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Bark beetle-caused mortality in a drought-affected ponderosa pine landscape in Arizona, USA

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ABSTRACT

Extensive ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) mortality associated with a widespread severe drought and increased bark beetle (Coleoptera: Curculionidae, Scolytinae) populations occurred in Arizona from 2001 to 2004. A complex of *Ips* beetles including: the Arizona fivespined ips, *Ips lecontei* Swaine, the pine engraver beetle, *Ips pini* (Say), *Ips calligraphus* (Germar), *Ips latidens* (LeConte), *Ips knausi* Swaine and *Ips integer* (Eichhoff) were the primary bark beetle species associated with ponderosa pine mortality. In this study we examine stand conditions and physiographic factors associated with bark beetle-caused tree mortality in ponderosa pine forests across five National Forests in Arizona. A total of 633 fixed-radius plots were established across five National Forests in Arizona: Apache-Sitgreaves, Coconino, Kaibab, Prescott, and Tonto. Prior to the bark beetle outbreak, plots with mortality had higher tree and stocking compared with plots without pine mortality. Logistic regression modeling found that probability of ponderosa pine mortality caused by bark beetles was positively correlated with tree density and inversely related with elevation and tree diameter. Given the large geographical extent of this study resulting logistic models to estimate the likelihood of bark beetle attack should have wide applicability across similar ponderosa pine forests across the Southwest. This is particularly true of a model driven by tree density and elevation constructed by combining all forests. Tree mortality resulted in significant reductions in basal area, tree density, stand density index, and mean tree diameter for ponderosa pine and for all species combined in these forests. Most of the observed pine mortality was in the 10–35 cm diameter class, which comprise much of the increase in tree density over the past century as a result of fire suppression and grazing practices. Ecological implications of tree mortality are discussed.

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1. Introduction

Bark beetles (Coleoptera: Curculionidae: Scolytinae) are important natural disturbance agents of forest ecosystems, with various species periodically causing extensive tree mortality across large landscapes. Eruptive populations are currently active in many parts of the West in forest types from piñon-juniper woodlands to spruce-fir forests (USDA Forest Service, 2006). Factors commonly associated with bark beetle outbreaks include climatic effects such as drought, pre-disposing disturbance events such as blowdowns and defoliation, forest stand conditions, and site characteristics favorable for bark beetle populations (reviewed by Fettig et al., 2007).

The genesis of extensive recent bark beetle outbreaks in the western US coincided with a period of extended, severe drought since about 2000 (Breshears et al., 2005; Shaw et al., 2005). For example, in southern California the amount of ponderosa pine, *Pinus ponderosa* Lawson, mortality associated with western pine beetle, *Dendroctonus brevicomis* LeConte, infestations reached unusually elevated levels after years of extended drought (USDA Forest Service, 2002). Mechanisms by which drought can incite insect outbreaks include a more favorable thermal environment for insect development, drought-stressed plants being more attractive and physiologically suitable for insects, insects being able to better detoxify plant defensive compounds, stimulation of physiological symbiotic organisms, and induction of genetic characteristics of insect populations that promote insect population development (Mattson and Haack, 1987). As it relates to bark beetles, drought may negatively influence the resin production mechanisms in conifers (Mattson and Haack, 1987) which is the

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primary defense against these herbivores (Vité, 1961; Rudinsky, 1966; Reid et al., 1967; Smith, 1975; Hodges et al., 1979; Nebeker et al., 1992, 1995; Strom et al., 2002). In addition, wood boring insects may acoustically sense drought-induced cavitations (Haack et al., 1988). Drought may also result in increased production or imbalances in terpenes which are attractive to bark beetles and can cause increases in certain sugars which become carbon sources for the insects (Mattson and Haack, 1987).

Stand conditions often influence bark beetle-caused tree mortality and discerning these factors can lead to silvicultural and restoration approaches (Hedden, 1981; Fettig et al., 2007). Dense conditions are a common characteristic of forests that experience epidemic bark beetle populations (Fettig et al., 2007). Although rating systems that associate stand environment and likelihood of bark beetle infestation are available for some bark beetle species (Steele et al., 1996; Fettig et al., 2007), physiographic characteristics have received little consideration. Site quality, latitude, and elevation impact insects and their hosts, thereby, influencing susceptibility to bark beetles (Sartwell, 1971; Amman, 1973; Sartwell and Stevens, 1975; Hansen, 1996; Fettig et al., 2004; Fettig et al., 2005). Moisture availability and temperature can influence tree vigor (Furniss and Carolin, 1977; Ayres and Lombardero, 2000; Sheppard et al., 2002), affect the distribution of insects (Furniss and Carolin, 1977; Ungerer et al., 1999; Ayres and Lombardero, 2000; Bale et al., 2002) and modify insect phenology (Furniss and Carolin, 1977; Ungerer et al., 1999; Ayres and Lombardero, 2000; Hansen et al., 2001; Bale et al., 2002). Hazard rating systems have not been fully developed for bark beetles in the Southwestern U.S., in particular for *Ips* species.

Ponderosa pine forests in the southwestern United States prior to Euro-American settlement were open with mostly large-diameter trees, abundant grass cover and scant regeneration (Covington and Moore, 1994a, 1994b). Fire suppression, logging, and grazing have changed these forests dramatically (Holsinger, 1902 as cited by Cooper, 1960); Cooper, 1960; Weaver, 1951, 1955; Covington and Moore, 1994a, 1994b; Johnson, 1994; Fulé et al., 1997). Covington and Moore (1994a) suggested that consequences of fire suppression, logging, and grazing include high tree density, reduced tree growth, increased insect and disease activity, increased fuel loadings and vertical continuity of fuels, and increased canopy cover.

