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Rapid vegetation redistribution in Southern California during the early 2000s drought

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[1] Climate change in semi-arid, midlatitude mountain environments is expected to shift the spatial patterns of temperature, water availability, and vegetation upslope. Vegetation growing near its low-elevation range limit may prove especially vulnerable to mortality and decline. We investigated the altitudinal pattern of conifer mortality that occurred from 2002 to 2004 in Southern California's San Jacinto Mountains. We found that conifer mortality was focused in the lower portion of the midmontane conifer range, which drove the midmontane conifer distribution upslope. We investigated past reports of conifer mortality in Southern California by searching historical newspaper accounts. We found evidence of previous episodes of conifer mortality that coincided with past droughts, and which may have caused vegetation redistribution in the past. We interpret the early 2000s mortality and associated vegetation redistribution as a response to natural decadal to centennial climate variability. Moreover, we hypothesize this response mode will dominate the early impact of global climate change on semi-arid forest, which, in turn, may complicate efforts to distinguish between ecological changes attributable to natural climate variability and those attributable to global climate change.

1. Introduction

[2] The broad distribution of natural vegetation in California is expected to move upslope and poleward by 2100 with global climate change [*Hayhoe et al.*, 2004; *Loarie et al.*, 2008]. Individual plants near the dry or warm parts of their species' fundamental niche are expected to decline or die, while areas upslope and poleward are newly opened to expansion and recruitment. Mortality at a species' low elevation limit combined with expansion at its high elevation limit may drive that species' distribution upslope.

[3] Abrupt shifts in the location of vegetation ecotones have been attributed to plant mortality caused by weather and climate extremes [e.g., *Allen and Breshears*, 1998]. Widespread tree mortality associated with drought and pest or pathogen outbreak occurred in Western North America over the last decade [*Allen et al.*, 2010; *Breshears et al.*, 2005; *Raffa et al.*, 2008; *Walker et al.*, 2006], and there has been speculation this mortality is similar to what would occur with climate change [*Allen et al.*, 2010]. This mortality generally coincided with or followed a series of unusually dry and warm years [*Breshears et al.*, 2005]. Reduced plant water availability may directly cause conifer mortality by hydraulic failure or carbon starvation associated with declining translocation and metabolism [*McDowell et al.*, 2008; *Sala et al.*, 2010]. Moreover, drought-stressed conifers are susceptible to pest and pathogen outbreaks, including bark beetles, which are often the proximate cause of mortality.

[4] Very high levels of mortality, especially among Ponderosa Pine, Pinyon Pine, and White Fir, were observed in Southern California's montane forest in 2002–04 during and following a severe and prolonged drought [*Minnich*, 2007b]. Much of this mortality was attributable to outbreaks and attacks by Western Pine, Mountain Pine, and Jeffrey Pine Beetles [*Walker et al.*, 2006; *Savage*, 1994]. The mortality coincided with and was similar to that reported for other areas of the southwestern U.S. *Kelly and Goulden* [2008] investigated the distribution of plants in Southern California's Santa Rosa Mountains following this mortality, and found the cover-weighted mean elevation of the most widespread species shifted upslope by ~65 m from 1977 to 2007. This redistribution was caused by the combined effect of plant mortality in the lower parts of species ranges and plant expansion in the upper parts of ranges, a pattern that resembles what may be expected with global climate change.

[5] We investigated the distribution of live and dead trees in Southern California's San Jacinto Mountains to better

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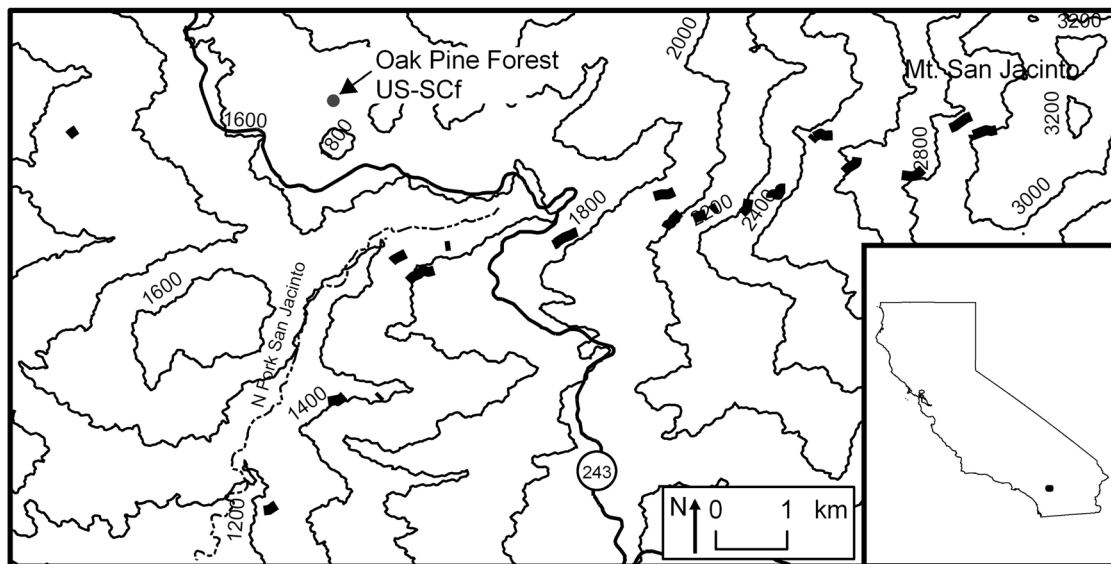
Figure 1. Map of elevation gradient. Topographic map of the elevation gradient established in 2007–08 in the San Jacinto Mountains, CA. Contour lines are meters above sea level. Bold black lines are sampling transects. The lowest and most westerly sampling transect is located at 116°48′17.6″W; 33°48′13.2″N. The highest and most easterly transect is located at 116°41′17″W; 33°48′15.1″N. Sampling transects were split into segments if the aspect deviated from north-northwest. The Ameriflux Oak Pine Forest eddy covariance site (U.S.-SCf) is indicated on the map.

understand the altitudinal patterns of the recent mortality and to place it into a longer, historical context. We focused on three questions: (1) How did mortality vary with elevation? (2) How were vegetation distributions impacted? (3) Was the mortality unique in a historical context?

2. Methods

2.1. Elevation Gradient

[6] We established a series of vegetation sampling transects in 2007–08 along an elevation gradient on the western slope of the San Jacinto Mountains in Southern California (Figure 1). Our gradient was ∼40 km northwest of that studied by *Kelly and Goulden* [2008]. Our gradient was on the western (windward) side of the mountains, and was wetter than the area investigated by Kelly and Goulden. Kelly and Goulden's gradient was on the eastern (leeward) side of the mountains, and was in a montane rain shadow, especially at lower elevations. Both studies investigated recent shifts in plant distribution, including those associated with the regional plant die-off in the early 2000s. Our gradient was independent of Kelly and Goulden's with regard to sampling locations, and our work can be interpreted as a test of whether the patterns Kelly and Goulden reported were widespread.

