Why do trees die? Characterizing the drivers of background tree mortality

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Abstract. The drivers of background tree mortality rates—the typical low rates of tree mortality found in forests in the absence of acute stresses like drought—are central to our understanding of forest dynamics, the effects of ongoing environmental changes on forests, and the causes and consequences of geographical gradients in the nature and strength of biotic interactions. To shed light on factors contributing to background tree mortality, we analyzed detailed pathological data from 200,668 tree-years of observation and 3,729 individual tree deaths, recorded over a 13-yr period in a network of old-growth forest plots in California's Sierra Nevada mountain range. We found that: (1) Biotic mortality factors (mostly insects and pathogens) dominated (58%), particularly in larger trees (86%). Bark beetles were the most prevalent (40%), even though there were no outbreaks during the study period; in contrast, the contribution of defoliators was negligible. (2) Relative occurrences of broad classes of mortality factors (biotic, 58%; suppression, 51%; and mechanical, 25%) are similar among tree taxa, but may vary with tree size and growth rate. (3) We found little evidence of distinct groups of mortality factors that predictably occur together on trees. Our results have at least three sets of implications. First, rather than being driven by abiotic factors such as lightning or windstorms, the "ambient" or "random" background mortality that many forest models presume to be independent of tree growth rate is instead dominated by biotic agents of tree mortality, with potentially critical implications for forecasting future mortality. Mechanistic models of background mortality, even for healthy, rapidly growing trees, must therefore include the insects and pathogens that kill trees. Second, the biotic agents of tree mortality, instead of occurring in a few predictable combinations, may generally act opportunistically and with a relatively large degree of independence from one another. Finally, beyond the current emphasis on folivory and leaf defenses, studies of broad-scale gradients in the nature and strength of biotic interactions should also include biotic attacks on, and defenses of, tree stems and roots.

Key words: bark beetles; biotic interactions; competition; suppression; tree mortality; tree mortality factors; tree pathogens.

INTRODUCTION

At the heart of much recent research in forest dynamics lies a deceptively simple question: Why do trees die? The answer is central to our ability to forecast changes in forest structure, composition, and feedback to ongoing global changes (Bonan 2008, Adams et al. 2010, Dietze and Matthes 2014). In particular, much recent work has focused on elucidating mechanisms contributing to forest die-back, when an unusually high proportion of trees die relatively abruptly in response to drought, heat, insect outbreaks, or other causes (Bréda et al. 2006, Sala et al. 2010, McDowell et al. 2011, Anderegg et al. 2015). In contrast, less attention has been paid to mechanisms driving background tree mortality—the typical low rates of mortality (usually ~0.5% to 2% per year; Stephenson and van Mantgem 2005) that occur in otherwise healthy forests that are not experiencing die-back.

Yet at broad scales, seemingly minor changes in background tree mortality rates can have substantial effects, exceeding even those of forest die-backs. For example, during a 14-yr period of notably extensive forest die-back in the western United States, insect outbreaks killed trees containing as much as 340 Tg of carbon (Hicke et al. 2013). Over the same period, in forests unaffected by die-back, an increase in background mortality rates of only 0.5%/yr—comparable to the increase observed across the western U.S. since the 1980s (van Mantgem et al. 2009)—would have killed trees containing at least an additional 380 Tg of carbon in excess of the amount if background mortality had not increased.

An understanding of the drivers of background mortality can also contribute to the ongoing debate about the relative strength, and the associated ecological and evolutionary consequences, of biotic interactions along environmental gradients (e.g., Schemske et al. 2009, Moles et al. 2011*a, b*, Moles 2013, Rodríguez-Castañeda 2013, Lim et al. 2015). For example, much of the data mustered in the debate has focused on the strength of leaf defenses and the intensity of folivory along environmental

gradients. But if folivory is typically not a major contributor to tree mortality relative to biotic attacks on tree stems and roots, then extra research emphasis is needed to improve our understanding of the latter.

Despite its importance, our understanding of why trees die under typical forest conditions—and thus our understanding of mechanisms driving background tree mortality rates—remains limited (but see Lutz and Halpern 2006, Lannenpaa et al. 2008, Hawkins and Henkel 2011). In large part, this is due to a paucity of studies on the full suite of factors that can contribute to tree death, as opposed to targeted studies of individual mortality agents, which are often conducted in response to insect or pathogen outbreaks. Additionally, most permanent forest plots are revisited at intervals of 5–10 yr, which is usually too long to confidently identify such factors. Long intervals between observations mean that signs of pathology preceding tree death can be missed, and the opportunistic insects and fungi that move into a tree after its death can obscure or destroy evidence of the actual mortality agents. Consequently, most studies of background mortality simply report how many trees died standing or were uprooted, broken, or crushed by another falling tree (e.g., Chao et al. 2009, de Toledo et al. 2012, Holzwarth et al. 2013).

This scarcity of detailed studies of the drivers of background tree mortality means that several hypotheses and assumptions remain largely untested. For example, the assumptions underlying the mortality algorithms of most individual-based forest models have remained essentially unchanged for more than 40 yr, and have increasingly been called into question (Kobe 1996, Loehle and LeBlanc 1996, Hawkes 2000, Keane et al. 2001, Das et al. 2008, Bircher et al. 2015). Such models typically assume that probability of tree death can be understood in terms of two broad classes of death: ambient mortality and vigor mortality, with vigor mortality representing an inverse relationship between tree growth and mortality probability (Shugart 1984, Botkin 1993, Bugmann 2001). Ambient mortality, in contrast, is death that is independent of growth rate and therefore affects trees growing at all rates with equal probability. Some authors have attributed ambient mortality to unspecified "intrinsic" causes of death, whereas others have assumed it to be caused by exogenous abiotic factors such as lightning, hurricanes, and fire.

