurred during the years since the late 1990s. The latter period had greater and more persistent stress as indicated by CWD than any other interval, including the 1930s.

Climate estimates from PRISM (1961–2009 data) for the central-eastern Sierran Nevada subregion indicate that mortality stands for the ecology plots and air survey pixels were drier and warmer and had higher CWD values ($p < 0.0001$) relative to the climate envelope for WBP in this subregion (Table 6). North slopes had significantly higher CWD values ($p < 0.0001$) than south slopes.

Table 6. Estimates of current (1971–2000) climate for whitebark pine (*Pinus albicaultis*) in the central-eastern Sierra Nevada subregion extracted from the 800 m PRISM climate model (Daly et al. 1994) downscaled to 400 m as in Millar et al. (2006) and modeled climatic water deficit (CWD) downscaled to 270 m (L.E. Flint and A.L. Flint, unpublished).

Site/health condition	Code/N pixels	Annual precipitation (mm)	January precipitation (mm)	July precipitation (mm)	Minimum annual temperature (°C)	Minimum January temperature (°C)	Minimum July temperature (°C)	Maximum annual temperature (°C)	Maximum January temperature (°C)	Maximum July temperature (°C)	Annual CWD (mm)
Ecology plot mortality stands											
Gibbs Cyn	GIBB	766.2	132.4	22.8	-3.5	-10.4	5.6	10.3	2.1	20.7	144
June Mtn East	JUNE	942.6	170.4	15.1	-2.5	-9.5	6.3	10.8	2.7	21.1	314
June Mtn West	JUNW	1003.3	183.2	18.7	-2.9	-10.1	6.4	9.5	1.2	19.7	222
Glass Cr	GLAS	975.6	178.6	16.0	-2.9	-10.0	6.3	10.2	1.6	20.3	236
Hilton Cr	HILT	658.3	101.6	10.2	-3.7	-10.7	5.6	8.9	1.4	19.0	32
Rock Cr	ROCK	562.1	79.3	10.6	-3.9	-10.6	5.3	9.2	1.6	19.3	41
Overall mean		818.0	140.9	15.6	-3.2	-10.2	5.9	9.8	1.8	20.0	165
Air surveys of dead, live, and all whitebark pine pixels in the subregion combined											
Dead	20 726	734.7	124.5	14.1	-3.0	-9.9	6.2	9.9	2.0	20.1	387
Live	257 111	844.3	147.5	15.0	-3.6	-10.4	5.7	8.9	1.3	18.9	307
Overall mean	277 837	836.1	145.8	14.9	-3.6	-10.4	5.7	9.0	1.4	19.0	347

Climate interactions with growth and mortality

Mortality in all WBP ecology stands was strongly associated with a multiyear drought that began in 2006 and continued through 2010 (Figs. 2 and 3). Correlations of tree growth, measured by standardized ring widths, for the past 115 years with climatic variables were significant although low (Table 7). In some cases, responses among the live and dead tree sets differed. The strongest correlations were to 2-year-lagged CWD and 2-year-lagged WY precipitation; current-year CWD was also significant. Growth in live trees had significant positive correlation with the Pacific Decadal Oscillation. Values of the Palmer Drought Severity Index, North Atlantic Oscillation, and Arctic Oscillation did not show significant correlations with growth, nor did maximum temperature. These correlations are reflected in growth over the 20th century, which declined during the multiyear periods of high CWD, including the 1920s and 1930s, late 1980s and early 1990s, and late 2000s, and increased in intervals of high precipitation, such as the early 1940s and early 1980s (Fig. 3A). The highly significant 2-year-lagged correlations of CWD and WY precipitation were strongest with the dead tree set (Table 7), suggesting greater sensitivity to low soil moisture stress in trees that eventually died.

Interactions of 20th century growth with climate were complex; only significant results are shown (Fig. 7). In the mixed-model response-surface analysis, overall growth (pooled ring width data set) was most strongly related to 2-year-lagged CWD ($p < 0.0001$). With CWD partialled out, minimum temperature was also highly related ($p < 0.01$), in contrast with the simple correlations. Interactions were next in importance ($p < 0.05$). Growth of live trees was more responsive to changes in 2-year-lagged CWD and minimum temperature (Figs. 7A and 7C) than the dead tree set (Figs. 7B and 7D), although the nature of response by live trees differed under conditions of low versus high maximum temperature. Similarly, growth of live trees was more sensitive than dead trees to changes in minimum and maximum temperatures under conditions of mean CWD (Figs. 7E and 7F, respectively).