[7] Our sampling transects were 300 m long and were located at 122 m elevation intervals from 1295 m to 3002 m (Figure 1). The transects followed elevation contours, and we controlled for non-elevation factors that might influence vegetation distributions. All transects were placed on consistent slopes and within a horizontal distance of 11 km. Transects were positioned on slopes with north to northwest aspect and were broken into segments if the aspect deviated. There were no reported fires along our elevation gradient,

except for a small segment of the lowest sampling transect that last burned in 1974, and sampling transects below 1661 m, which last burned in 1924 (http://frap.fire.ca.gov). Timber harvest and grazing ended in the early 1900s. Soils were coarse and derived from granodiorite across the entire elevation gradient (Soil Map from http://websoilsurvey.nrcs. usda.gov/).

2.2. Climate

[8] The climate was Mediterranean with most precipitation falling from November to April. The warmest temperatures occurred from June to September. The annual average temperature at 1645 m was 11.6 +/− 0.66°C (mean +/− SD) and the average precipitation was 648 +/− 256 mm (mean +/− SD; Idyllwild, CA; Western Regional Climate Center; accessed Feb. 9, 2011, http://www.wrcc.dri.edu).

2.3. Field Observations of Species Distributions and Mortality

2.3.1. Cover

[9] We determined vegetation cover in 2007–08 by measuring the length of each plant's canopy projected onto a 300-m-long one-dimensional sampling transect. This was done by extending a tape across the forest floor and recording the length of a plant's crown that extended over the tape. We recorded live and dead conifer tree cover by species along each transect including overlapping tree crowns such that total cover could exceed one on a sampling transect. Dead conifers had died within five years; they had lost most or all of their needles, retained branches to ∼.6 cm in, had some bark sloughing off, and were in a similar state of decay. Almost all the dead conifers remained standing at the time of the survey and only a few trees had broken stems. The state of conifer decay was consistent with death during

Table 1. Terms and Calculations

Term	Definition	Calculation
$Live_{07-08}$	Sum of live cover in 2007–08 divided by sampling transect length	Σ measured live cover (m)/300 m
$Dead_{07-08}$	Sum of dead cover in 2007–08 divided by sampling transect length	Σ measured dead cover (m)/300 m
$Live_{02}$	Estimated fraction of live cover on transect in 2002	$Live_{07-08} + Dead_{07-08}$
Cover-weighted mean elevation	Center of a species' distribution; calculated separately for $Live_{07-08}$, $Live_{02}$, or $Dead_{07-08}$	Σ (Fraction cover*elevation) at each elevation / Σ Fraction cover over all elevations
Mortality	Proportion of dead cover	$Dead_{07-08}/Live_{02}$
Normalized cover	Species' fraction cover normalized by the largest fraction cover of that species on any one transect along the entire elevation gradient	Σ (Fraction cover for sp_j/ Maximum Fraction cover for sp_j on gradient)

the reported 2002–04 conifer mortality period [*Minnich*, 2007b].

2.3.2. Calculations and Assumptions

[10] The fractional cover of a species or group of species was calculated as the sum of species or group cover divided by the length of the sampling transect (for species or group j: Fraction $cover_j = \Sigma$ $cover_j$ on sampling transect in m / 300 m). $Live_{07-08}$ was calculated as the fraction cover of live vegetation measured in 2007–08 (for species or group j: $Live_{07-08j} = \Sigma$ live $cover_j$ on sampling transect in m / 300 m; Table 1). $Dead_{07-08}$ was the fraction cover of dead vegetation measured in 2007–08 (for species or group j: $Dead_{07-08j} = \Sigma$ dead $cover_j$ on sampling transect in m / 300 m). $Live_{02}$ was the sum of live and dead fraction cover measured in 2007–08 (for species or group j: $Live_{02j} = Live_{07-08j} + Dead_{07-08j}$). Mortality was calculated as the sum of a species dead fraction cover divided by the sum of live and dead fraction cover (for species or group j: $Mortality_j = Dead_{07-08j} / Live_{02j}$).

[11] Our approach assumed that live cover prior to the tree mortality in 2002 was equal to the sum of live and dead cover measured in 2007–08. One possible source of error is the inclusion of conifer trees that had died before 2002, which would have caused us to overestimate recent mortality. However, we believe this effect was slight, since the last reported episode of elevated conifer mortality before the early 2000s occurred around 1991 [*Savage*, 1994], and these trees would have fallen or lost branches after 16 years. A more significant source of uncertainty in our approach is associated with the possible contraction of dead tree crowns from their original shape by the time we measured cover, which would have led us to underestimate $Dead_{07-08}$. Additionally, growth and infilling of living trees may have increased $Live_{07-08}$. Our measurements, therefore, provide a conservative estimate of mortality and would tend to minimize any trend in mortality with elevation.

[12] We determined fraction cover and mortality for two broad conifer tree groups: midmontane and subalpine. The midmontane conifer group included *Abies concolor*, *Pinus lambertiana*, *P. coulteri*, *P. jeffreyi*, *P. ponderosa*, and *Calocedrus decurrens*. The subalpine conifer group included *Pinus contorta* and *P. flexilis*.

[13] We analyzed conifer distribution and mortality at the species level. The cover-weighted mean elevation for each species was calculated by summing the product of species' cover and elevation over all elevations for a species and dividing by the sum of that species' cover over all elevations (for species j: cover-weighted mean $elevation_j = \Sigma$ (fraction $cover_j$ on sampling transect * elevation of that sampling transect)/Σ fraction $cover_j$ over all sampling transects; Table 1).

[14] We pooled *Pinus coulteri*, *P. jeffreyi*, and *P. ponderosa* into a yellow pine group, and *P. contorta* and *P. flexilis* into a subalpine group. In both cases, we were unable to unambiguously identify all dead trees in a group to species. The effect of tree mortality on species' cover-weighted mean elevation was determined by subtracting the estimated 2002 cover-weighted mean elevation from the 2007–08 cover-weighted mean elevation. We tested if this difference was significantly different from zero using a two tailed t-test.

[15] We normalized the fraction cover of each species on each transect by the maximum fraction cover of that species found on any sampling transect on the entire elevation gradient (for species j: normalized $cover_j$ = fraction $cover_j$ on sampling transect/fraction $cover_{max,j}$; where fraction $cover_{max,j}$ = maximum fraction cover of species j found on the entire elevation gradient; Table 1). We constructed normalized distributions averaged across species by setting the transect nearest the cover-weighted mean elevation of each species to zero and averaging the normalized covers corresponding at 122 m intervals above and below the center for each species.

2.3.3. Size Distribution

[16] Diameter at breast height (DBH) of all conifers greater than or equal to 138 cm tall was recorded in ten 100-m^2 subplots equally spaced along each sampling transect. Conifer seedlings (less than 138 cm tall) were counted in subplots above 1661 m elevation. We determined the population size structure of stands below 2150 m and stands above 2270 m by binning the sum of live and dead conifers (e.g., $Live_{02}$) with a DBH less than 100 cm into 10-cm DBH size classes. We did not consider trees with broken tops. We further analyzed the population size structure between high and low elevation by comparing the slopes of the best fit lines between $\log_{10}$(stem density) and $\log_{10}$(tree size).