To shed light on the factors contributing to background tree mortality ("mortality factors"), we followed the fates of 23,657 living trees belonging to 14 species in 23 old-growth forest plots arrayed across a broad elevational gradient in California's Sierra Nevada mountain range. Over a 13-yr period (with three plots having shorter intervals), each tree was visited annually and assessed for signs of pathology, for a total of 200,668 tree-years of observation. There were no severe disturbances, severe insect or pathogen outbreaks, or unusual droughts during this period. Each of the 3,729 trees that died during the period was systematically evaluated for

mortality factors within a year of its death. We asked the following questions:

1. What types of mortality factors appear to dominate tree mortality processes?
2. How does the distribution of these factors vary by tree size, growth rate, and species?
3. Is there evidence for strong organization among mortality factors, suggesting distinct disease complexes?
4. What are some implications for how we study forest processes and forecast forest change?

METHODS

Study sites

Twenty-three permanent study plots ranging in size from 0.9 to 2.5 ha were established between 1982 and 2001 in old-growth stands within the coniferous forests of Sequoia and Yosemite national parks, Sierra Nevada, California, USA (Appendix S1). These plots are located in old-growth forests, in which recruitment and mortality are roughly balanced (i.e., while competitive effects may still be important, the stand is no longer in the stage of self-thinning). Other plots in our network were excluded due to disturbances (fire) prior to the study period. Two plots burned during the study period, and only those trees that died prior to those fires were considered. The plots are arranged along a steep elevational gradient (~1,900 m) from near lower to upper treeline and encompass several different forest types, including ponderosa pine-mixed conifer, white fir-mixed conifer, Jeffrey pine, red fir, and subalpine forests (Fites-Kaufman et al. 2007). The sites have never been logged. Frequent fires characterized many of the forest types prior to Euro-American settlement, but the areas containing the study plots had not burned since the late 1800s (Caprio and Swetnam 1993). The climate is montane mediterranean, with hot, dry summers and cool, wet winters in which ~25–95% of annual precipitation (which averages 1,100 to 1,400 mm) falls as snow, depending on elevation (Stephenson 1988). Mean annual temperature declines sharply with elevation (~5.2°C for every 1 km increase in elevation), ranging from roughly 11°C at the lowest plots to 1°C at the highest. Soils are relatively young (mostly inceptisols), derived from granitic parent material.

Data collection

Within each plot, all trees ≥1.37 m in height were tagged, mapped, measured for diameter, and identified to species. We censused all plots annually for tree mortality and new recruitment, and at intervals of ~5 yr, we re-measured diameter at breast height (dbh, 1.37 m above ground level) of living trees. The consecutive diameter measurements allowed us to calculate diameter growth rates for each tree. We scanned trees' crowns with binoculars to ensure no green foliage remained before we

declared them dead, and each dead tree was revisited annually for at least 5 yr to ensure no misclassifications. Field crews were trained at the beginning of each season to identify known biotic attackers in these forests, learning to distinguish between primary tree-killing attackers and those likely to have entered the tree after mortality. This training included a short field course given by the regional U.S. Forest Service pathologist and entomologist, who were also consulted throughout the season when their expertise was required. Each living tree was examined for indications of poor health, damage (e.g., broken crowns or bark-stripping caused by a falling tree), or biotic attack (e.g., thinning crown, pitch tubes, fungal conks), and these conditions were recorded. Trees that died within the last year were evaluated for factors potentially contributing to mortality; the evaluations included careful inspection for signs of physical damage and signs of tree-killing or tree-weakening pathogens and insects. Bark was removed to locate and identify beetle galleries and to search for signs of fungal attack, and some minor excavation was done around the base of each dead tree to look for conks. Comments about the given tree's condition in previous years were used to assist in the evaluation. Whenever possible, attacking agents were identified to species. In addition, field crews made a visual assessment of a given tree's competitive environment and listed "suppression" as a potential mortality factor when crowding among trees appeared to be important. (We compared our visual assessments of suppression against a competition index and found that, as expected, trees with suppression listed as a mortality factor usually had a significantly higher competition index than those without.) We include only the data collected starting in 1998, when our field pathology procedures were improved, giving us a total 3,729 dead trees.

Our ability to identify some mortality factors—particularly those whose signs are most often found belowground or in treetops—was limited. For example, although root rots can often be identified by direct observation of conks, the presence of mycelial mats beneath the bark near ground level, and supporting circumstantial evidence (e.g., field comments noting that a tree's canopy became more sparse through time, evidence of the rot on nearby trees, and slowly spreading clumps of tree mortality), absence of these observations on a dead tree cannot rule out a role for root rots. Similarly, beetle attacks that usually occur at the tops of standing trees (e.g., by *Ips paraconfusus*) are likely to go unrecorded beyond notation of a dead top in the years preceding mortality. Finally, field personnel did not make the direct physiological measurements that could reveal certain abiotic factors contributing to mortality, such as effects of drought stress (although our period of study was free of any unusual droughts). Thus, our analyses of mortality factors are based on a comprehensive list of visible factors that likely contributed to tree mortality (including those beneath the bark in the lower portion of the tree), but not a complete list. Nonetheless, our data provide the most robust community-level analysis of mortality factors of which we are aware.

Importantly, the results we present for this analysis are the proportions of tree deaths that were associated with the different mortality factors (that is, they are not the annual rates of occurrence of the factors in the population of surviving plus recently dead trees). For reference, the average annual mortality rate for all trees in our study was 1.80% per year (1.35% to 2.25% per year 95% CI). Mortality rates for each of the four most abundant species were 1.39% per year (0.93% to 1.84% per year 95% CI) for *Abies concolor*; 1.55% per year (1.07% to 2.04% per year 95% CI) for *Abies magnifica*; 1.26% per year (0.73% to 1.79% per year 95% CI) for *Calocedrus decurrens*; and 6.69% per year (4.37% to 9.02% per year 95% CI) for *Pinus lambertiana*.