Discussion

Status of whitebark pine in eastern California

The WBP mortality event that began in eastern California in 2007 extended by 2010 to affect a total of 7395 ha (8.8% of the WBP forest), with mortality greatest in the north (Warner Mountains, 38%) and declining southward (Sierra Nevada, 5%). While apparently unprecedented in recent centuries in the California subalpine forest zone, WBP mortality has become far more extensive in other parts of western North America (Logan et al. 2010; Tomback and Achuff 2010). Observations in California at this stage inform understanding of the process and provide a baseline for future assessments.

A potential difference in California relative to elsewhere is that WPBR appears to be much less, or not at all, implicated in mortality. No sign of WPBR infection was evident in the affected stands in the central-eastern Sierra Nevada. Although WPBR has been in California for decades, levels remain low throughout the WBP forest, with highest levels in the northern and western Sierra (Maloney and Dunlap 2007; J.M.

Table 7. Correlations of growth (standardized tree-ring widths) at six ecology plot stands with composite climate station records, modeled climatic water deficit, and Pacific Decadal Oscillation indices (Mantua et al. 2005), central-eastern Sierra Nevada (period of records for correlations is 1898–2008).

Standardized tree-ring width	Water-year precipitation	Water-year precipitation 2 years lagged	Minimum temperature	Maximum temperature	Climatic water deficit	Climatic water deficit 2 years lagged	Pacific Decadal Oscillation
Live trees	0.15	0.29**	0.11	0.00	-0.19*	-0.43****	0.23*
Dead trees	0.18	0.34***	0.13	-0.08	-0.19*	-0.46****	0.06

Note: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.00001$.

Dunlap, US Forest Service, personal communication (2011)). Thus, it appears that WPBR is unlikely to have been an important stress correlate in the mortality episode to date. In situations outside California where WPBR infection levels are high, rust is an important stressor of WBP, heightening vulnerability to climatic stress and beetle-related mortality (Campbell and Antos 2000; Smith et al. 2008; Tomback and Achuff 2010).

Environmental context and stand structure

Despite the limited extent of WBP mortality in California, the environmental context of affected stands was highly consistent across the regions surveyed. For all regions except the north Warner Mountains, mortality was concentrated in the lower elevation, upright-tree zones of the WBP forest and on northerly aspects. In the exceptional north Warner Mountains, mortality increased with elevation, although as elsewhere, mortality stands were more abundant on northerly aspects than on other slopes. Absolute elevations varied as expected across the 6° of latitude surveyed (36°–42°N), with both the zone of mortality and the elevational range of the species lower in the north (Warner Mountains) than in the south (southern Sierra Nevada).

These environmental and silvical contexts for WBP were nearly identical to the situation of the 1988–1994 mortality in subalpine limber pine forests of the central-eastern Sierra Nevada (Millar et al. 2007). In that case, limber pine mortality occurred also in dense, young to mature, upright, closed-canopy, and monotypic stands on northerly aspects in the lower elevation zone for the species. Mountain pine beetle and dwarf mistletoe infestations interacted complexly with climate to cause tree death; WPBR was not present. Mortality was slightly lower in the limber pine event relative to WBP, with a mean mortality of 50%–75%. Aside from the higher within-stand mortality in WBP, however, live and dead trees in both species were growing together in affected stands; limber pine trees that died were codominant to those that survived, as in the WBP situation. Further, long-term trends in growth between live and dead tree groups were similar in both species: trees that eventually died had significantly greater annual growth in the 19th century than live trees whereas the opposite situation occurred in the 20th century.

Similar patterns characterized prior mortality events in the Sierra Nevada and montane forests elsewhere. In Yosemite National Park, for instance, forests on north slopes were more likely to have died during the late 1980s' drought than forests on other aspects; north slopes also had the highest stand density of all aspects (Guarin and Taylor 2005). High tree density is a common attribute of montane forest stands

throughout western North America that experience periodic mortality, especially during drought (Breshears et al. 2005; Campbell et al. 2007; Fettig et al. 2007).