[17] We determined live and dead aboveground biomass for all conifers with greater than 2.5 cm DBH using generalized allometric equations [*Jenkins et al.*, 2003]. We compared the sum of live and dead conifer biomass with dead conifer biomass to assess the impact of mortality on biomass. While the possible inclusion of dead conifers that had died before 2002 would have a small effect on cover, the inclusion of only a few large snags could substantially increase dead biomass. These estimates should therefore be considered an upper bound.

2.4. Historical Weather

[18] We obtained historical records of annual precipitation, monthly mean temperature, and annual temperature for the California Southern Interior Region from the California climate tracker website ([Abatzoglou et al., 2009]; downloaded Jan. 19, 2011; http://www.wrcc.dri.edu). The Southern Interior Region encompasses Southern California's Mountains. The climate tracker record combines reports from multiple weather stations into a homogenous record of precipitation and temperature from 1895 to 2009. Inspection of the metadata showed that 1 of the 17 stations reported data during 1895, 6 stations reported data by 1905 and 14 stations reported data by 1949. We used the entire Southern Interior precipitation record to examine relative precipitation amounts over the past ~100 years, and data from 1949 onward to examine quantitative trends in precipitation and temperature.

2.5. Historic Tree Mortality

[19] We used the Proquest database to search The Los Angeles Times newspaper for historic reports of tree mortality in Southern California's mountains (accessed in 2011 and 2012, http://www.proquest.com/en-US/). We searched the following combinations of terms: ("beetle" and ("san jacinto" or "san bernardino" or "angeles national forest" or "san bernardino national forest" or "idyllwild")) or "pine beetle" or "dead trees." Our search focused on the San Jacinto and San Bernardino Mountains, which are two of the primary ranges in Southern California, and included the Angeles and San Bernardino National Forests, which manage and administer much of the undeveloped area. We included the village of Idyllwild, which is the main town in the San Jacinto Mountains. Articles identified by the Proquest search were read to confirm that they described widespread mortality among native trees. Articles that reported ongoing tree mortality, evidence of widespread tree mortality, or bark beetle outbreaks in Southern California's conifer forests were recorded to year and verified with governmental and scientific reports when possible.

3. Results

3.1. Weather and Climate Trends

[20] The local climate was montane Mediterranean, with cool, wet winters and warm, dry summers [Minnich, 2007a]. Air temperature decreased with elevation at an average lapse of $-5.4°C$ km^{-1} [Fellows, 2012]. Mean precipitation generally increased with elevation [Minnich, 1986]. Available rain gauge data indicate precipitation increased to ~1500-m elevation, at which point it leveled off [Fellows, 2012]. The snowline in Southern California varies markedly from storm to storm, and averaged 2300 m during the 1950s through the 1970s [Minnich, 1986].

[21] The Southern Interior Region of Southern California warmed on average by $0.0208°C$ yr^{-1} from 1949 to 2009 (p < 0.01; linear regression, slope different from 0). Precipitation variability, as measured by the 11-year running standard deviation and coefficient of variation, increased from 1949 to the 1980s and then declined. Precipitation amount did not change significantly since 1949 (p = 0.53; linear regression, slope different from 0).

[22] Lower than average annual precipitation and above average air temperatures preceded the 2002–04 conifer mortality. Annual southern interior precipitation was 48% of average in 2002, which was the 8th driest year in the 116 year record. The mean precipitation during the preceding five years was 84% of average in 2002 and 69% of average in 2003. Annual temperature was $0.82°C$ above average in 2002 and $1.34°C$ above average in 2003.

3.2. Species and Plant Functional Type Distribution

[23] Plant distribution with elevation was roughly bell-shaped within a species, and overlapping and offset between species (Figure 2). Midmontane conifer distributions were generally skewed upslope. Midmontane conifers spanned 1417 m to 2758 m and subalpine conifers spanned 2637 m to 3002 m (Figure 3). Total conifer cover peaked at 2271 m, which was near the midpoint of the overall conifer range. Evergreen and deciduous oaks, including Quercus chrysolepis, Q. kelloggii, and Q. wislizeni, contributed to non-conifer cover below 2149 m. Chaparral shrubs, mostly Arctostaphylos spp. and Adenostoma fasciculatum, contributed to non-conifer cover below 1539 m (Figure 3a).

3.3. Mortality Patterns

[24] Conifer mortality on a cover basis averaged 15% over the entire elevation range (Figure 3b). $Dead_{07-08}$ was increased from 1783 m to 2271 m, with dead conifers covering 9 to 18% of the 300 m transects. Conifer mortality decreased with increasing elevation (Figure 3c; p < 0.01; linear regression; slope different from zero). Nearly 40% of the 2002 conifer cover near the lower conifer ecotone had died by 2008.

[25] Midmontane conifer mortality exceeded subalpine conifer mortality. Total midmontane conifer mortality was 17% and subalpine conifer mortality was 3% (Figure 3b). Midmontane conifer mortality decreased with increasing elevation (Figure 4, p = 0.02; linear regression on mean mortality; slope different from zero), causing a large reduction in live cover at low elevation and further skewing the mean midmontane species' distribution upslope. Subalpine conifer mortality was independent of elevation and did not have a noticeable effect on the shape of subalpine species' distribution (Figure 5, p = 0.32; linear regression; slope different from zero).

[26] We compared mortality between the midmontane species. Abies concolor, Calocedrus deccurrens, Pinus lambertiana, and Yellow Pine (Pinus coulteri, ponderosa, jeffreyi) mortality was high, ranging from 10% to 25% over the elevation range (Table 2). The cover-weighted mean elevation of $Dead_{07-08}$ was below the mean elevation of $Live_{02}$ for each midmontane species (Table 2). This mortality caused a 37 +/− 33 m (mean +/− 95% CI) upslope shift in midmontane species distribution (p = 0.04). The pattern of subalpine conifer mortality paralleled the $Live_{02}$ subalpine species' cover, resulting in a small and insignificant change in cover-weighted mean elevation (−2 m).