Defining size and growth-rate classes

To determine how mortality factors vary by tree size and growth rate, we defined three size and three growth-rate classes. Diameter size classes were <10 cm (small trees, often exposed to overtopping and shading), ≥10 and ≤50 cm (intermediate), and >50 cm (usually canopy trees). Diameter growth-rate classes were determined from data in Das and Stephenson (2015) as <0.5 mm/yr (low vigor; mortality rates are extremely high), ≥0.5 mm/yr and ≤4.0 mm/yr (intermediate vigor; mortality rates decline rapidly with increasing growth rates), and >4.0 mm/yr (high vigor; mortality rates are low and mostly independent of growth rate). We could not calculate growth rates for 29 trees due to missing diameter measurements, which were excluded from growth-rate analyses.

Variation with elevation

To explore how mortality factors varied in space, we examined patterns of occurrence across the elevational gradient (Appendix S1: Table S1). We used generalized linear mixed effects models with a binomial error distribution and the logit link function (i.e., a mixed effects logistic regression). The dependent variable was the occurrence (1 or 0) of a given biotic factor on a given tree, with the independent variable being elevation. Plot identity was treated as a random effect on the intercept. We fit elevation as first through third polynomial functions, and we present the model with the lowest AIC value.

Co-occurrence analyses

To examine whether some mortality factors were predictably associated with one another, we performed chi-squared tests between pairs of mortality factors, using the chisq.test function in the R statistical software (R Core Team 2013). Analyses were done separately for only the four most abundant species (*Abies concolor, Abies*

magnifica, Calocedrus decurrens, and *Pinus lambertiana.*), including only factors that had occurred on at least 10 dead trees within a given species. Statistical significance was determined using a Bonferroni correction for multiple tests within each species.

Pairwise tests might fail to detect larger groupings of mortality factors. Also, the large number of pairwise tests reduces our statistical power. Therefore, we performed an additional "community" analysis that allowed for the consideration of multiple factors simultaneously. For this purpose, we used nonmetric multidimensional scaling (NMDS). In these analyses the "site" was the individual tree and the "species" were the mortality factors associated with each tree. We considered only those trees that had two or more mortality factors listed in their mortality evaluations and included only those mortality factors that occurred on at least 10 trees in this subset, leaving us with a final sample of 1,786 dead trees.

We performed NMDS for all trees combined and separately for each of the four most abundant tree species in the dataset. Where sample sizes were adequate, we also performed analyses by size classes; we do not present these results because they did not differ meaningfully from those including all trees. NMDS was calculated using metaMDS in the VEGAN package with R statistical software, version 2.15.2. We used the Jaccard dissimilarity index and considered between two and 10 axes. Analyses were run without relativization, with relativization by column total, and with double relativization by column and row totals. Relativizations were performed to test whether the large disparities in occurrence among factors might affect our ability to detect groupings.

RESULTS

For each dead tree, mortality evaluations resulted in a list of 1–6 mortality factors (mean = 1.6). Half of all dead trees had only one mortality factor (including "unknown" as a mortality factor), and nearly 90% had only one or two factors.

We grouped mortality factors hierarchically and by frequency of occurrence (Appendix S3: Tables S1–S7); a detailed breakdown of specific mortality factors is given in Appendix S2 and Appendix S3. Biotic agents were the most frequent mortality factor (58% of dead trees overall; Fig. 1), ranging from 51% in small, slowly growing trees to 92% in large, slowly growing trees (Fig. 2). Occurrence of biotic factors generally increased with tree size (Fig. 2). Biotic factors were primarily insects (43%) and diseases (23%), with insects being dominated by bark beetles (40%) and diseases being fairly evenly distributed among a variety of agents. Notably, defoliators were a factor for less than 3% of dead trees. Bark beetles occurred frequently on trees ≥10 cm dbh, without a strong pattern relative to growth rate (vigor), but occurred far more frequently on small, fast-growing trees than on small, slow-growing trees (Fig. 3). Diseases showed a similar pattern to bark beetles, though at lower proportions.
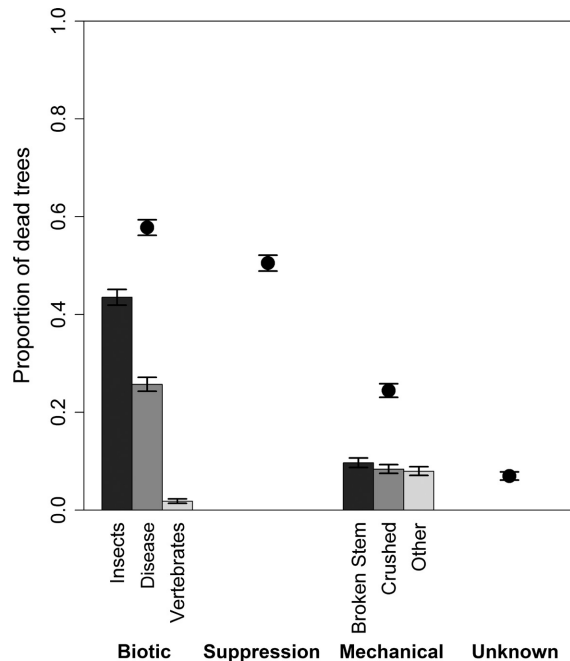

FIG. 1. Proportional occurrences of mortality factors in all 3,729 dead trees. Black dots indicate proportions within four broad classes; bars show finer subdivisions within the biotic and mechanical classes. Error bars represent 95% binomial confidence intervals. Proportions need not sum to one because each dead tree can have more than one mortality factor.