As in California, elevation has been important in explaining variability in mortality elsewhere. In general, mortality decreases with increasing elevation (Smith et al. 2008). Given ecological control of bark beetles by climate, especially temperature (Thomson 2009), upslope movement of beetles is expected with warming (Logan and Powell 2001), making lower elevation zones susceptible first. Mortality caused by WPBR, in contrast, affects forests at many elevations, including WBP *krummholz* and upper treeline zones (Resler and Tomback 2008). Similarities in silvical contexts to the California situation are more common in situations where bark beetles are implicated, especially in regard to age, stand density, and low species diversity (Campbell and Antos 2000; Fettig et al. 2007; Smith et al. 2008).

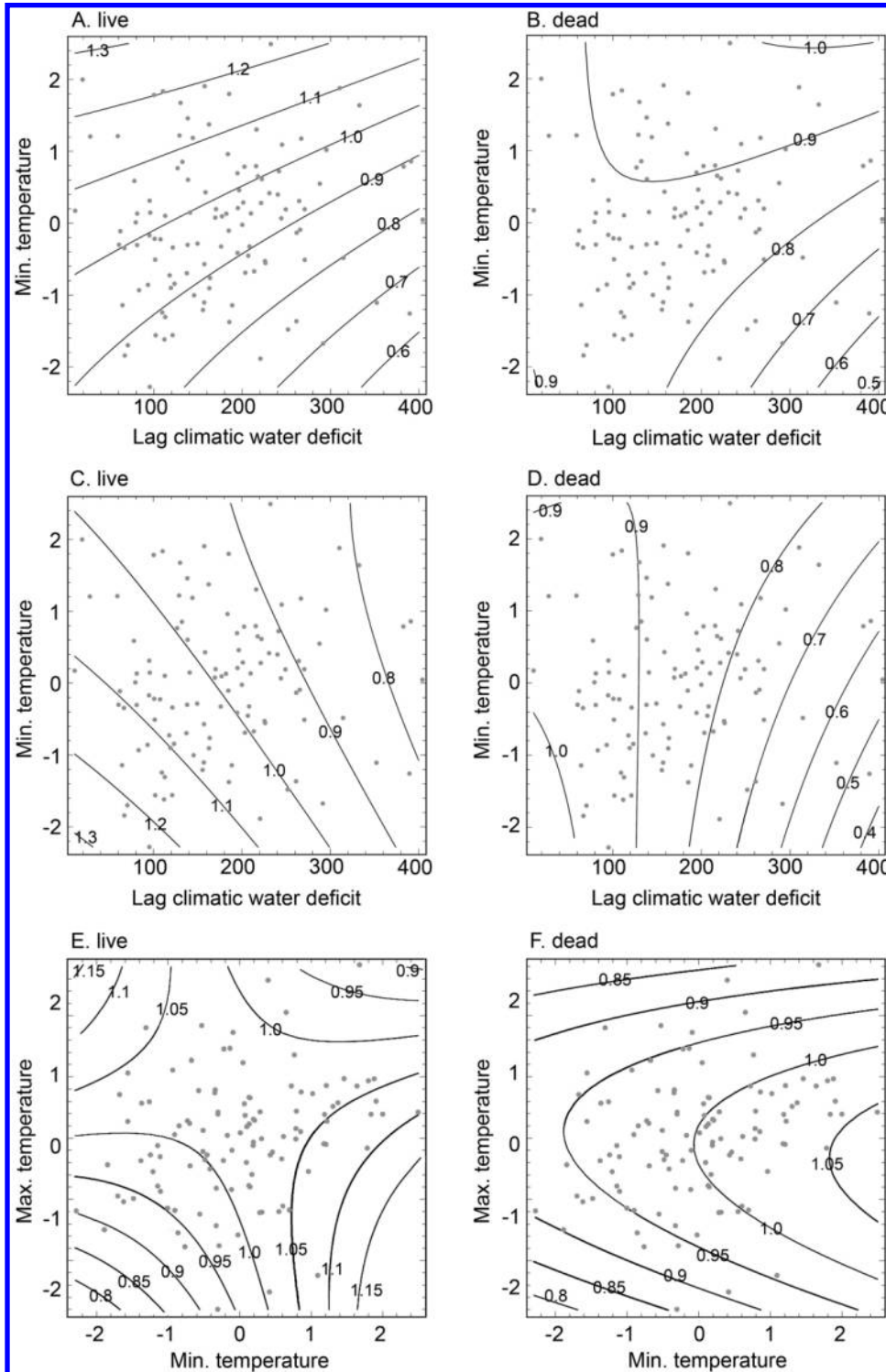
Climatic interactions

The trend of increasing minimum temperature over the past 120 years evident in our composite record of weather stations has been observed previously for the Sierra Nevada (Millar et al. 2006, 2007; Moritz et al. 2008) and other mountain regions of the west (Stewart et al. 2005). By contrast, precipitation trends over the century vary inconsistently around the west. In our composite record, we detected no long-term trend in WY precipitation except an increase in variability after ~1940. Values and interannual variability of CWD also increased after 1980, reaching their highest values in 2007 for the period of record. Mortality stands of WBP had similar climate niches to those of limber pine in an earlier drought (Millar et al. 2007). That is, dead stands of both species were located in significantly drier and warmer sites relative to the species' range.

A similar relationship of forest mortality has been correlated with environments exposed to drought and increasing temperature throughout western North America (Allen et al. 2010). In mixed-conifer forests of Yosemite National Park, for example, mortality was related to multiyear episodes of high spring and summer temperatures and low annual and seasonal precipitation (Guarin and Taylor 2005). Such "global warming style drought" effects have been most extensive for pinyon pine (*Pinus edulis* Engelm.) and ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) forests of the American Southwest (Breshears et al. 2005; Williams et al. 2010) and in lodgepole pine forests of the Canadian Pacific (Carroll and Safranyik 2004).

By contrast with weak linear climate correlations, significant growth × climate interactions and lagged responses