3.4. Forest Size Structure

[27] We recorded the diameter at breast height (DBH) of 720 live and dead conifers in the survey plots at the various elevations. The low elevation stands showed a comparatively more exaggerated J-shape size structure, which was
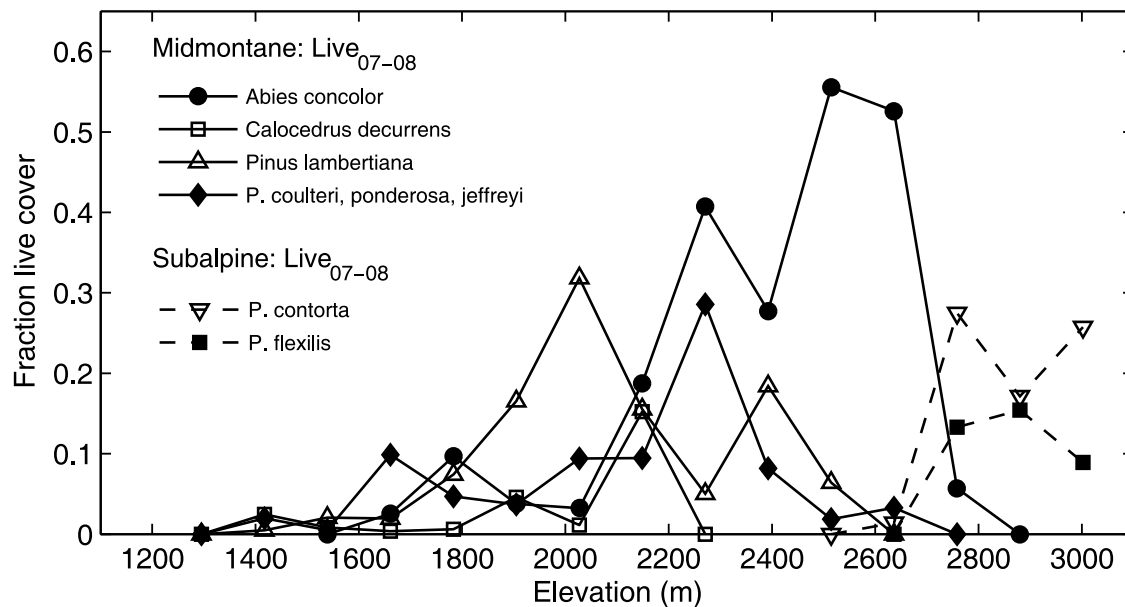
Figure 2. Species fraction cover with elevation. $Live_{07-08}$ measured at each sampling transect on the elevation gradient. Midmontane species were: *Abies concolor* (black circle), *Calocedrus decurrens* (open square), *Pinus lambertiana* (open triangle), and a yellow pine group composed of *Pinus coulteri*, *P. ponderosa*, and *P. jeffreyi* (black diamond). Subalpine species were: *Pinus contorta* (inverted open triangle) and *P. flexilis* (black square).

characterized by a low density of intermediate and large diameter trees and a high density of small trees (Figure 6). The slope of the best fit line between $\log_{10}$(stem density) and $\log_{10}$(tree size) in the low elevation plots had a steeper negative slope (p = 0.03; analysis of covariance), indicating that low elevation forests contained significantly fewer intermediate and large trees than high elevation forests.

[28] We found 111 dead conifers ha^{-1} below 2150 m in the smallest 10 cm size class, and 67 dead conifer trees ha^{-1} in all other size classes. Low elevation stands retained a strong J-shape after excluding dead conifers (Figure 7a).

[29] We counted 313 conifer seedlings: 61% were *Abies concolor*, 33% were *Pinus spp.* and 7% were *Calocedrus decurrens*. The highest seedling density was found at 1783 m, which was in the lower midmontane forest (Table 3). We did not find a statistically significant trend in seedling density with elevation. Similarly, we did not find any seedlings above the current ranges of adult trees of the corresponding species.

[30] We used generalized allometric equations to calculate the $Live_{07-08}$, $Dead_{07-08}$ and $Live_{02}$ biomass in the survey plots. $Dead_{07-08}$ conifers accounted for 36% of the $Live_{02}$ biomass in all of the survey plots, and 70% in the survey plots below 2150 m. The biomass of a tree is a sharply nonlinear function of DBH; mid-to-large conifer trees account for a relatively small fraction of a stand on the basis of number of stems, and a very large fraction of a stand on the basis of biomass (Figure 7). The marked mortality of large trees below 2150 m, especially those above 60 cm DBH, caused a large loss of biomass between 2002 and 2007–08. These larger trees contained a disproportionate amount of biomass, and died at a disproportionate rate, resulting in a large loss of overall stand biomass (Figure 7b).

3.5. Historical Context

[31] The Los Angeles Times contained occasional reports of tree mortality in Southern California's mountains, beginning with an article in 1903 (Figure 8). Conifer mortality associated with bark beetle outbreak was reported approximately every 15 years, with an especially large number of articles published in the 1950s and early 1960s. Nearly all reports indicated beetle outbreaks were the cause of conifer mortality. Many of the articles described a situation that appears similar to that observed in the early 2000s. A September 30, 1903 article titled "Pine Forests Doomed by Dakota Beetle" speculated that "at the present rate of death among the large pine trees, it will be only a matter of a few years before the forest will be destroyed." A January 29, 1950 article titled "Pine Beetle Infestation Fight Began" reported that the "greatest damage from the pine bark beetles has occurred in the regions bordering the chaparral belts," providing anecdotal evidence for tree mortality that focused at the lower parts of the conifer range (e.g., Figure 3).

[32] Reported beetle outbreaks were episodic and clustered, and usually occurred after several years with below average precipitation (Figure 8). Years with reported bark beetle outbreak had significantly lower mean precipitation in the preceding five years than years with no reports (p < 0.05). We found no correlation between annual temperature and reported beetle outbreak (p > 0.05; Figure 8).

4. Discussion

4.1. Rates and Patterns of Tree Mortality

[33] The rates of mortality we observed are consistent with those reported for the early 2000s by other researchers working in Southern California's mountains. We found 15%
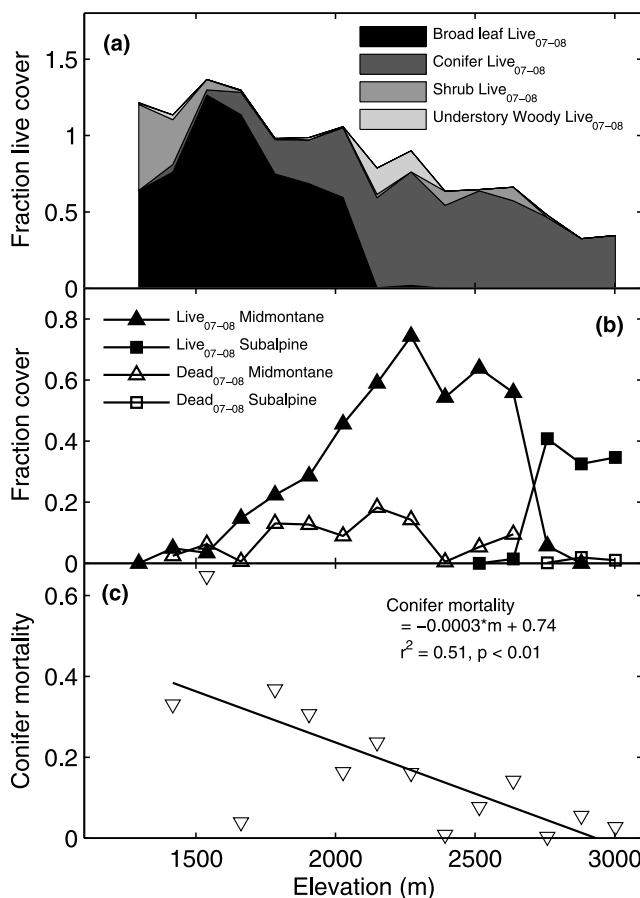
Figure 3. Plant functional type, live and dead conifer fraction cover, and conifer mortality. (a) Live$_{07-08}$ grouped by plant function type. Broadleaf species were: *Quercus* spp. and *Salix* sp. Conifer species were: *Abies* sp., *Calocedrus* sp., *and Pinus* spp. Shrub species were: *Arctostaphylos* spp., *Ceanothus* spp., *Cercocarpus* sp., *Adenostoma* sp., *and Chrysolepis* sp. Understory woody species were a variety of understory woody species including *Ribes* spp. (b) Live$_{07-08}$ midmontane (filled triangle), Dead$_{07-08}$ midmontane (open triangle), Live$_{07-08}$ subalpine (filled square), and Dead$_{07-08}$ subalpine (open square) fraction conifer cover with elevation. Midmontane species were: *Abies concolor, Calocedrus decurrens, Pinus lambertiana, P. coulteri, P. ponderosa, and P. jeffreyi.* Subalpine species were: *Pinus contorta* and *P. flexilis.* (c) Conifer mortality for all conifers over the elevation gradient (open triangle). Elevation is meters above sea level.

