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ORIGINAL ARTICLE

Multi-temporal ecological analysis of Jeffrey pine beetle outbreak dynamics within the Lake Tahoe Basin

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Abstract From 1991 to 1996, Jeffrey pine beetles (*Dendroctonus jeffreyi* Hopkins) (JPB) caused tree mortality throughout the Lake Tahoe Basin during a severe drought. Census data were collected annually on 10,721 trees to assess patterns of JPB-caused mortality. This represents the most extensive tree-level, spatiotemporal dataset collected to-date documenting bark beetle activity. Our study was an exploratory assessment of characteristics associated with the probability of successful JPB mass-attack (P_{JPB}) and group aggregation behavior that occurred throughout various outbreak phases. Numerous characteristics associated with P_{JPB} varied by outbreak phase although population pressure and forest density had positive associations during all phases. During the incipient phase, JPBs caused mortality in individual trees and small groups within toeslope topographic positions and P_{JPB} had a negative relationship with stem diameter. In the epidemic phase, JPB activity occurred in all topographic positions and caused mortality in spatially expanding clusters. P_{JPB} had a curvilinear relationship with tree diameter and a negative relationship with proximity to nearest brood tree. Majority (92–96 %) of mass-attacked trees were within 30 m of a brood tree during the peak epidemic years. During the post-epidemic phase, mortality clusters progressively decreased while dispersal distances between mass-attacked and brood trees increased. Post-epidemic P_{JPB} had a negative relationship with stem diameter and mortality was concentrated in the mid and upper-slope topographic positions. Results indicate mortality predictions are reasonable for the epidemic phase but not for incipient and post-epidemic phases. Ecological factors influencing JPB-caused tree mortality, clustered mortality patterns, and transitions from environmental to dynamic determinism are discussed.

Keywords Bark beetles · *Dendroctonus jeffreyi* · Disturbance ecology · Epidemiology · Spatial aggregation · Tree physiology

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Introduction

Bark beetles (Coleoptera: Curculionidae: Scolytinae) are native disturbance agents in western North America coniferous forests. At endemic states, individual-tree and small-group mortality creates canopy gaps for new cohort recruitment by killing older, diseased or declining trees (Sartwell and Stevens 1975; Furniss and Carolin 1977; Lundquist and Negrón 2000). When populations reach an epidemic state, extensive tree mortality can occur across

landscape spatial scales. In recent years, outbreaks of numerous bark beetle species have occurred in regions throughout western North America (Man 2012). Some of these mortality events have exceeded the intensity and spatial magnitude of outbreaks documented within the past 125 years (Raffa et al. 2008). Extensive mortality can conflict with resource management values including wildlife habitat conservation, regulating surface and canopy fuel structure and loadings, carbon sequestration, timber production, and recreation (Martin et al. 2006; Axelson et al. 2009; Allen et al. 2010; Pfeifer et al. 2011; Hicke et al. 2012a, b).

The Jeffrey pine beetle (*Dendroctonus jeffreyi* Hopkins; JPB) is the primary insect disturbance agent in mature Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) stands (Furniss and Carolin 1977; Wood et al. 2003). JPBs occur throughout the range of Jeffrey pine, which occurs in pure and mixed-species forests distributed on cold and dry sites of lower site-quality from the southern Klamath and Sierra Nevada ranges to the Baja Peninsula (Jenkinson 1990; Wood et al. 2003; Smith et al. 2009). Jeffrey pines also grow in pure composition forests in limited areas of this range, including within the Lake Tahoe Basin.

Outbreaks of JPB near the Lake Tahoe Basin, along with outbreaks of other bark beetles in the Sierra Nevada, are highly correlated with multiple years of below average precipitation and related drought conditions (Guarin and Taylor 2005; Egan et al. 2011). Historical reconstructions indicate JPB outbreaks in the Lake Tahoe Basin typically occurred in conjunction with drought periods between 1910 and 2010 (Egan 2009), at an average frequency of one outbreak per decade between 1960 and the early 2000s. These recent outbreaks persisted for an average of 5 years and most reached an incipient (i.e., pre-epidemic) or epidemic phase where mortality occurred at limited spatial scales. Two JPB outbreaks within the past century have reached epidemic phases to cause extensive levels of mortality at a landscape-scale in the Lake Tahoe Basin, one of which was evaluated for this study (Egan 2009).