Bark beetles in association with drought recently caused high levels of ponderosa pine mortality throughout Arizona (USDA Forest Service, 2001, 2002). In general, aerial survey information collected by forest health specialists indicate the large extent and distribution of insect populations across all aspects and elevations. The majority of the mortality was attributed to a complex of *Ips* beetles including: the Arizona fivespined ips, *Ips lecontei* Swaine, the pine engraver beetle, *Ips pini* (Say), *Ips calligraphus* (Germar), *Ips latidens* (LeConte), *Ips knausi* Swaine and *Ips integer* (Eichhoff). To a lesser extent other bark beetles involved include the roundheaded pine beetle, *Dendroctonus adjunctus* (Blandford), the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, and the western pine beetle, *Dendroctonus brevicomis* (Le Conte) (USDA Forest Service, 2001, 2002). The relative abundance of these species was found to vary by elevation in north-central Arizona, with greater populations of *I. lecontei* and *D. brevicomis* at low to mid elevations (<2000 m), while *I. pini* was found in similar numbers across all elevations evaluated (Williams et al., 2008). While Williams et al. (2008) provided important information on the relative abundance of bark beetle species by elevation, tree mortality caused by them has not been examined or quantified.

The objective of this study was to examine stand conditions and physiographic factors associated with the occurrence of bark beetle-caused tree mortality in ponderosa pine forests across five National Forests in Arizona. Specifically: (1) Given a landscape with high populations of *Ips* beetles, are particular stand structures or environmental conditions associated with *Ips*-caused tree mortality? (2) What is the structure of the stands after a successful *Ips* outbreak? We developed models to identify conditions under which mortality is more likely to occur in association with bark beetles, compared stand conditions in affected stands before and after the mortality, compared stand conditions in areas with and without tree mortality, and compared distributions of tree diameters of live and bark beetle-killed trees in affected areas. This information can be used to identify conditions which may be more conducive to the occurrence of bark beetle-caused tree mortality in the future, help in the development of vegetation management approaches to reduce susceptibility and relevant for restoration projects and to better understand how these disturbance agents can contribute to forest stand structure and composition.

2. Materials and methods

2.1. Study site

Ponderosa pine forests in Arizona cover 1.2 million ha representing 16% of the forest land in the state (O'Brien, 2002), with an approximate elevation range from 1850 to 2460 m and precipitation averaging ca. 18 cm. Our sampling was conducted in 2003–2004 by establishing a network of plots across five National Forests in Arizona. Study sites were located on the Apache-Sitgreaves, Coconino, Kaibab, Prescott, and Tonto, National Forests (Fig. 1).[1] Geographic information system maps showing the distribution of ponderosa pine forests,[2] National Forest boundaries, and Forest Service road system for each National Forest were prepared. These maps were then populated with sampling points using a 5-km grid randomly laid over the map; however, for accessibility each sampling point was constrained to be within 40–400 m of a road with the number of sample points proportional to the area of ponderosa pine forest per National Forest. All plots were located in unburned areas. Primary tree species in the study sites included ponderosa pine, piñon pine, *Pinus edulis* Engelm., Rocky Mountain juniper, *Juniperus scopulorum* Sarg., and oneseed juniper, *Juniperus monosperma* (Engelm.) Sarg.

2.2. Plot establishment and data collection

To explore the relationship between stand characteristics and occurrence of tree mortality we installed clusters of four plots; three organized in a triangle and a fourth plot at a random distance and azimuth. Plots in triangles were separated by 200 m starting from a randomly selected sampling point. The location of plots was independent of previous land management history; areas of obvious thinning or harvesting were not avoided or encouraged. Plots were 0.08 ha fixed radius (8 m radius) with all trees $\geq$2.54 cm measured and the following information recorded: tree species, diameter at breast height (dbh) for ponderosa pine (diameter at root collar for piñon pines and junipers), tree condition, and damaging agent if any. Tree condition was recorded as green live tree, currently infested by bark beetles or killed by bark beetles within the current outbreak, or dead to other causes. Presence of boring dust, pitch tubes, exit holes, galleries, and life stages were used to determine if bark beetles were or had been present. Site characteristics were recorded for each plot, including: aspect, slope, and elevation. A total of 633 plots were established over two

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[1] Hereafter, for simplicity we often refer to the forests by their names without stating their National Forest status.

[2] It is understood that a variety of habitat types occur within the ponderosa pine type. For simplicity we refer to these as ponderosa pine forests.

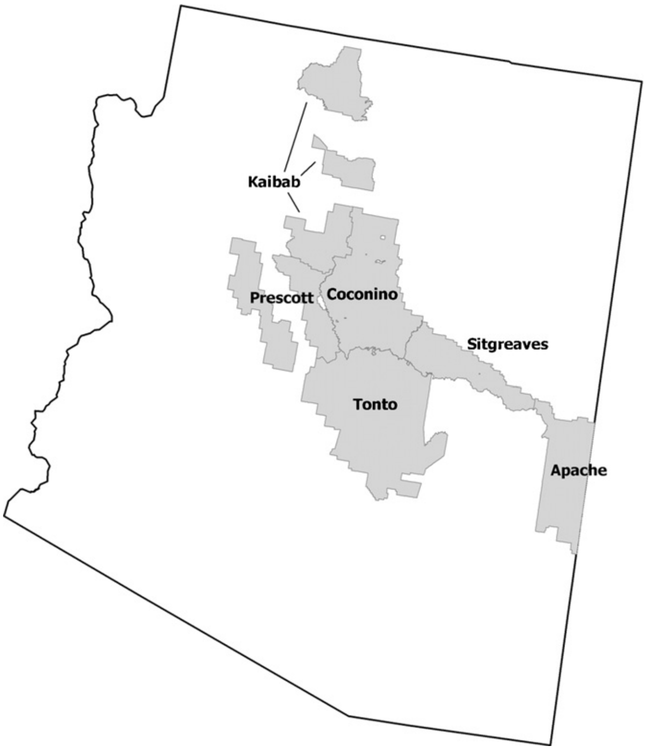

Fig. 1. National Forests in Arizona where ponderosa pine, *Pinus ponderosa*, forests were sampled, 2003–2004.

years, and distributed as follows: 172 in the Apache-Sitgreaves, 270 in the Coconino, 29 in the Kaibab, 82 in the Prescott, and 80 in the Tonto.

2.3. Data analysis

Since our sampling was conducted across five different National Forests, the first consideration was whether all forests could be combined into a single analysis, whether each forest should be considered separate, or were there were some ecologically sound combinations of forests. To accomplish this, we examined all variables with analysis of variance and the extent to which pair-wise differences of variables measured were significant. This was followed by logistic regression modeling where we examined if there were stand attributes or physiographic characteristics that could be used to discriminate between plots with beetle-caused tree mortality (at any level) from plots with no mortality. Using the logistic approach, models take the form:

$$P(\text{infestation}) = \frac{1}{1 + e^{-b'X}},$$

where $b'X$ represents a linear combination of explanatory variables X with their estimated parameters b, and e is the base of natural logarithms. Logistic regression model responses were portrayed by graphing model outputs across the range of values sampled for the predictor variable(s).