California during 2002–04 exceeded the cumulative regional tree mortality over the last century.

[34] Midmontane conifer mortality was greatest at lower elevations (Figure 3). This focused decline further skewed the distribution of midmontane conifers upslope (Figure 4), and led to an average 37-m rise in cover-weighted elevation (Table 2). Most species did not show a change in range extent. *Abies concolor* was the exception, with an apparent lower range retraction caused by 100% mortality at 1540 m. In general, low elevation conifer mortality broadened the ecotonal transition from shrubs and evergreen broadleaf trees at low elevation to broad and needleleaf trees at higher elevations, without shifting the lower conifer tree boundary [*Jump et al.*, 2009]. We found no evidence of seedling recruitment to higher elevations, suggesting the upper range extent was also static.

[35] *Breshears et al.* [2008] classified the possible forms of plant population redistribution along a climate gradient into three categories: "march," "lean," and "crash." A march occurs when decline at the trailing edge of a distribution is
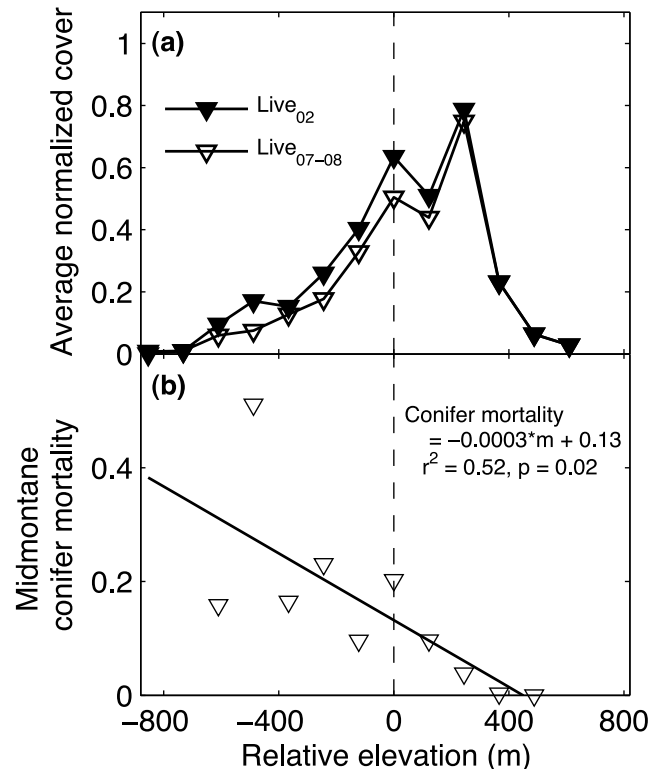

Figure 4. Midmontane conifer group distribution. (a) Live$_{02}$ (black triangle) and Live$_{07-08}$ (open triangle) midmontane distributions. The distributions were determined by setting the central transect (the sampling transect nearest the Live$_{02}$ cover-weighted mean elevation) for each midmontane species to zero and then averaging the normalized cover of each species at the corresponding sampling transects above and below the central transect. Relative elevation is the elevation above or below the central transect with positive indicating meters above the central transect. (b) Conifer mortality (open triangle) is mean midmontane conifer mortality for elevations with at least two species. Elevation is meters above sea level.

conifer mortality by cover, and 25% mortality of conifers with at least 12.7 cm DBH over the entire gradient, which is somewhat greater than the 12.7% mortality of conifers with at least 12.7 cm DBH reported for Southern California's mountains during this period [*Walker et al.*, 2006]. The tree death we observed is well above the long-term mean mortality reported for Californian montane forest. *Ansley and Battles* [1998] found baseline mortality in a Sierra Nevada old growth forest was 0.6% yr^{-1}. *Stephenson and van Mantgem* [2005] reported average tree mortality in the Sierra Nevada Mountains is less than 2% yr^{-1}. *Minnich* [2007b] speculated the total tree mortality in Southern
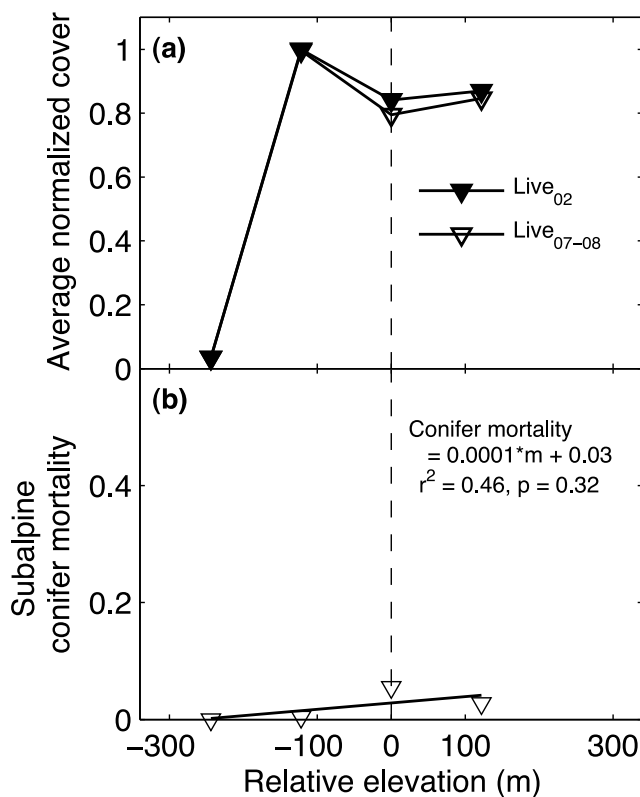
Figure 5. Subalpine conifer group distribution. (a) $Live_{02}$ (black triangle) and $Live_{07-08}$ (open triangle) subalpine conifer distributions. (b) Conifer mortality (open triangle) is subalpine conifer mortality. Elevation is meters above sea level.