After biotic factors, suppression was most frequent (51% overall; Fig. 1). Unsurprisingly, the occurrence of suppression was highest in small, slowly growing trees (66%) and decreased dramatically with both tree size and growth rate (Fig. 2).

Mechanical factors were associated with 24% of dead trees and were dominated by broken stems (most commonly in intermediate and large trees) and trees that were crushed by other falling trees (most commonly in small and intermediate trees). Incidence of mechanical factors increased modestly from small to mid-size and showed some tendency to increase from slow to moderate growth rates, though the latter pattern was not strong (Fig. 2). Lightning damage was nearly absent in the dataset (found on only three out of 3,729 dead trees).

Taxon-specific results

Patterns within genera and species tended to be qualitatively similar to those for all taxa combined, with biotic factors dominating, followed by suppression and mechanical factors (Appendix S3: Tables S1–S7, Fig. S1). Biotic factors again tended to increase with tree size; suppression occurred as a factor most commonly among small, slow-growing trees; and among mechanical causes, stem breakage occurred mostly on large trees and crushing mostly on small. *C. decurrens* made an exception to some of these patterns. While biotic factors were
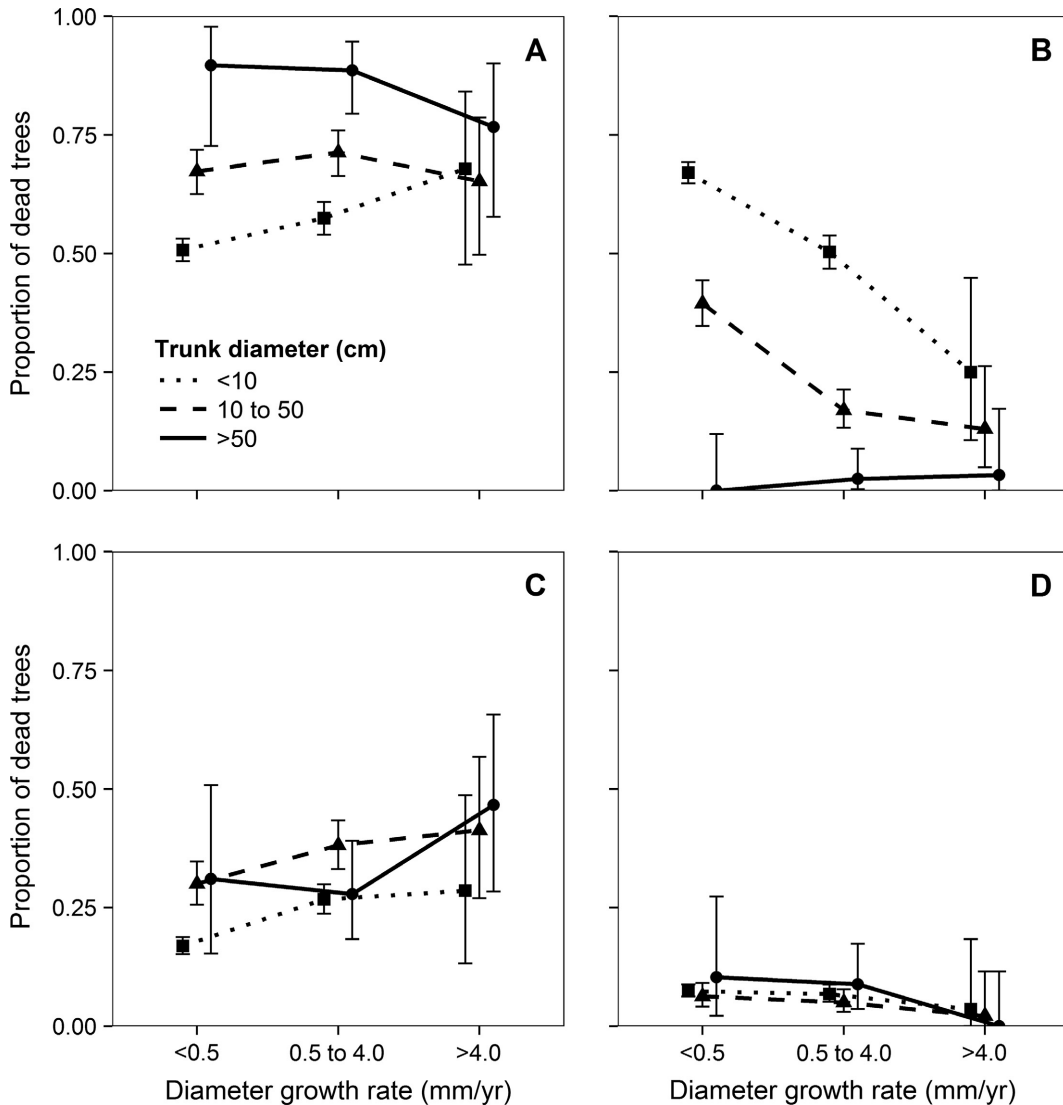
Fig. 2. Proportional occurrences of broad classes of mortality factors by tree size and pre-death growth rate, for all dead trees. A, biotic; B, suppression; C, mechanical; D, unknown. Error bars represent 95% binomial confidence intervals.

prevalent (49%), suppression dominated (68%). Additionally, biotic factors occurred more frequently in the smallest *C. decurrens* rather than the largest. The genus of bark beetles that most commonly attacks incense cedars, *Phloeosinus*, apparently prefers smaller trees – the opposite of the primary beetles that attack other species in this forest (Appendix S3: Fig. S6).