We also calculated stand attributes between mortality and no mortality plots for the different forests and compared them with a *t*-test assuming unequal variances. We compared reconstructed stand conditions before the beginning of the mortality event with residual stand conditions with a *t*-test, quantified percent changes in stocking levels and tree diameters, and prepared graphs portraying the number of trees per diameter classes for live and bark beetle-killed ponderosa pines. The distribution of tree mortality across diameter classes was tested with a chi-square.

3. Results

Elevation for ponderosa pine plots ranged from 1494 to 2861 m with slopes from level ground to 56% and all aspects represented. An examination of pair-wise comparisons in average diameter and stocking densities suggests that the Apache-Sitgreaves and the Coconino are quite similar as no differences in the variables measured were significant (not shown). This in combination to their proximity suggests that these forests could be treated as one. We report the results for the Apache Sitgreaves/Coconino aggregate and also for these forests separately. The Prescott and Tonto are each treated separately. Only 4 plots out of 29 in the Kaibab exhibited tree mortality, therefore that forest is excluded from further discussion.

3.1. Probability of tree mortality

Logistic models to estimate the probability of observing tree mortality were formulated for all forests combined, the Apache-Sitgreaves/Coconino aggregate, and each individual forest. For all forests combined and for the Apache-Sitgreaves/Coconino aggregate, models were constructed which included tree density of all species and elevation. The all forests model and the Apache-Sitgreaves/Coconino aggregate had correct classification rates of 69% and 67%, respectively (Table 1). These models indicated that tree density (all species included) and elevation could be used to separate mortality plots from no mortality plots. The probability of mortality was positively related to tree density, as indicated by a positive coefficient, and negatively related to elevation, as indicated by a negative coefficient in the logistic regression parameter estimates. The models response across a range of tree densities for various elevation levels portrays the influence of elevation in the probability of observing tree mortality (Fig. 2a and b). For a given tree density, the probability of tree mortality increased as elevation decreased. Conversely, within each elevation the probability of observing tree mortality increases with tree density. For the Apache-Sitgreaves alone a model using elevation had a correct classification rate of 71% (Table 1). The model response indicates how the probability of tree mortality decreases with elevation (Fig. 2c). For the Coconino (as a separate forest) and the Tonto, models using tree density of all species had the same correct classification rate of 71% (Table 1). Again, tree density was positively related to the probability of mortality as indicated by a positive coefficient of the parameter estimate. Models response depict how the probability of mortality increases with increasing tree density (Fig. 2d). For the Prescott, a model with mean tree diameter for all species had a correct classification rate of 63% (Table 1). Mean tree diameter was inversely related to the probability of mortality as indicated by the negative coefficient of the parameter estimate. The response shows how the probability of mortality decreases with increasing mean tree diameter at breast height (Fig. 2e).

3.2. Stand and tree variables associated with plots containing tree mortality

Several forest condition characteristics differed significantly between plots with and without tree mortality (Table 2). The Apache-Sitgreaves plots with mortality had smaller ponderosa pine mean diameter and higher ponderosa pine tree density than no mortality plots. In the Coconino there were differences in all variables measured with the exception of ponderosa pine basal area. In the Tonto there were differences in mean diameter for all species and for tree density for all species while in the Prescott there were only differences in ponderosa pine and all species mean diameter. In all cases where differences were observed, plots with

Table 1
Logistic regression models for estimating the probability of occurrence of mortality associated with bark beetles in plots in ponderosa pine stands across four National Forests in Arizona, 2003–2004.

Forest	Variable	B	Std. error	Chi-square	Significance	% Correct
Combined forests						
All Forests	Intercept	1.2	0.8	2.1	0.1	68.5
	Trees/ha all spp	0.001	0.0003	30.9	<0.01	
	Elevation (m)	−0.001	0.0004	14.0	<0.01	
Apache-Sitgreaves/Coconino	Intercept	1.1	1.4	0.6	0.43	67.0
	Trees/ha all spp	0.002	0.0003	22.2	<0.01	
	Elevation (m)	−0.001	0.0006	5.6	0.02	
Individual forests						
Apache-Sitgreaves	Intercept	5.3	1.9	8.1	<0.01	71.3
	Elevation (m)	−0.003	0.0008	11.7	<0.01	
Coconino	Intercept	−2.5	0.3	68.1	<0.01	70.7
	Trees/ha all spp	0.002	0.0004	21.0	<0.01	
Tonto	Intercept	−2.6	0.7	12.4	<0.01	71.3
	Trees/ha all spp	0.003	0.001	10.1	<0.01	
Prescott	Intercept	1.7	1.0	3.1	0.08	62.6
	Tree DBH (cm) all spp	−0.07	0.03	4.0	0.04	

mortality exhibited increased stocking and reduced mean tree diameters.

3.3. Comparison of stand structure pre- and post-outbreak

An examination of differences in forest conditions between original stand conditions and after the mortality event within plots exhibiting tree mortality revealed significant changes in stand structure (Table 3). In the Apache-Sitgreaves and the Coconino there were differences in all variables with mean diameter of all species significant at the $P < 0.07$ level for both forests. In the Tonto and the Prescott we observed differences in all variables measured. In all cases where differences were significant, reductions in mean tree diameter and stocking levels were observed for all species combined and for ponderosa pine.

3.4. Changes in mean tree diameters and stocking levels

Bark beetle-caused reductions in tree diameters, stand density, and basal area varied across the Forests (Table 4). Reductions in ponderosa pine tree diameter were larger in the Tonto and the Prescott and about the same in the Apache-Sitgreaves and the Coconino. Reductions in tree diameter for all species were highest at the Prescott and much less in the Coconino and the Tonto. Ponderosa pine basal area and tree density reductions were much larger in the Tonto and the Prescott. Basal area reductions for all species were also higher in the Tonto and the Prescott while reductions in tree density for all species were higher in the Prescott and the Apache-Sitgreaves.