matched by expansion at the leading edge: the species' distribution "marches" uphill. A lean occurs when decline at the trailing edge outpaces expansion at the leading edge: the species' distribution "leans" or skews uphill. A crash occurs when a species' abundance decreases throughout its range: the species' density declines or "crashes" throughout its range. Our observations are consistent with an enhanced lean among midmontane conifers in the early 2000s (Figure 4). This pattern is similar to that reported between 1977 and 2006–07 along a nearby montane transect [*Kelly and Goulden*, 2008]. The rate of upslope redistribution we observed (37 m) is less than that reported by Kelly and Goulden (~65 m). This difference may be partially methodological. The approach we used is sensitive to only the effects of recent crown mortality on cover-weighted species
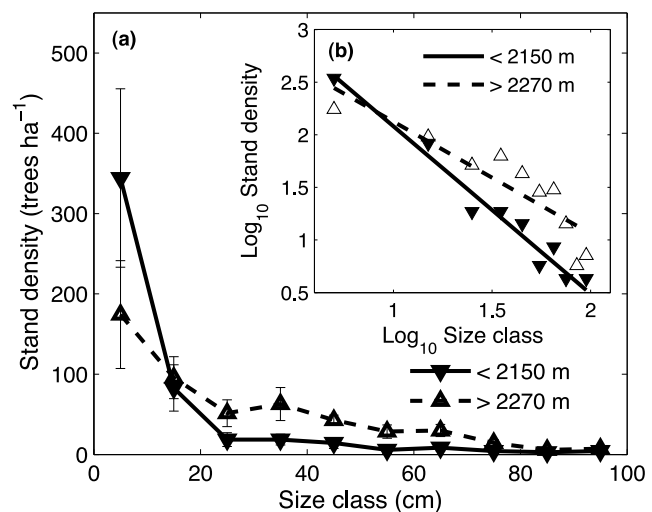

Figure 6. Conifer diameter size distribution. (a) Conifer diameter size distribution for lower (<2150 m; black triangle) and upper (>2270 m; open triangle) elevation stands. Live and dead conifer trees were binned into 10-cm diameter at breast height (DBH) size classes. Each marker is plotted at the center of the corresponding 10-cm diameter size bin. Stand density (trees ha^{-1}) is mean +/− standard error. (b) Log_{10}(conifer stand density) versus Log_{10}(size class) for lower (<2150 m; black triangle) and upper (>2270 m, open triangle) elevation stands.

distribution, whereas Kelly and Goulden's approach is sensitive to both crown mortality and expansion.

4.2. What Caused the 2002–2004 Mortality?

[36] There is consensus in the literature that drought was the primary immediate cause of the 2002–04 mortality [*Minnich*, 2007b; *Walker et al.*, 2006]. Southern California's Southern Interior Region received 48% of average precipitation in 2002, making it the 8th driest year in the 116 year record. The preceding five year mean precipitation was 84% of average in 2002, and 69% of average in 2003. Bark or engraver beetles were responsible for most of the pine mortality in the area [*Walker et al.*, 2006]. Water-stressed trees are considered susceptible to beetle attack due to reductions in photosynthesis, energy reserves, and the production of secondary defense compounds [*Adams et al.*, 2009]. Non-pine conifers in Southern California, including white fir, are thought to have died as the direct result of drought [*Minnich*, 2007b]. Additional factors beyond drought may have contributed to mortality. Predisposing

Table 2. Species Distribution Properties[a]

Species	$Live_{02}$ Elevation (m)	$Live_{07-08}$ Elevation (m)	$Dead_{07-08}$ Elevation (m)	Elevation Change (m)	Norm Cover	D (%)	N
Abies concolor	2353	2399	2188	46	0.19	22	11
Calocedrus decurrens	1934	1991	1763	57	0.02	25	7
Pinus lambertiana	2086	2095	2019	9	0.08	11	10
P. coulteri, ponderosa, jeffreyi	2079	2117	1717	38	0.06	10	11
P. contorta, flexilis	2872	2870	2913	−2	0.07	3	4

[a]$Live_{02}$ elevation is the estimated cover-weighted mean elevation before tree mortality. $Live_{07-08}$ elevation is the cover-weighted mean elevation of live vegetation measured during the survey. $Dead_{07-08}$ elevation is the cover-weighted mean elevation of dead vegetation measured during the survey. Elevation change is the difference between the $Live_{02}$ cover-weighted mean elevation and the $Live_{07-08}$ cover-weighted mean elevation. Norm cover is the fraction of the survey covered by that species. D (%) is the conifer mortality of that species over the entire survey. N is the number of transects that the species spanned.
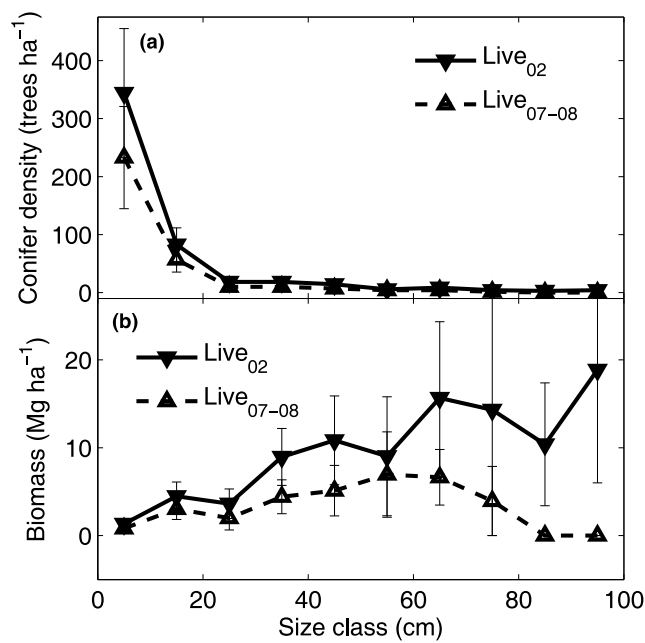
Figure 7. Lower elevation live and dead conifer stem density and biomass by size class. (a) Conifer density (trees ha^{-1}) is mean +/− standard error for all stems (Live$_{02}$; black triangle) and for live stems (Live$_{07-08}$; open triangle) below 2150 m. (b) Conifer biomass (Mg ha^{-1}) is mean +/− standard error for all stems within a size class (Live$_{02}$; black triangle) and for live stems within a size class (Live$_{07-08}$; open triangle) below 2150 m.

conditions such as air pollution or stand densification with fire suppression may have weakened trees and left them vulnerable to beetles and drought [*Mueller-Dombois*, 1988; *Savage*, 1994]. Southern interior temperatures preceding and during the bark beetle outbreak in the early 2000s were above average. Warmer temperatures may increase forest vulnerability either by exacerbating drought stress or by increasing beetle metabolism and reproduction [*Raffa et al.*, 2008]. Regional temperature trends may have predisposed low elevation conifers to mortality. The 0.0208°C yr^{-1} warming trend over the last 60 years (Figure 8) resulted in a ~3.9 m yr^{-1} upslope shift in temperature with elevation, assuming a −0.0054°C m^{-1} lapse rate.

[37] Fellows and Goulden (Controls on gross production by a semiarid forest growing near its warm and dry ecotonal limit, submitted to *Agricultural and Forest Meteorology*, 2012) analyzed the CO_2 and water exchange by a conifer and oak stand at 1708-m elevation and 3.5-km northwest of the transect (Figure 1; Oak Pine Forest U.S.-SCf). The 1708-m stand experienced considerable mortality in 2002–04, and had species that were similar to the 1661 and 1783 m sites we report here. Fellows and Goulden selected the 1708-m stand because it was near the lower conifer range limit, and in the belt of greatest 2002–04 tree mortality (e.g., Figure 3). The 1708-m stand maintained high rates of CO_2 uptake throughout the summer drought during an average rainfall year, apparently as a result of deep rooting and access to soil water at 2 to 5-m depth. The rates of CO_2 uptake during a drier-than-average year were markedly reduced from mid-summer to fall, presumably as a result of deep soil drying.