There were other differences among genera. For example, *Pinus* had a higher incidence of biotic factors (66%), bark beetle attack (53%), and disease (30%) than the collection of dead trees as a whole (Appendix S3: Tables S1–S7, Figs. S1–S6). The *Dendroctonus* bark beetles that attack pines are generally considered more aggressive than *Scolytus ventralis*, the primary species that attacks *Abies* (Wood et al. 2003), perhaps accounting for the difference. The higher incidence of disease on *Pinus* was mostly driven by the

exotic fungal pathogen *Cronartium ribicola* on *P. lambertiana*. Compared to all dead trees taken together, *A. magnifica* had relatively high occurrences of bark beetles and dwarf mistletoe and a notably higher incidence of mechanical mortality factors. *A. concolor* had a higher incidence of defoliators (7.3%)—a consequence of some of our plots being in the vicinity of an outbreak of *Orgyia pseduotsugata* in the late 1990s—but this value is still substantially lower than the incidence of bark beetles. Compared to all taxa combined, *C. decurrens* had a higher proportion of trees with suppression listed as a factor and a relatively low occurrence of diseases, in keeping with the observation that this species is subject to relatively fewer strong pathogens (Wood et al. 2003). *Quercus* showed a much lower proportion of biotic factors than the dataset as a whole, with suppression appearing to be the dominant factor.
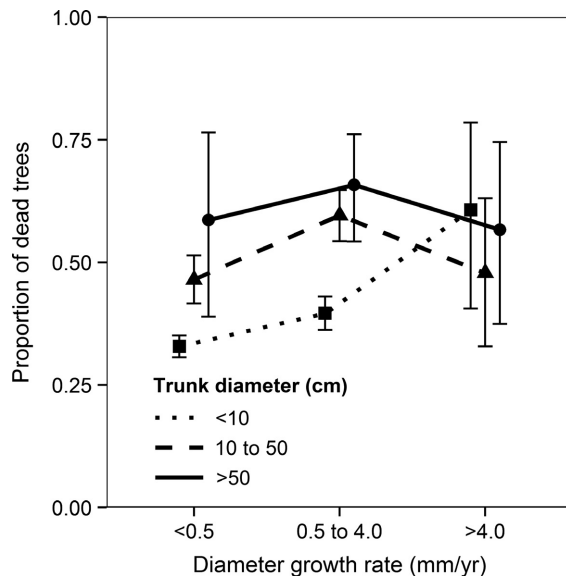
Fig. 3. Proportional occurrences of bark beetles by tree size and pre-death growth rate, for all dead trees. Error bars represent 95% binomial confidence intervals.

Variation in space

The prevalence of mortality factors also varied in space: biotic factors appeared to peak at middle elevations, suppression generally declined with elevation, and mechanical factors increased with elevation (Fig. 4). These patterns are almost certainly influenced by elevational changes in stand structure, species composition, soil properties, climate, and their interactions. A thorough analysis of mechanisms is beyond the scope of this paper but remains an important future goal.

Relationships among mortality factors

Our co-occurrence analysis found very few significant positive associations among mortality factors (Table 1; Appendix S4). For *A. concolor*, there was a predictable association between heart rot and stem breakage. The lack of detection of such an association in other species is almost certainly due to small sample sizes, as heart rot as a mortality factor is rare in these stands (Appendix S3: Table S1). For *P. lambertiana*, there was an association between bark beetles and white pine blister rust. For *C. decurrens,* there was a positive association between bark beetles and other and unknown diseases, which upon closer examination appears to primarily be due to apparent association between beetles and a sooty mold. The sample size of the latter association, however, is small and would require further investigation to verify.

Most of the significant associations (16 of 20) for all four species were negative. Eleven of these involved a mechanical factor. The most likely explanation for these mechanical "repulsions" is that when a tree is crushed, broken or otherwise severely damaged the mechanical

effect supersedes and is usually unrelated to any other conditions that the tree might have. (Similarly, a human with terminal cancer who is struck by a car is killed by the car, not by the cancer.) Most of the negative mechanical associations (seven) were with suppression; this is likely a consequence of high sample size—and thus higher statistical power—for suppression.

The remaining five negative associations also involve suppression. A repulsion between bark beetles and suppression for *A. concolor* and *P. lambertiana* might be expected because the bark beetle attackers for those species tend to prefer larger trees. But the other three – between suppression and rot in *A. concolor*, suppression and mistletoe in *A. magnifica*, and suppression and white pine blister rust in *P. lambertiana*—require further investigation.

For all NMDS ordinations, the ordination stress continued to decrease notably with increasing dimensions, not leveling out until at least six or eight dimensions had been added (Appendix S5). This property was more pronounced with relativized versions of the data. In all cases, two or three dimensions (which would allow for easy visual representation) appeared to be inadequate, with Kruskal's stress values not dropping below 0.1 until after three dimensions and the "elbow" in the stress plot not occurring until after this point as well. Randomization tests for a subset of the analyses indicated that the NMDS solutions for up to 10 dimensions provided significantly more reduction in stress than expected by chance.

Consistent with our pairwise analyses, ordinations as a whole did not reveal strong clustering among mortality factors (i.e., there did not appear to be several distinct groups of associated factors). Some factors were relatively close in ordination space, including broken stems and heart rot and suppression and bark beetles (Appendix S5).

On the other hand, two factors, suppression and bark beetles, appeared to be located centrally relative to several other factors (i.e., suppression and bark beetles had relatively short ordination distances to several other mortality factors, even if those other factors were not close to one another). This suggests that suppressed trees are vulnerable to a variety of other mortality agents and that bark beetles tend to attack trees that are stressed by a variety of other agents. Notably, for *P. lambertiana*, bark beetles tended to be very central to a wide array of other factors, and for *A. concolor* suppression was.