3.5. Distribution of tree mortality by tree diameter class

Examination of the number of ponderosa pine trees per diameter class depicts the uneven-aged nature of the ponderosa pine stands in all forests. The majority of the trees was in the 15–25 cm classes for all forests combined (Fig. 3a) and in the 15 cm class for the Apache-Sitgreaves (Fig. 3b). The majority of the bark beetle-killed trees in the Apache-Sitgreaves NF was in the 10 and 15 cm class, whereas in the Coconino NF trees killed were primarily in the 10–30 cm classes (Figs. 3b and c). In the Tonto NF the majority of the trees killed was in the 15–25 cm classes but trees were killed in all diameter classes except the 5 cm class (Fig. 3d). In the Prescott NF, tree mortality occurred in all diameter classes (Fig. 3e). We observed a significant departure in the distribution of killed trees from that of the live trees in all forests combined, the Apache Sitgreaves, and the Tonto. When trees from all forests are combined the chi-square test was significant as a result of higher that expected mortality in the 15–30 cm diameter classes (Chi-square = 57.3, $p < 0.0001$) (Fig. 3a). In the Apache-Sitgreaves significance was the result of large numbers of trees killed in the 10–30 cm diameter classes (Chi-square = 64.6, $p < 0.0001$) while in the Tonto it was the result of all trees killed in the larger diameter classes (Chi-square = 33.1, $p < 0.002$). In every forest mortality occurred in the larger diameter classes which contributed to average reductions in tree diameters (Table 3).

4. Discussion

This study comprised a large geographical area with diverse forest conditions sampled across a range of elevation, aspects, and slopes. Within the heterogeneous landscape there were areas of similarity. Ponderosa pine forests in the Apache-Sitgreaves NF and the Coconino NF were similar in forest conditions and a logistic model was built for each separate forest and for both forests together. This forest combination may not be the result of similar past management or disturbance history, nor translate into similar future management or restoration approaches, but provide a larger system from which ecological processes can be described.

We formulated logistic regression models of tree mortality for all forests combined, for the Apache-Sitgreaves/Coconino aggregate, and for each individual forest (Table 1). The full model and the Apache-Sitgreaves/Coconino aggregate included tree density of all species and elevation as predictor variables. Coefficients and model response indicated that increased tree density and lower elevation are associated with an increased likelihood of tree mortality to bark beetles (Fig. 2a and b, Table 1). The model for the Apache Sitgreaves used elevation as the best predictor variable of mortality, also with a negative coefficient (Table 1), indicating an inverse relationship between elevation and the likelihood of tree mortality. Decreasing elevation was associated with an increased probability of tree mortality (Fig. 2c). Models for the Coconino and the Tonto included tree density of all species, with a higher likelihood of mortality with increasing tree density (Table 1; Fig. 2d). The model for the Prescott included mean tree diameter for all species with larger diameter associated with a reduced probability of tree mortality (Table 1, Fig. 2e).