Fig. 7. Contour maps showing the effects of second-order interactions between (*Pinus albicaulis*) growth and climate. (A and B) Conditions of low maximum temperature: (A) live tree response to 2-year-lagged climatic water deficit (CWD) and minimum temperature; (B) dead tree response to 2-year-lagged CWD and minimum temperature. (C and D) Conditions of high maximum temperature: (C) live tree response to 2-year-lagged CWD and minimum temperature; (D) dead tree response to 2-year-lagged CWD and minimum temperature. (E and F) Conditions of mean CWD: (E) live tree response to minimum and maximum temperature; (F) dead tree response to minimum and maximum temperature. In each case, tree growth increases as contour values increase. Contour intervals are in units of standardized tree-ring growth. Main axis units are standard deviations from the mean of each variable. The scatter of dots in each graph is the set of recorded values from the composite 1895–2009 instrumental weather record.



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point to complex responses of WBP to variable annual conditions and climate phases. As with limber pine, surviving WBP within dying stands were better able to take advantage of warm temperatures and grow faster (more responsive to decreasing water deficit) in cool years than trees that died; the latter were less able to take advantage of reductions in water stress and increase in temperature. Under conditions of high minimum temperatures, trees that died grew poorly relative to surviving trees and responded only to reductions in water stress. These and other complex interactions corroborate the hypothesis that at least two genotypic groups exist in WBP as well as limber pine stands, having differential responses to water deficit and maximum temperatures. Trees that eventually died reveal in their growth behavior a greater vulnerability than surviving trees to high temperatures and water stress and poorer capacity to take advantage of warm conditions, suggesting greater adaptedness to cool, wet conditions of the Little Ice Age when they established.

In that drought is widely implicated in conifer mortality and growth depression, correlations with direct climate variables have been less important for understanding process than relationships to seasonal water availability (Stephenson 1990, 1998). Even indices such as the Palmer Drought Severity Index, which attempt to measure integrated response of plants to moisture availability, often lack useful resolution. Direct estimates of CWD, by contrast, reveal water relationships that are biologically meaningful to plant function. These have high predictive power to explain conifer distribution, vigor, and survival (Stephenson 1990, 1998); correlations of forest mortality with CWD are often stronger than with other climate variables or drought indices (Raffa et al. 2008; Crimmins et al. 2011). For instance, high values of water deficit at low elevations in the Swiss Alps better explained conifer mortality and growth declines during the 2003 heat wave in Europe than direct correlations with climatic variables (Jolly et al. 2005). In our case, CWD values of WBP mortality stands were at and above the high range of values that Stephenson (1990) indicated as defining conifer forest biome ecotones, pointing to high stress conditions at these locations.