Discussion

Importance of biotic factors

Most models of forest dynamics assume that probability of tree mortality is a function of tree growth rate, with slowly growing trees having a much higher probability of mortality than rapidly growing trees (Kobe 1996, Loehle and LeBlanc 1996, Hawkes 2000, Keane et al. 2001). While this assumption is well supported by
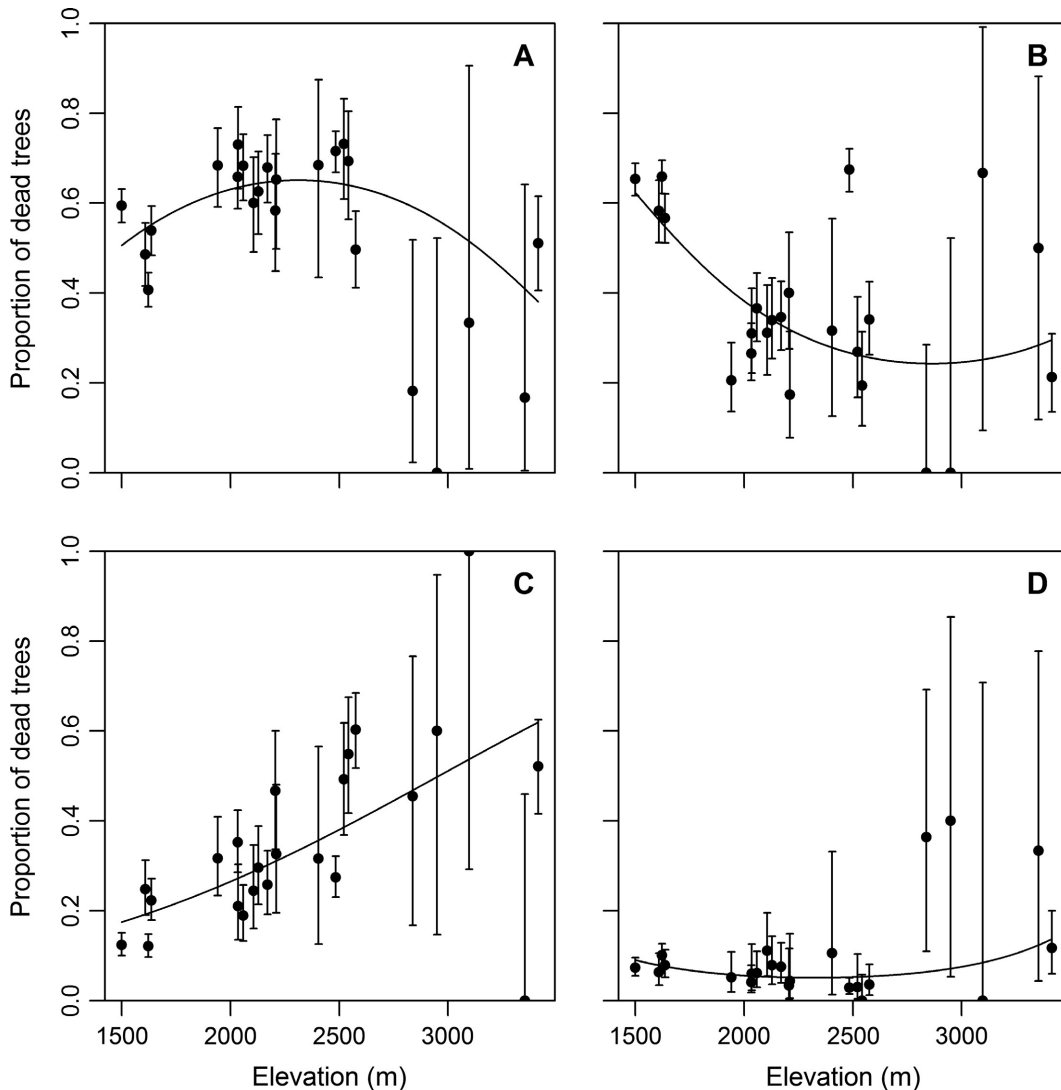
Fig. 4. Occurrence of broad classes of mortality factors by elevation, for all dead trees. Curves are fit using mixed effects models (see *Methods*). Individual points represent occurrence for a given plot. Note that model fits were based on individual trees, while the plot values are given as a useful summary of the underlying data. A, biotic; B, suppression; C, mechanical; D, unknown. Error bars represent 95% binomial confidence intervals.

empirical observations, the magnitude of the relationship appears to be under strong environmental control (Stephenson et al. 2011). Accurate model representation of environmentally induced changes in tree mortality thus requires a mechanistic understanding of mortality, which in turn requires an understanding of what kills trees under typical forest conditions. Our work particularly highlights the substantial contribution of biotic agents to background tree mortality.

Biotic mortality factors appear to be the most prevalent agents of background mortality in old-growth Sierra Nevada forests, even more so than competition (suppression), with biotic factors occurring on at least 50% of dead trees regardless of tree size and growth rate. Biotic factors dominated at all elevations except the

highest. The general prevalence of biotic mortality factors is consistent with previous work in these forests, which found that competition alone could not account for the temporal dynamics of spatial patterns in these forests (Das et al. 2011), and that factors other than competition appear to influence risk of mortality (Das et al. 2008).

Although more work is needed, the importance of biotic mortality agents as significant contributors to background tree mortality may be global. While dead trees in old-growth forests of the Pacific Northwest had a substantially higher occurrence of mechanical mortality factors than ours, at least half of them also had non-mechanical factors (biotic and suppression), and 80% of mechanical mortalities in larger trees were associated with rot (Larson and

TABLE 1.   Significant pairwise co-occurrences of mortality factors.