Fellows and Goulden hypothesized this deep soil reservoir becomes depleted during a sequence of particularly dry years, and that this deep drying results in unusually severe summer drought stress, a decline in GPP, and increased tree mortality. This mechanism is consistent with the spatial (Figures 3 and 4) and temporal (Figure 8) patterns of mortality we observed: widespread mortality focused in lower elevation stands following a sequence of drier than usual years.

[38] *Kelly and Goulden* [2008] reported a similar upslope shift in vegetation cover along a nearby altitudinal gradient and also attributed it to recent meteorological conditions, including the occurrence of extended drought. *Schwilk and Keeley* [2012] subsequently criticized Kelly and Goulden's attribution of the upslope species redistribution to climatic conditions. Schwilk and Keeley developed an alternative hypothesis, suggesting the upslope redistribution during this period was caused by stand self-thinning in the lower parts of species' ranges associated with long-term vegetation dynamics following historic fires. Goulden and Kelly (http://www.plosone.org/attachments/pone.0034798.comment1.pdf) rebutted Schwilk and Keeley's interpretation based on both theoretical (Schwilk and Keeley incorrectly assumed trends in plant stem density mirror trends in plant cover during stand thinning) and prior publication (Schwilk and Keeley 's hypothesized pattern of postfire recovery dynamics is inconsistent with previous work [e.g., *Zammit and Zedler*, 1993]).

[39] Our results add two arguments that further counter Schwilk and Keeley's hypothesis. First, our investigation was spatially independent of Kelly and Goulden's, and can be viewed as replicating their work. Schwilk and Keeley's hypothesis requires a complex and speculative mosaic of fire history, such that the lower part of each of the individual species' ranges last burned during a time window that would have caused recent age-related mortality, whereas the upper part of each range last burned at a time that would have caused recent cover stasis. Kelly and Goulden reported that 9 of 10 species redistributed upslope over the last 30 years, and we found that 4 of 5 species or groups redistributed upslope with recent mortality. The probability that a mosaic of fire histories and stand ages could have caused such a large fraction of species to redistribute upslope appears low. Second, Schwilk and Keeley hypothesized the mortality in the lower reach of a species' range was caused by natural stand thinning, rather than meteorological conditions. Natural stand thinning is greatest among smaller, suppressed members

Table 3. Conifer Seedlings[a]

Elevation (m)	Midmontane Seedlings (ha^{-1})	Subalpine Seedlings (ha^{-1})
1661	170	0
1783	950	0
1905	670	0
2027	160	0
2149	260	0
2271	50	0
2393	40	0
2515	50	0
2637	150	10
2758	260	40
2880	0	30
3002	0	290

[a]Midmontane and subalpine conifer seedling density (conifer trees with a height less than 138 cm).
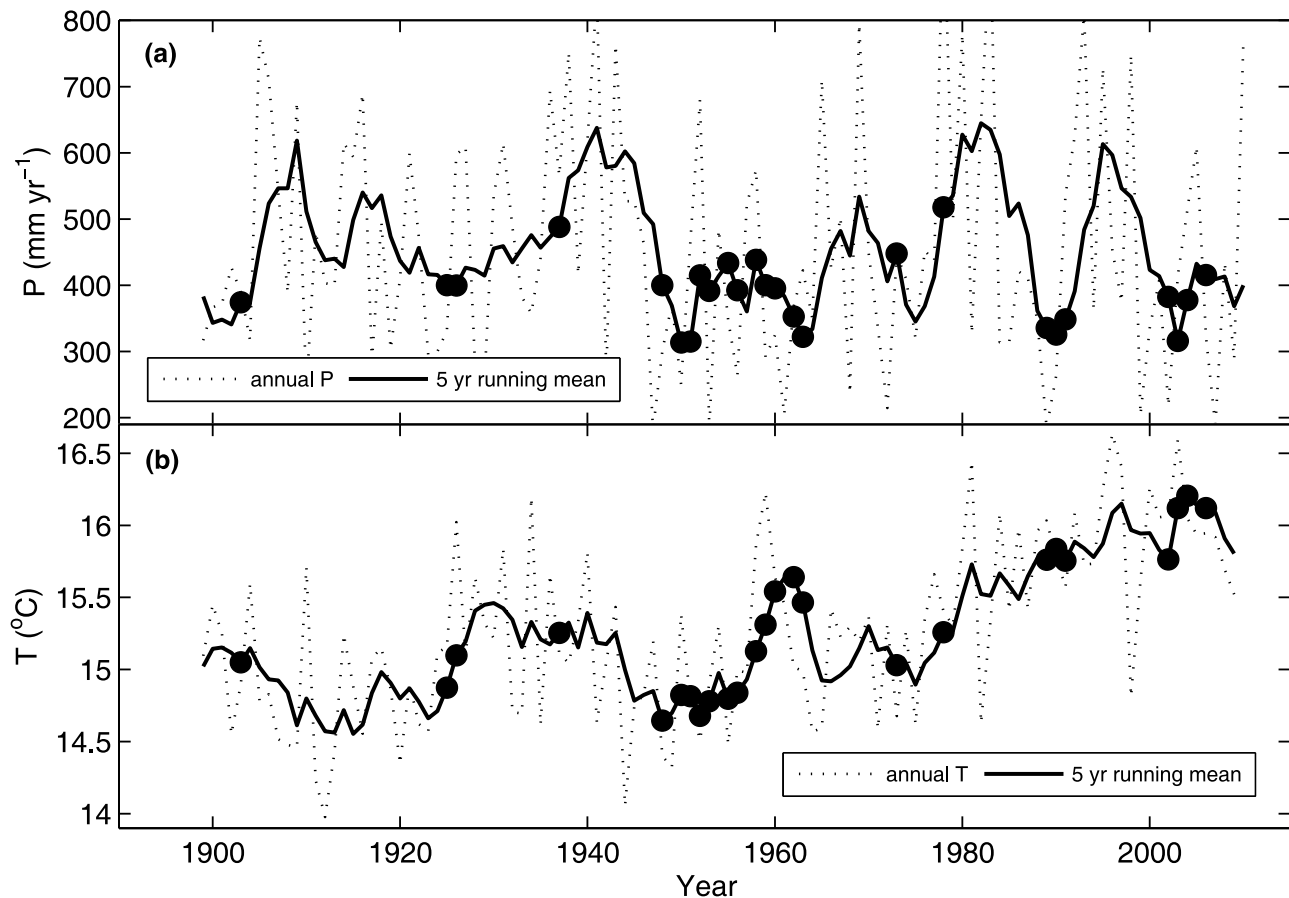
Figure 8. Reports of bark beetle outbreaks with precipitation and temperature record. (a) Bark beetle outbreaks reported in the Los Angeles Times newspaper (black circles) are plotted with the previous five-year moving average (bold black line) and the annual southern interior precipitation record (annual P; dotted line). Bark beetle outbreaks are plotted on top of the previous five-year moving average of precipitation. (b) Reported bark beetle outbreaks (black circles) are plotted with the previous five-year moving average (bold black line) and the annual mean southern interior temperature record (annual T; dotted line). The beetle outbreaks are plotted on top of the previous five-year moving average of temperature.

of the community: thinning is a consequence of competition and the mortality of smaller, less competitive plants [*Oliver and Larson*, 1996]. However, we found the mortality rate was greatest among large trees (Figure 7), a pattern that is inconsistent with Schwilk and Keeley's hypothesis.