Higher values of CWD on north slopes, where mortality most often occurred, than south slopes seems counterintuitive but might relate to the fact that WBP occurs lower in elevation on north slopes than on south slopes in the eastern Sierra Nevada. Further, environmental context of the mortality stands in the Sierra might expose them to soil water stress despite north aspects. These stands are on mild slopes of morainal till or on structural ridges overlain at four of the stands by deep Holocene tephra with minimal soil development, predisposing them to CWD stress. Heightened exposure to evaporative stress at mid elevations in the Sierra Nevada has been modeled by Lundquist and Loheide (2011), who demonstrated that annual evapotranspiration at mid elevations is sensitive to groundwater transfer from higher slopes. The six mortality sites are situated in contexts where no or minimal slopes exist above them, meaning that water transfer from above would not be available to provide late-season groundwater, thus exposing these sites to relatively greater CWD than other situations.

The strongest correlation of growth variability in WBP forests of eastern California was with CWD in prior years

(2 year, 1 year) and also with lagged WY precipitation, a situation that has also been associated with spruce beetle (*Dendroctonus rufipennis* (Kirby)) outbreaks in Colorado and Utah (Herbertson and Jenkins 2008). These lag relations suggest that WBP are stressed by seasonal-specific climate and hydrologic response and various timing combinations, such as warm winters and early spring snowmelt, that lead to water deficits even in times when annual precipitation is not unusually low. Prolonged stress experienced by WBP appears to precondition stands (growth depression and declining trends) to years of extreme precipitation or temperature anomalies. A mechanism for this is suggested by the timing of bud development, which in year 1 affects stem elongation, hormone production, and carbohydrate accumulation and thus cambial growth and wood formation in the subsequent year. Deficit in one year thereby affects resource accumulation in subsequent years. This lag effect may be responding to high-resolution precipitation cycles that have been observed in the California region and associated with the 2.16-year quasi-biennial oscillation, a North Pacific ocean mode that has been compared with the strength of the El Niño – Southern Oscillation (Johnstone 2011). Spectral decomposition of significant ~2.2-year power in WY precipitation and CWD from our analyses suggests a potential connection of the lag effect that we observed with quasi-biennial oscillation type variation in precipitation.

Differences in growth between surviving trees and trees that died suggest that adaptive genetic differences exist within stands. Trees that died and trees that survived were codominants: the groups were not significantly different in age, diameter, mean growth over their lifespans, or location within stands. Superior relative growth of the dead tree group in the first century of stand establishment, however, suggests that those trees were better adapted to cool, wet conditions of the Little Ice Age when they established than trees that survived. The switch in rank to live trees growing consistently better than dead trees after the early 1920s coincides with a transition to warming and drying trends that persisted thereafter (Stine 1996). The extreme low growth of the dead tree group during the warmest and driest years of the 20th century, the higher sensitivity to maximum temperatures, and the differential susceptibility to bark beetles further suggest adaptive differences. The beetle-related mortality appears to have been a successful natural selection event that removed trees less fit under current climates and to increase population adaptedness to current high CWD, warming trends, and increased interannual variability. A silvical benefit likely also accrued wherein stands were reduced in basal area and remaining trees are left dispersed, creating conditions less favorable for successful beetle outbreak (Fettig et al. 2007), approaching conditions more typical of old-growth stands. Improvement in stand cultural health and opportunity for reproduction in openings created by beetle kill have been proposed for WBP (Tomback and Achuff 2010), observed as growth release after beetle-mediated thinning events in lodgepole pine (Campbell et al. 2007), and suggested as a widespread process following recent forest mortality events (Rocca and Romme 2009). Lack of limber pine mortality in eastern Sierran forests during the 2007–2010 drought is tentative evidence that a selection event in the drought of the late 1980s did in fact occur as speculated.