Species	Number of dead trees	Numbers of pairs of mortality factors with (without) significant associations	Significant assocations	Expected	Observed	Effect size	P-value
Abies concolor	1,101	6 (114)	*Broken stem (n = 104) and Heartrot (n = 15)*	*1.4*	*9*	*+542%*	*0.000002*
			Broken stem (*n* = 104) and Suppression (*n* = 541)	51.1	16	−69%	0.000001
			Bark beetle (*n* = 331) and Suppression (*n* = 541)	162.6	109	−33%	0.000001
			Uprooted (*n* = 27) and Suppression (*n* = 541)	13.3	0	−100%	0.000001
			Crushed (*n* = 85) and Suppression (*n* = 541)	41.8	20	−52%	0.000001
			Unspecified rot (*n* = 32) & Suppression (*n* = 541)	15.7	5	−68%	0.000010
Abies magnifica	727	4 (87)	Broken stem (*n* = 95) and Suppression (*n* = 362)	47.3	7	−85%	0.000001
			Mistletoe (*n* = 96) and Suppression (*n* = 362)	48.3	25	−48%	0.000002
			Uprooted (*n* = 13) and Suppression (*n* = 362)	6.5	0	−100%	0.000202
			Bark beetle (*n* = 356) and Crushed (*n* = 113)	55.3	25	−55%	0.000001
Calocedrus decurrens	495	4 (32)	*Bark beetle (n = 186) and Other or unknown disease (n = 27)*	*10.1*	*19*	*+88%*	*0.000450*
			Broken stem (*n* = 42) and Suppression (*n* = 336)	28.5	4	−86%	0.000001
			Bark beetle (*n* = 187) and Broken stem (*n* = 42)	15.9	6	−62%	0.001310
			Bark beetle (*n* = 187) and Crushed (*n* = 32)	12.1	3	−75%	0.000467
Pinus lambertiana	832	5 (40)	*Bark beetle (n = 485) and white pine blister rust (n = 203)*	*118.3*	*140*	*+18%*	*0.000444*
			Broken stem (*n* = 28) and Suppression (*n* = 375)	12.6	4	−68%	0.000419
			Bark beetle (*n* = 485) and Suppression (*n* = 375)	218.6	160	−27%	0.000746
			White pine blister rust (*n* = 203) and Suppression (*n* = 375)	91.5	27	−70%	0.000001
			Bark beetle (*n* = 485) and Crushed (*n* = 48)	28.0	16	−43%	0.000444

Notes: Significant associations shown in italic are positive; all others are negative. Results of all pairwise comparison (including non-significant comparisons) are shown in Appendix S4.

Franklin 2010). An association between mechanical mortality and rot has also been noted in mature temperate deciduous forest in Europe (Holzwarth et al. 2013). Biotic mortality agents have also been found to be common contributors to background mortality in boreal forests (Rouvinen et al. 2002, Lannenpaa et al. 2008) and tropical forests (Nair 2007, Stephenson et al. 2011).

Even in the absence of outbreaks, bark beetles were the dominant biotic mortality agent, occurring on 40% of all dead trees and as many as 91% of large, dead pines. Even on small trees, where our bark beetle species have previously been thought to occur very rarely (Furniss et al. 1977, Wood et al. 2003), we found bark beetles on 35% of

dead trees and 45% of dead pines. Beetles are not simply attacking trees that have already been weakened by other causes; even vigorous trees (as indicated by growth rate preceding death) had a high occurrence of bark beetles (55%). Accurate prediction of tree mortality under climatic or other environmental changes may thus depend in part on our ability to model bark beetle dynamics even in the absence of outbreaks (Dukes et al. 2009 and see below).

Associations among mortality factors

One of the most commonly referenced conceptual models of tree mortality is the "mortality spiral"—proposed by

Manion (1981) and modified by Franklin et al. (1987)—which posits that tree death is the final result of a cumulative set of environmental and biotic stressors. Manion further defined his "decline disease spiral" by placing various stressors into categories, with each type of factor playing a particular role in the cycle. In the same vein, Franklin et al. (1987) proposed that there might be a "limited number of mortality spirals … each with strongly linked factors." In other words, the mortality spiral model often includes the idea that there might be a set of linked factors that act sequentially and in predefined roles to kill a tree. Hawkins and Henkel (2011) found some evidence of disease complexes in coniferous forests of northern California, though their study was a single survey that diagnosed trees that had often been dead for many years.

The model of "accumulating stresses" is compelling, as is the idea that agents of mortality might act in an organized fashion. Indeed, the core idea of the model—that tree mortality can be the result of accumulating stressors—is consistent with our findings, given the relatively common occurrence of multiple mortality factors on individual trees. This is in keeping with studies that have shown increased risk of biotic attack for trees that are already weakened by other biotic and abiotic factors (e.g., Stark et al. 1968, Cobb et al. 1974).

However, we found little evidence of strong organization among mortality factors or of "mortality spirals" characterized by specific sequences of mortality agents. First, half of all dead trees had only a single mortality factor. Second, our pairwise comparisons found very few positive associations, indicating little strong association in the community of mortality factors as a whole. For the ordinations, beyond expected associations, such as stem breakage being associated with rot, we found no strong groupings. (Note that for this study we treat well-known obligate symbiotic associations, as that between bark beetle species and blue stain fungi, as a single factor). We did find bark beetles and suppression to be fairly close in ordination space to a variety of other factors, but there were no apparent groupings among those associated factors (e.g., bark beetles might occur frequently with several other factors, but those other factors did not occur frequently with one another, and there was no evidence in the pairwise comparisons that the occurrence was greater than one would expect randomly). Thus, rather than organized sequences of factors contributing to tree mortality, mortality factors may usually act opportunistically—simply showing up whenever they are both present in the area and able to overcome tree defenses, regardless of the reason.