[40] In short, our results confirm Kelly and Goulden's finding of a recent, rapid upslope movement of plant distribution in Southern California's mountains. Moreover, our results are consistent with Kelly and Goulden's conclusion that this redistribution was attributable in large part to recent meteorological conditions.

4.3. Comparison of Vegetation Redistribution and Mortality Between Midmontane and Subalpine Forests

[41] Total conifer cover peaked at 2271 m (Figure 3), and a reasonable working hypothesis is that sparser conifer cover below this elevation is caused by increasing drought stress, and sparser cover above this elevation is caused by increasing cold limitation. The pattern of mortality with elevation, and especially the comparison between midmontane and subalpine forest, supports this idea. The early 2000s mortality coincided with severe drought, and mortality was

much more prevalent among midmontane species, especially at and below 2271 m. In contrast, subalpine conifer mortality was low and independent of elevation, a pattern that is consistent with background mortality rates. Midmontane conifer distributions ranged from 1417 m to 2758 m (Figure 3) and presumably spanned a gradient of decreasing water limitation from low to high elevation. Subalpine conifer tree distributions ranged above 2637 m, an area where water limitation may be uncommon and production is more typically limited by winter cold.

4.4. Effect of Mortality on Aboveground Biomass

[42] Large trees comprise only a small fraction of the number of individuals in a stand, but contain most of a stand's biomass (Figure 7). Large conifers, especially those greater than 60-cm DBH and those growing below 2150 m, died at a disproportionately high rate in the early 2000s relative to small trees (Figure 7a). *Walker et al.* [2006] reported a similar pattern in Southern California's mountains: large conifers died at twice the rate of small ones. The loss of only a few large trees can drive substantial changes in forest biomass. The death of 26 conifers ha^{-1} with a DBH

between 10 and 20 cm reduced aboveground biomass by 1.4 Mg ha^{-1} in stands below 2150 m (Figure 7b). The death of 4 conifers ha^{-1} with a DBH between 90 and 100 cm reduced biomass by 18.9 Mg ha^{-1}. Mortality drove a 36% reduction in conifer biomass averaged across all elevations, and a 70% reduction in conifer biomass in stands below 2150 m (Figure 7b). These reductions exceeded the 21% loss of conifer biomass reported by *Walker et al.* [2006] but are similar to declines due to beetle attacks elsewhere [*Pfeifer et al.*, 2011]. Focused mortality on large trees has the potential to amplify the ultimate loss of carbon associated with stand dieback, beyond what would be predicted with size-independent mortality.

4.5. Is Mortality and Vegetation Redistribution a Common Occurrence?

[43] The identification of early ecological impacts of global climate change is a difficult and contentious problem, with major attribution challenges [*Parmesan et al.*, 2011]. In principle, the early 2000s mortality described by *Breshears et al.* [2005], *Kelly and Goulden* [2008], and others can be interpreted in three ways: (1) as an early ecological impact of a changing mean climate associated with global climate change, (2) as a consequence of low-frequency natural climate variability, or (3) as a consequence of natural climate variability that has been amplified or modified to an unknown extent by global climate change and other human-driven factors.

[44] We feel there is strong evidence the upslope species redistribution we describe is not a new or exclusively modern phenomenon. Bark beetle outbreaks and conifer mortality have occurred repeatedly in Southern California over the past 100 years and are strongly associated with extended drought (Figure 8). The precipitation record in Southern California shows marked low-frequency variability with a period of 10 to 15 years. Decadal climate patterns in California have been linked to natural variability, such as the Pacific Decadal Oscillation [*Biondi et al.*, 2001; *McCabe et al.*, 2004]. Bark beetle outbreak and conifer mortality track this decadal variability, with peaks in the early 1960s, mid 1970s, early 1990s, and early 2000s (Figure 8). Redistribution of vegetation would have occurred during these previous outbreaks, provided mortality was focused in the lower parts of species distributions. The contrasting patterns of tree size distribution between the lower and upper stands supports the notion that past mortality was greater at lower elevations. The size distribution of conifers in lower elevation stands was comparatively more strongly J-shaped, with relatively fewer large trees (Figure 6). This size structure may be explained by previous episodes of mortality that were focused at lower elevation and on larger trees. Similarly, the upward skew in Live$_{02}$ vegetation (Figure 4) may be explained by previous mortality and an associated upward "lean" of conifer vegetation.

[45] The vegetation redistribution we observed may therefore be part of a long-running natural cycle, consisting of: (1) focused mortality and crown dieback at lower elevation during multiyear drought and an associated upward vegetation "lean," followed by (2) focused establishment and crown expansion at lower elevation during multiyear wet periods and an associated downward "lean." Seedling recruitment is also episodic in Western conifer forests and depends on

multiple biotic and abiotic factors that include meteorological extremes [*North et al.*, 2005; *van Mantgem et al.*, 2006].

[46] These considerations lead us to reject the notion that the patterns we observed are the exclusive result of a changing mean climate associated with global climate change. Rather, our findings are most consistent with the interpretation that the redistribution of species in the early 2000s was primarily a consequence of low-frequency natural climate variability. Our findings do not shed light on the possibility that the occurrence, intensity, or impact of drought was amplified by global climate change or other human-driven factors. In particular, we are unable to determine whether mortality in the early 2000s was amplified by above average temperatures (Figure 8). The likelihood of an interaction between drought and warming remains an outstanding and largely unresolved question (a "global-change-type drought"; [*Breshears et al.*, 2005]). Climate change is expected to decrease mean precipitation in the southwestern U.S. [*Seager and Vecchi*, 2010], and cause further warming-driven intensification of evapotranspiration and drought [*Huntington*, 2006; *Walter et al.*, 2004], especially at higher elevation [*Bradley et al.*, 2004]. Some analyses suggest the hydrology of the western U.S. is already changing [*Barnett et al.*, 2008].

[47] The mortality observed in the early 2000s points to a natural and rapid ecological response to decadal to centennial climate change. We hypothesize this natural mode of response will dominate the early response of semi-arid forest to global climate change, and will complicate efforts to identify and attribute the local impacts of climate change. Attribution of biotic responses to global climate change is especially difficult at small spatial scales, over short time periods, and for single events [*Parmesan et al.*, 2011]. Attribution may prove particularly difficult in the Southwestern U.S., where the initial impact of global climate change on vegetation may prove almost identical to the impact of natural climate variability.

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