Improved fitness through forest dieback has been observed in other situations and is expected by evolutionary theory, assuming there is genetic diversity for climate response. The 1996 drought-related mortality in pinyon pine forests of northern Arizona was interpreted as evidence for genetic selection to heightened drought hardiness (Ogle et al. 2000). A similar situation was described for 1998–1999 drought-killed forests of *Nothofagus* in Patagonia whereby stand-level fitness improved following mortality as a result of removing trees with lower and more sensitive growth rates (Suarez et al. 2004). Expanding on classic evolutionary theory, Gutschick and BassiriRad (2003) suggested that selection is virtually ineffective except during extreme events that drive strong directional selection. Kuparinen et al. (2010) used quantitative genetic, individual-based selection simulations to assess responsiveness of Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth) to 100 years of change in length (increase) of growing season. Under background mortality rates, the simulations predict that adaptation in both species lags more than 50% behind the climatic optimum. The lag was greatly reduced when mortality rates increased, with implications that populations experiencing high mortality rates would be quickest to adapt to warming climates.

Conclusion: contrasting scenarios for whitebark pine in eastern California

Although it is early to project the future of WBP in California forests, two trajectories are feasible scenarios. These underlie a question of whether recent events portend “normative disturbance” or “catastrophic” outcomes (sensu Rocca and Romme 2009; Logan et al. 2010). In the latter case, stress from climatic change and increased mobility and efficacy of native insects, combined with novel stressors such as WPBR, other invasive species, and fire exclusion, would expand rapidly throughout the WBP forest. These would outpace the capacity of WBP to reproduce and adapt in situ. As a result, WBP forests would progressively disappear from the landscape, and type conversions would be expected. A contrasting normative disturbance scenario is one wherein stresses would affect only limited and specific environmental, genetic, and silvical contexts of WBP forests, mortality events would occur episodically but remain localized, and consequence to the overall forest would be improvement in health through silvical thinning and natural selection for adaptation to current climates.

Factors in support of the first scenario include the experience throughout most of the WBP range outside California. Mortality patterns developed in the 1990s similar to the California event and over the course of a decade continued until the scale and scope exceeded historic levels in many regions of the species’ range, implicating widespread population extirpations (Logan et al. 2010; Tomback and Achuff 2010). The situation in California, wherein mortality in the northern region (Warner Mountains) currently affects 10 times more area than in the southern region (Sierra Nevada), suggests that a north-to-south wave might be underway. Aside from WBP, the recent effects of drought, elevated temperatures, and mortality experienced in other conifers around North America suggest that type conversion and ecosystem collapse are logical outcomes (Breshears et al. 2005; Allen et al. 2010; Williams et al. 2010).

There are reasons, on the other hand, to infer that the current mortality is a normative disturbance episode. Importantly, WPBR does not appear to be widespread or advancing into the upper subalpine zones despite its long history in montane California. The restriction of mortality to specific environmental contexts and stand age and structure suggests that the event might remain limited to such areas, as is the case to date for limber pine. The apparent silvical and genetic benefits accruing during the mortality event in WBP are corroborated also by the situation in limber pine where no significant mortality beyond background levels has been observed in the last 8–10 years, suggesting that the effects of the 1988–1992 drought mortality were adaptive.

Real futures usually unfold as combinations of scenarios, including novel and unexpected ones. Northern regions of California, by virtue of their cooler, more mesic climates, might move toward precipitous declines of WBP across many elevations and aspects, as have been seen in other parts of the species’ range. These areas might also become increasingly favorable for expansion of WPBR into subalpine forests, given moister conditions for effective rust dispersal and life cycle completion and potentially higher abundance of alternate host species. Populations at Mt. Shasta, for similar reasons, or exceptional Sierran locations such as Mt. Rose might also follow this path. In the southern Sierra Nevada, however, especially east of the crest, water deficits are likely to increase in future decades at ever higher elevations. WBP stands on aspects other than north might be adequately preadapted to these conditions, given their exposure historically to Mediterranean fluctuations, to continue to adapt in situ. Thus, even with potential expansion of beetles upward under warming conditions, assuming that WPBR continues to be excluded and selection continues to support pines adapted to deficit conditions, beetle outbreaks might remain normative and adaptive into the future in those regions.

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