Implications for characterizing the strength of biotic interactions

An ongoing debate centers on whether the strength of biotic interactions and consequent evolutionary pressures vary predictably along environmental gradients. In particular, the debate has focused on the existence—or
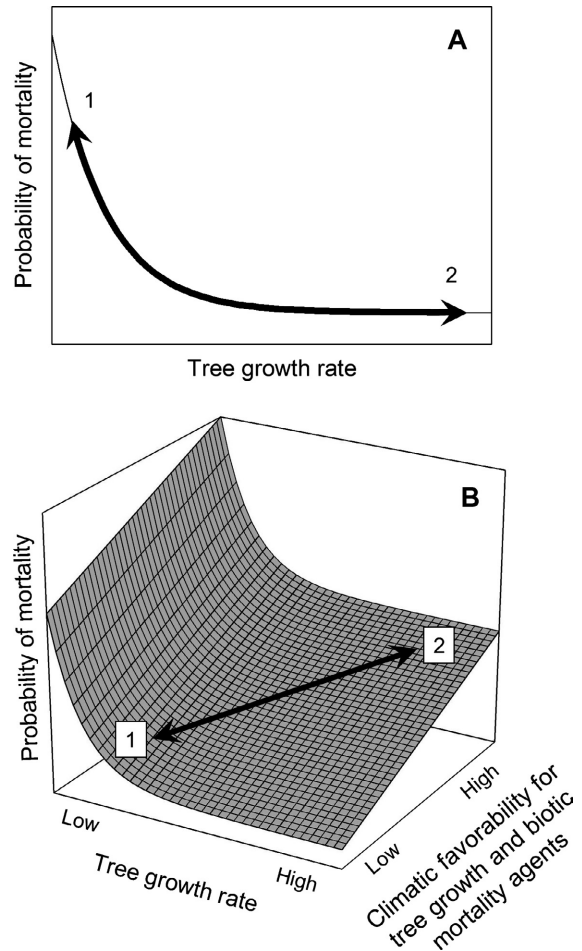

FIG. 5. Potential effects of biotic mortality agents (insects and pathogens) on the relationship between tree growth rate and probability of mortality in a changing climate (modified from Stephenson et al. 2011). (A) Individual-based forest models typically assume that within a species, tree growth rate, and probability of mortality are inversely related. For example, trees in a highly competitive environment will grow more slowly, and will thus have a higher probability of mortality. But regardless of competitive environment, climatic changes that decrease a tree's growth must also increase the tree's probability of mortality (e.g., location 1), and vice-versa (e.g., location 2). (B) However, climatic changes that favor tree growth also often favor the insects and pathogens that attack trees (Stephenson et al. 2011). Unlike the simple model presented in frame A, it is also possible for probability of mortality to decline with declining growth rate (e.g., location 1), and vice-versa (e.g., location 2). Other outcomes are also possible, depending on site- and species-specific circumstances.

lack thereof—of latitudinal gradients in folivory and leaf defenses (e.g., Schemske et al. 2009, Moles et al. 2011a, b, Moles 2013, Rodríguez-Castañeda 2013, Lim et al. 2015). Our results add to a growing body of evidence (Stephenson et al. 2011, Stephens and Westoby 2015) suggesting that the focus on folivory and leaf defenses is, at best, incomplete. Specifically, the contributions of insects and pathogens to background tree mortality in our study were overwhelmingly through

attacks on stems and roots, not foliage. Our results thus align with other evidence that, for woody plants, attacks on stems may have greater effects on plant fitness than those on leaves (Stephens and Westoby 2015). However, data on broad geographic patterns of biotic attacks on, and defenses of, tree stems and roots are nearly nonexistent (Stephenson et al. 2011), highlighting a major research need.

Implications for forecasting change

Our findings may be relevant to understanding and predicting the potential effects of environmental changes on forests. For example, mortality algorithms in individual-based forest models typically assume that probability of tree mortality is inversely related to growth rate (e.g., Botkin 1993, Bugmann 2001) (Fig. 5A). In the absence of directional environmental changes, this assumption is usually accurate; empirical studies show that within a species and site, slowly growing trees are more likely to die than rapidly-growing trees (Stephenson et al. 2011). But the fact that biotic mortality agents are substantial contributors to background tree mortality suggests that this simple inverse relationship between growth and mortality may not always hold in the face of directional environmental changes.

For example, consider a tree species growing in a mesic environment, where growth is not limited by water availability. If we assume an unchanging relationship between growth and mortality, a warming climate would increase tree growth rate, potentially lowering a tree's probability of mortality (Fig. 5A). Conversely, a cooling climate would reduce growth rate, increasing the tree's probability of mortality. However, temperature also affects the biotic agents that attack trees. For example, warming temperatures often increase the individual- and population-level growth and survival of insects, and thus their attack rates on trees (e.g., Frazier et al. 2006, Currano et al. 2010, Weed et al. 2013). Thus, through its effects on biotic mortality agents, a temperature change that increases tree growth could potentially increase rather than decrease a tree's probability of mortality, and a change that decreases growth could potentially decrease rather than increase a tree's probability of mortality (Fig. 5B); indeed, this is a probable mechanism contributing to the higher background mortality rates found in tropical compared to temperate forests (Stephenson et al. 2011). While the presence or importance of such a mechanism might vary according to circumstances, there is little doubt that the effects of environmental changes on forests will at least partly depend on the effects of those environmental changes on the organisms that attack trees.

Conclusions

Regardless of tree size or vigor, biotic agents—predominantly insects and pathogens that attack tree stems and roots—are dominant and apparently opportunistic contributors to background tree mortality in old-growth forests of California's Sierra Nevada. While we suspect this generalization will hold across many of the world's forests (e.g., Lannenpaa et al. 2008, Stephenson et al. 2011), much more research is needed, particularly in tropical forests. Our findings imply that mechanistic models of forest responses to environmental changes should explicitly consider the effects of environmental changes on biotic agents of tree mortality, even in the absence of outbreaks. Finally, research on the nature and strength of biotic interactions along environmental gradients, which commonly focus on folivory and leaf defenses, will do well to additionally consider attack rates on, and defenses of, tree stems and roots.

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