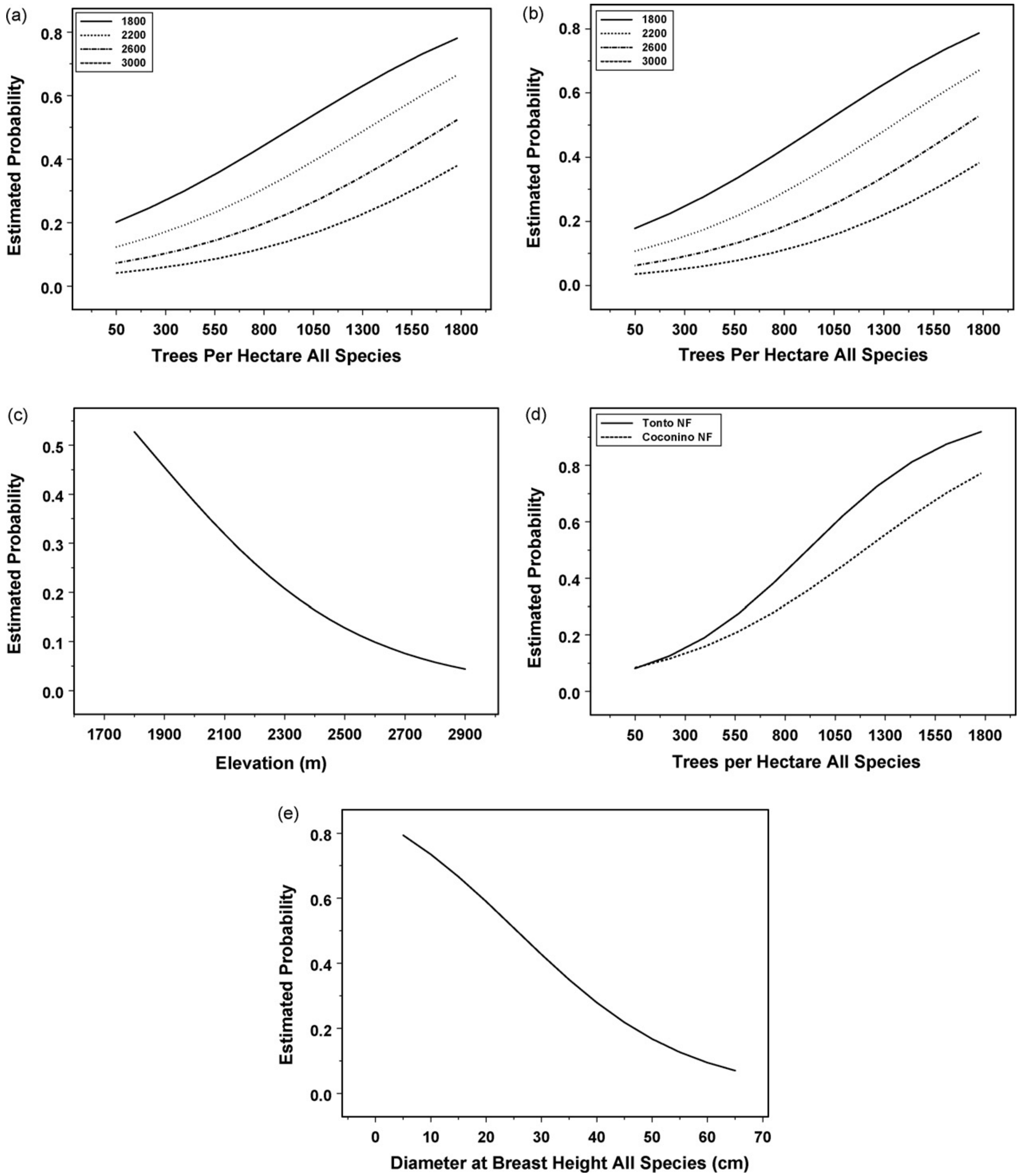

Fig. 2. Logistic model response for estimating probability of observing tree mortality in ponderosa pine, *Pinus ponderosa*, forests as a function of: (a) tree density and elevation, all forests combined; (b) tree density and elevation, Apache-Sitgreaves/Coconino National Forests aggregate; (c) elevation, Apache-Sitgreaves National Forest; (d) tree density (all species), Coconino and Tonto National Forests; and (e) tree diameter (all species), Prescott National Forest, Arizona, 2003–2004.

Many studies have previously documented that given the presence of suitable diameter classes, there is a positive relationship between increased stocking levels and the likelihood of bark beetle-caused tree mortality (See Fettig et al., 2007). This has been attributed to reduced tree vigor under high stocking levels and/or unfavorable microclimate for bark beetles under lower stocking, although the latter may not be a factor with *Ips* beetles as these insects, in general, thrive under hot weather conditions. However, to our knowledge no studies have been conducted to determine stocking levels that render ponderosa pine stands more susceptible to mortality by *Ips* beetles. Studies in even-aged ponderosa pine in the Black Hills of South Dakota and Wyoming suggest that basal area levels above about 18.4 m^2/ha make stands more susceptible to mountain pine beetle attack (Schmid and Mata, 1992, 2005). In uneven-aged ponderosa pines stands in the Black Hills increased stand susceptibility occurs when basal area of Trees 25.4 cm and larger is greater than 6.1 m^2/ha (Negrón et al., 2008). In uneven-aged ponderosa pine in Colorado, Negrón and Popp (2004) established susceptibility levels to bark beetle-caused mortality at a ponderosa pine basal area of 17.1 (m^2/ha). In the absence of specific data for *Ips* beetles, if these levels are used guidelines for increased likelihood of *Ips* attacks in ponderosa pine stands, all

Table 2
Differences in stand conditions between plots with ponderosa pine mortality and those without mortality across four National Forests in Arizona, 2003–2004.

Forest	Variable	No mortality plots	Mortality plots	Difference	Standard error	*t*-value	*p*-value
Apache-Sitgreaves	Number of Plots	127	38				
	DBH all spp (cm)	27.3	25.8	1.6	1.8	0.8	0.41
	DBH ponderosa pine (cm)	31.2	25.8	5.4	2.7	2.4	0.02
	Basal Area all spp (m^2/ha)	27.7	26.1	1.6	3.3	0.6	0.54
	Basal Area ponderosa pine (m^2/ha)	19.4	18.0	1.4	2.7	0.6	0.57
	SDI all spp	482.5	479.7	2.9	51.4	0.1	0.95
	SDI ponderosa pine	334.2	336.5	−2.3	43.1	−0.1	0.95
	Trees/ha all spp	441.9	530.4	−88.5	57.6	−1.5	0.15
	Trees/ha ponderosa pine	284.3	380.9	−96.6	45.5	−2.1	0.05
Coconino	Number of Plots	216	51				
	DBH all spp (cm)	29.8	24.4	5.4	1.6	4.6	<0.01
	DBH ponderosa pine (cm)	31.7	26.8	4.9	2.0	2.7	0.01
	Basal Area all spp (m^2/ha)	24.3	32.3	−8.0	2.3	−3.3	<0.01
	Basal Area ponderosa pine (m^2/ha)	21.0	24.9	−3.9	2.3	−1.6	0.11
	SDI all spp	428.8	598.1	−169.3	40.4	−4.1	<0.01
	SDI ponderosa pine	366.7	456.4	−89.6	40.1	−2.1	0.04
	Trees/ha all spp	389.9	648.0	−258.1	49.7	−4.8	<0.01
	Trees/ha ponderosa pine	315.4	464.9	−149.6	46.4	−3.0	<0.01
Tonto	Number of Plots	44	28				
	DBH all spp (cm)	26.5	20.9	5.6	1.9	3.4	<0.01
	DBH ponderosa pine (cm)	30.3	30.5	−0.2	3.2	−0.1	0.96
	Basal Area all spp (m^2/ha)	36.6	41.7	−5.1	4.5	−1.1	0.29
	Basal Area ponderosa pine (m^2/ha)	16.5	16.1	0.4	3.1	0.1	0.90
	SDI all spp	632.9	758.9	−126.0	68.8	−1.8	0.08
	SDI ponderosa pine	281.0	290.2	−9.1	51.2	−0.2	0.86
	Trees/ha all spp	605.2	912.1	−307.0	80.3	−3.9	<0.01
	Trees/ha ponderosa pine	227.9	275.2	−47.3	50.9	−0.9	0.39
Prescott	Number of Plots	44	36				
	DBH all spp (cm)	30.5	26.9	3.6	1.7	2.1	0.04
	DBH ponderosa pine (cm)	33.9	29.6	4.3	2.3	2.0	0.05
	Basal Area all spp (m^2/ha)	30.0	26.5	3.5	3.2	1.1	0.28
	Basal Area ponderosa pine (m^2/ha)	24.9	21.9	2.9	2.9	1.0	0.31
	SDI all spp	517.3	479.3	37.9	55.6	0.7	0.50
	SDI ponderosa pine	425.1	392.2	32.9	50.5	0.7	0.51
	Trees/ha all spp	398.6	462.4	−63.9	62.2	−1.0	0.32
	Trees/ha ponderosa pine	297.5	336.2	−38.7	53.7	−0.7	0.48

forests examined in this study can be considered to have high susceptibility as total basal area in all forests was above 26 m^2/ha and only the Tonto National Forest had a ponderosa pine basal area below 17.0 m^2/ha.

Most of the ponderosa pine mortality occurring in Arizona during this outbreak was attributed to a complex of *Ips* species (USDA Forest Service, 2005), which are typically associated with killing smaller diameter trees and the tops of larger diameter trees (Parker, 1991; Kegley et al., 1997). Similarly, in an *I. lecontei* outbreak on the San Carlos Indian Reservation in late 1970s, Parker (1991) found an inverse relationship between ponderosa pine mortality and pine diameter. Kolb et al. (2006) concluded that preference by *Ips pini* for small diameter pine or the tops of larger trees is inversely related to bark thickness. In contrast, stand hazard rating models for *Dendroctonus* species attacking conifers most often include a tree diameter factor, with stand susceptibility increasing with greater mean tree diameter (reviewed by Fettig et al., 2007).

Tree density may be a more accurate predictor of tree mortality for *Ips* outbreaks than basal area or stand density index because, as outlined above, these species of bark beetles do not prefer larger trees. Tree densities in ponderosa pine forests have increased across the Southwest over the last century as a result of anthropogenic factors (Cooper, 1960; Weaver, 1951, 1955; Covington and Moore, 1994a, 1994b; Johnson, 1994; Fulé et al., 1997) particularly in the small and mid-size diameter classes (e.g., Fig. 3). These changes in forest structure are likely to increase susceptibility to *Ips*-caused ponderosa pine mortality.

Elevation influences bark beetle distributions and mortality patterns (Hansen, 1996; Fettig et al., 2005; Williams et al., 2008). For example, lodgepole pine, *Pinus contorta* Dougl. ex Loud., mortality caused by mountain pine beetle is inversely related to increasing elevation (Amman et al., 1973). Moreover, at high elevations, mountain pine beetle life cycle is extended increasing exposure to lethal winter temperatures and greater exposure to natural enemies (Amman et al., 1973). As a result, elevation has also been incorporated into stand susceptibility rating systems for mountain pine beetle in lodgepole pine in Canada (Shore and Safranyik, 1992). Distributions and populations of several *Ips* species attacking ponderosa pine in Arizona are inversely related to elevation (Williams et al., 2008). Cooler temperatures and shorter growing season at higher elevations caused later flight initiation in the spring and earlier flight termination in the fall, resulting in at least one generation less per year for some multivoltine *Ips* species. Therefore, *Ips* populations have greater potential for population increase in ponderosa pine forests at lower elevations. In addition, warmer temperatures and possibly less precipitation at lower elevations probably increased tree stress and further increased stand susceptibility to bark beetle attacks. The elevation effects are magnified by densely stocked stands (i.e., Fig. 2a and b).

Percent of ponderosa pine basal area prior to mortality were 69%, 77%, 83%, and 39% in the Apache-Sitgreaves, Coconino, Prescott and Tonto, respectively. The percent of ponderosa pine trees per hectare were 72% for the Apacahe-Sitgreaves, Coconino, and the Prescott and 30% for the Tonto. Reductions in ponderosa pine stocking and ponderosa pine mean diameter were more pronounced in the Tonto and the Prescott. In general, the mortality may be ecologically beneficial for these ecosystems as stocking

Table 3
Mean stand conditions pre- and post-tree mortality in plots with tree mortality and their differences in ponderosa pine stands across four National Forests in Arizona, 2003–2004.

Forest	Variable	Pre- Mort	Post-Mort	Difference	Standard Error	t-value	*p*-value
Apache-Sitgreaves (*N* = 38)	DBH all spp (cm)	25.8	21.6	6.4	2.2	1.9	0.07
	DBH ponderosa pine (cm)	25.8	19.4	6.4	2.6	2.9	0.02
	Basal Area all spp (m^2/ha)	26.1	17.5	8.6	1.4	6.0	<0.01
	Basal Area ponderosa pine (m^2/ha)	18.0	11.4	6.7	1.2	5.5	<0.01
	SDI all spp	479.8	317.7	162.2	25.8	6.3	<0.01
	SDI ponderosa pine	336.6	210.6	126.0	20.5	6.1	<0.01
	Trees/ha all spp	530.6	318.6	212.0	45.5	4.6	<0.01
	Trees/ha ponderosa pine	381.1	213.3	167.8	35.2	4.8	<0.01
Coconino (*N* = 51)	DBH all spp (cm)	24.4	22.5	2.0	1.0	1.9	0.07
	DBH ponderosa pine (cm)	26.8	18.1	8.7	2.5	3.5	<0.01
	Basal Area all spp (m^2/ha)	32.3	23.7	8.6	1.6	5.4	<0.01
	Basal Area ponderosa pine (m^2/ha)	24.9	16.9	8.0	1.5	5.4	<0.01
	SDI all spp	598.4	446.6	151.7	24.1	6.3	<0.01
	SDI ponderosa pine	456.5	317.5	139.1	21.8	6.4	<0.01
	Trees/ha all spp	648.3	497.1	151.2	22.6	6.7	<0.01
	Trees/ha ponderosa pine	465.1	338.2	126.9	17.1	7.4	<0.01
Tonto (*N* = 28)	DBH all spp (cm)	20.9	19.8	1.1	0.5	2.4	0.03
	DBH ponderosa pine (cm)	30.5	17.6	12.9	3.9	3.3	<0.01
	Basal Area all spp (m^2/ha)	41.7	30.9	10.8	2.1	5.2	<0.01
	Basal Area ponderosa pine (m^2/ha)	16.1	6.1	10.0	2.1	4.8	<0.01
	SDI all spp	759.2	571.8	187.4	35.1	5.3	<0.01
	SDI ponderosa pine	290.3	119.0	171.3	34.9	4.9	<0.01
	Trees/ha all spp	912.5	757.2	155.3	27.8	5.6	<0.01
	Trees/ha ponderosa pine	275.3	141.2	134.1	27.2	4.9	<0.01
Prescott (*N* = 36)	DBH all spp (cm)	26.9	21.5	5.4	1.9	2.8	<0.01
	DBH ponderosa pine (cm)	29.6	22.1	7.5	2.4	3.1	<0.01
	Basal Area all spp (m^2/ha)	26.5	15.2	11.3	2.0	5.7	<0.01
	Basal Area ponderosa pine (m^2/ha)	21.9	10.8	11.1	2.0	5.6	<0.01
	SDI all spp	479.3	282.4	197.1	34.0	5.8	<0.01
	SDI ponderosa pine	392.2	199.2	193.1	34.0	5.7	<0.01
	Trees/ha all spp	462.6	310.2	152.4	24.3	6.3	<0.01
	Trees/ha ponderosa pine	336.3	189.4	146.9	24.2	6.1	<0.01

levels in smaller diameter classes were reduced, a trend towards historical levels. Moreover, increased growing space will foster faster increases in tree diameters in the residual trees.

The effects of extensive ponderosa pine mortality associated with bark beetles will change the current nature of these forests. Ecological effects will be varied and their magnitude may be temporally and spatially influenced. One of the immediate changes taking place soon after trees are killed by bark beetles is an increase in herbage production in affected areas. McCambridge et al. (1982) indicated that three years after initial attack by bark beetles, herbage production increased up to 674–898 kg/ha. McMillin and Allen (2000) indicated that in Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, forests understory plants increased 200% to 400% in stands where trees were killed by the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins. To a lesser extent, increases in understory vegetation have also been reported after tree mortality caused by *Dryocoetes confusus* Swaine in subalpine fir, *Abies lasiocarpa* (Hook.) Nutt., forests in Wyoming (McMillin et al., 2003). Based on these previous studies we should expect an increase in vegetation in the understory. This increase may be of benefit to wildlife species that utilize these resources but may reduce thermal cover for other species.

Snags provide resources for many wildlife species and a substrate for bacteria, fungi, and insects to contribute to decay processes in forest ecosystems. Some resources include nesting habitat and food such as insect larvae. Keen (1955) from long-term monitoring of ponderosa pines killed by the western pine beetle in Oregon indicated that fall rate was slow for the first 5 years and very rapid between 5 and 15 years. About 75% of the snags had fallen 14 years after infestation and after 25 years 90% of the snags had fallen. Keen (1955) also indicated that smaller diameter trees will fall faster than larger trees. Seven years after infestation 75% of trees 25.4–45.7 cm had fallen compared to only 30% of trees 127 cm or larger. Schmid et al. (1985) monitored fall rate from 1972 to 1984 of ponderosa pines killed by mountain pine beetle in the Colorado Front Range. Most trees broke off between ground level and 2 ft above the ground. Trees started falling 3 years after attack by bark beetles with most trees falling between 7 and

Table 4
Percent reductions (mean ± SE) in tree diameter, basal area, and tree density of ponderosa pine and all species in ponderosa pine forests across all plots (mortality and no-mortality) forest stands across four National Forests in Arizona, 2003–2004.

	Apache-Sitgreaves	Coconino	Tonto	Prescott
Number of pots	165	267	72	80
Diameter ponderosa pine (cm)	5.0 (0.2)	5.4 (0.2)	16.5 (0.4)	10.5 (0.3)
Diameter all species (cm)	3.4 (0.6)	1.3 (0.2)	1.8 (0.2)	8.4 (0.9)
Ponderosa pine basal area (m^2/ha)	8.0 (0.6)	7.0 (0.5)	23.8 (1.8)	21.3 (0.3)
Basal area all species (m^2/ha)	7.6 (0.1)	6.3 (0.1)	11.1 (0.3)	17.9 (0.4)
Ponderosa pine per ha	12.6 (0.2)	7.1 (0.1)	21.2 (0.3)	21.0 (0.3)
All species trees per ha	11.1 (0.3)	6.6 (0.1)	8.5 (0.2)	16.0 (0.3)

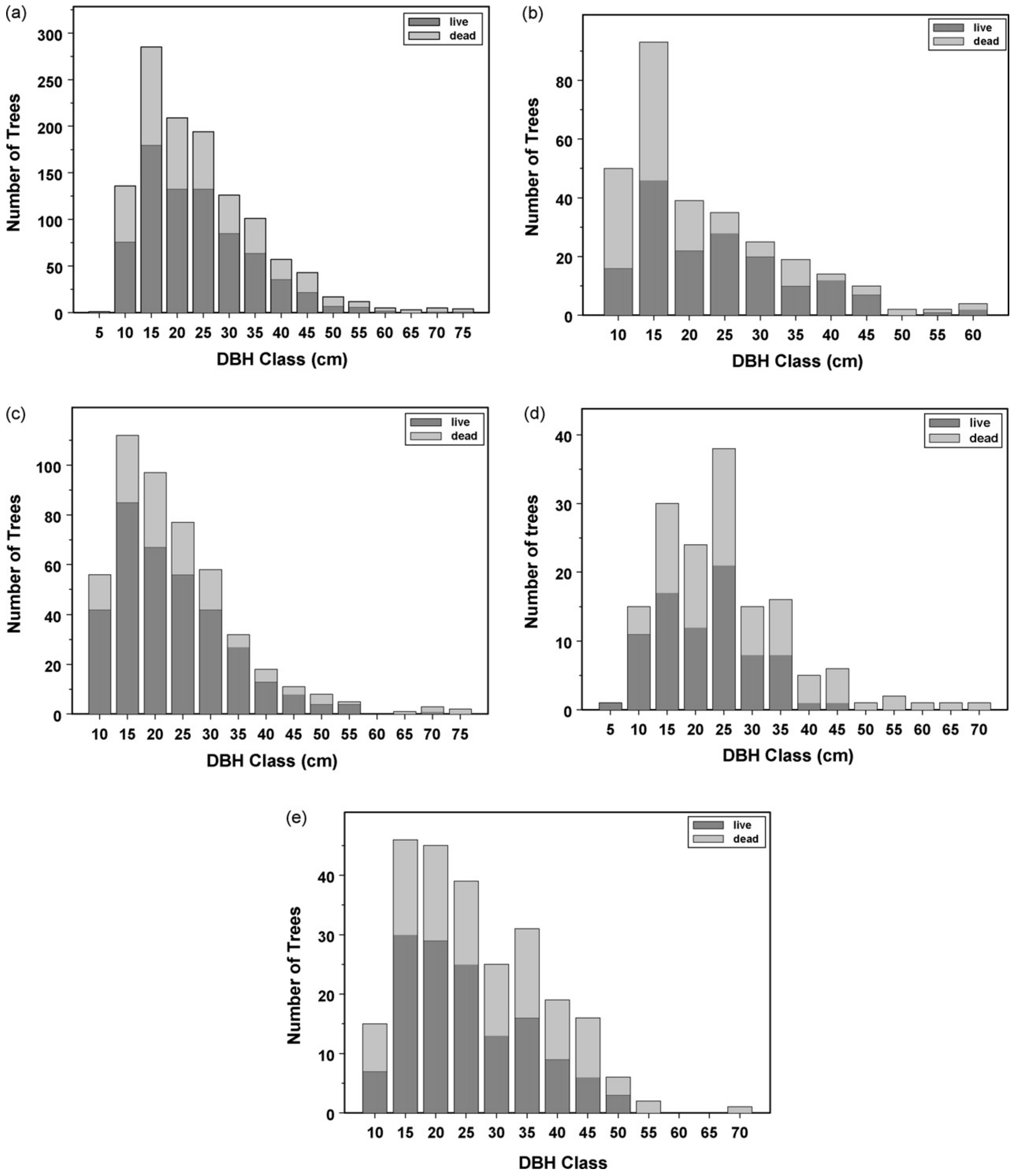

Fig. 3. Number of live and bark beetle-killed ponderosa pines, *Pinus ponderosa*, across diameter classes in the: (a) all forests combined [chi-square = 57.3, $p < 0.0001$]; (b) Apache Sitgreaves National Forest [chi-square = 64.6, $p < 0.001$]; (c) Coconino National Forest [chi-square = 15.8, $p = 0.3$]; (d) Tonto National Forest [chi-square = 33.1, $p < 0.002$]; and (e) Prescott National Forest [chi-square = 15.4, $p = 0.2$]; Chi-square compares the distribution of live and dead trees across diameter classes, Arizona, 2003–2004.

10 years after infestation. About 60% of the trees had fallen 10 years after infestation. Mitchell and Preisler (1998) indicated that lodgepole pine in Oregon killed by mountain pine beetle initiated fall 3 and 5 years after infestation in thinned and unthinned stands, respectively. Half of the trees were down after 8–9 years after tree death and 90% were down in 12–14 years. They also reported that smaller trees fell faster in thinned stands but not in unthinned stands. All of the study trees fell by breaking off at the ground line. Ganey and Vojta (2005) indicate that snags will increase in numbers in parts of the Southwestern U.S. as a result of current bark beetle outbreaks. Based on previous studies tree falls may initiate about 3 years after tree mortality in ponderosa pine forests with most down by about 15 years. It is important to note that as most of the ponderosa pine mortality in our ponderosa pine forests is occurring in the 10–30 cm classes more than likely tree fall rate may be faster than large diameter trees reducing snag longevity.

The implications of extensive bark beetle caused mortality and subsequent fires is poorly studied and not well understood. In ponderosa pine bark beetle-killed trees needles turn brown-orange in color and begin falling to the ground in about 1 year. Dry needles can play a role in the development of crown fires (Van Wagner, 1977; Chrosciewicz, 1986; Agee et al., 2002). Yet as the mortality is patchy across the landscape over a number of years and the needles are also continuously dropping from the trees the presence of combustible foliage varies spatially and temporally across the landscape resulting in discontinuous fuels. As trees begin to fall coarse woody debris accumulates rapidly with most of the trees down in about 15 years. Jenkins et al. (2008) examined fuel characteristics after bark beetles outbreaks in Douglas-fir, lodgepole pine, and Engelmann spruce, *Picea engelmannii* Parry ex Engelm., forests. The authors indicated that the insects, in addition to causing a change in species composition, significantly altered fuel complexes, which can result in changes in fire behavior over time. The type, amount, and spatial distribution of fuels will influence fire characteristics (Van Wagner, 1977; Agee, 1993). Forest structure, which is altered by bark beetles also influences fire severity (Lentile et al., 2006; Jain and Graham, 2004; Jenkins et al., 2008). The relationship between bark beetle-caused mortality and fire severity will vary from site to site depending on factors such as forest structure, time since mortality (Lynch et al., 2006), spatial distribution of fuels, and topography among others. Regardless, the likelihood of a fire is dependent on the occurrence of weather suitable for a fire.

It has been suggested by various authors that these events of extensive mortality contribute to defining the geographical distribution of the tree species involved and community structure (Breshears et al., 2005; Mueller et al., 2005). The mortality event that recently occurred in Arizona has been considered as a scenario under which species distributions may change. Ponderosa pine tree density reduction ranged from 7% in the Coconino to 21% for the Tonto and the Prescott. However only 25% of all ponderosa pine plots measured experienced mortality. Mortality levels are highly variable from one stand to another with few experiencing total mortality. Bark beetle-caused mortality varies at small scales within stands and landscapes (Olsen et al., 1996; Negrón et al., 2001), resulting in individual stands across the study area that are completely killed or relatively unaffected. It is unlikely that mortality levels observed in this study may foster significant landscape-level distributional changes but this will likely depend on interactions with other disturbances.

In their study in Yosemite National Park, Guarín and Taylor (2005) indicate that drought-caused mortality in ponderosa pine was the same across all diameter classes. Yet, in our study, most of the mortality observed in ponderosa pine was in the smaller diameter classes which is the size range preferred by the complex of *Ips* beetles present. We suggest that the extreme and extensive drought in the Southwest acted as an inciting factor for the dramatic increase in bark beetle populations. These insects then exacerbated mortality particularly in the diameter classes preferred by the insects. The magnitude of these influences is likely to be greatest in areas most prone to tree stress associated with densely stocked stands and elevation ranges more conducive to insect development.

Zausen et al. (2005) examined various factors that influence tree and stand susceptibility to bark beetles in thinned and thinned and prescribed burned ponderosa pine forests in Arizona 8–16 years after treatment. The authors determined that these techniques fostered reduced tree mortality by enhancing tree resistance Our study comprised a large geographical area and a large number of plots. Moreover, there was consistency in two variables identified in the logistic modeling as predictors of bark beetle-caused mortality; tree density and elevation. Therefore, applicability of these models, particularly the all forests model, should prove useful in identifying areas where vegetation management projects to reduce susceptibility to bark beetles and contribute to restoration efforts would be of benefit. Although extrapolation to other areas of site-specific models should be done with caution, in this case the models should have wide applicability in the Southwestern U.S. where similar ponderosa pine forests occur with a similar guild of tree killing bark beetles.

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