JPB outbreaks that reach epidemic levels at a landscape scale can cause high levels of tree mortality in large aggregations that can exceed 500 stems within a mortality cluster (Smith et al. 2009). Such extensive levels of mortality can conflict with resource management objectives aimed to sustain critical ecosystem processes and function (Ellison et al. 2005; Allen et al. 2010). For instance, extensive tree mortality can reduce wildlife habitat for sensitive avian species by reducing forest canopy cover (Martin et al. 2006). Beetle-caused mortality can affect wildfire hazard at various post-mortality temporal periods by influencing canopy fuel moisture content and volatility, changing canopy bulk density and fuel loadings, and influencing the juxtaposition of snags and down woody debris (Hicke et al. 2012a; Jolly et al. 2012). Furthermore, mortality caused by bark beetle outbreaks can have major impacts on timber management and road system maintenance as well as recreation and occupational safety (USFS 2011).

As a result, resource managers have long sought techniques to minimize mortality caused by bark beetles (Craighead 1925). Effective management techniques to prevent high levels of tree mortality in western pine systems include regulating inter-tree spacing and forest stocking through thinning and other silvicultural means (Fettig et al. 2007; Egan et al. 2010, 2014). Direct beetle suppression and brood destruction through sanitation treatments, such as debarking or infested-tree removal, can also reduce localized mortality over short-term time horizons (Miller 1944; Wulder et al. 2009; Coggins et al. 2011). However, this management practice is ineffective when epidemic populations occur at landscape scales as it is impractical to identify and treat all infested trees (Miller and Keen 1960; Amman and Baker 1972; Sartwell and Stevens 1975).

Epidemiological knowledge of bark beetle outbreak dynamics is critical to support robust resource management decisions. Such information can be used to evaluate the risk of tree mortality, location of anticipated beetle activity, and impacts of foregoing management activities to reduce beetle activity. Insect behavior during an outbreak fluctuates through various phases of an outbreak that lead to differences in the size, quality, and quantity of mass-attacked trees, degree of spatial clustering in host mortality, beetle dispersal distance to new host trees, and population control mechanisms (Sartwell and Stevens 1975; Safranyik and Carroll 2006; Kautz et al. 2011; Walter and Platt 2013). Common characteristics describing these phases have been summarized for the mountain pine beetle (*D. ponderosae*) (MPB) within lodgepole pine (*P. contorta*) forests (Safranyik and Carroll 2006; Wulder et al. 2006) and, to a lesser extent, for ponderosa pine (*P. ponderosa*) systems (Schmid et al. 2007). Only limited study of outbreak phases have occurred for other bark beetles in western North America, and no evaluation of JPB-caused mortality patterns during these phases has occurred to-date.

In this study, we conducted an exploratory analysis to investigate baseline epidemiological information and derive mechanistic hypothesis regarding ecological and spatiotemporal interactions of JPB-caused mortality from 1991 to 1996 with census data from the Lake Tahoe Basin. Our goal was to assess forest and site characteristics associated with successful JPB mass-attack, describe group mortality dynamics through time, and characterize variations in these behaviors and dynamics between the progressive phases of a JPB outbreak. Specific objectives were to (1) characterize forest attributes, rates of mortality, and

spatial aggregations that occurred during this JPB outbreak; (2) identify how spatial aggregations of mortality changed during the outbreak; (3) determine mathematical relationships between JPB mass-attacked trees and individual tree, neighborhood, and site characteristics; (4) compare how these relationships changed by outbreak phase; and (5) identify which variables had the strongest association with probability of JPB-attack.

Methods

A 24.3 ha study area was established on the east side of the Lake Tahoe Basin, approximately 600 m northwest of Spooner Lake, after elevated JPB-caused mortality was detected. Study area boundaries were delineated based on drainage boundaries, aspect, and forest type. Elevations within the study area ranged from 2090 to 2250 m and had south- to southwest-oriented slopes that ranged from 5 to 20 %. The soil association type was Cagwin-Toem, which is somewhat to excessively well-drained and comprised of loamy coarse to gravelly coarse sands situated over granitic rock deposits (Rogers 1974). The study area climate is montane Mediterranean, where majority of precipitation falls as snow from November to April. Precipitation averaged 87.5 cm year^{-1} from 1978 to 2010 and mid-summer daily temperatures averaged 14.8 °C with a mean summer daily maximum of 23.7 °C based on the Marlette Lake SNOTEL station located six miles from the study site (NRCS 2015). Our data were collected during a severe drought period that elevated populations of various bark beetle species throughout many central Sierra Nevada locations (Fig. 1; California Forest Pest Council 1994). However, forested vegetation within the study area was exposed to high JPB populations that originated locally rather than from an expansive beetle migration from an adjacent area.

Forest vegetation in the study area was primarily Jeffrey pine with scattered lodgepole pine (*P. contorta* ssp. *murrayana* Grev. & Balf.) and white fir (*Abies concolor* var *lowiana* Gordon). From Smith (1994), the best ecological type match was Jeffrey pine/bitterbrush-snowberry/bluegrass. This area had extensive timber extraction activities in the late nineteenth century when majority of stems were harvested with clearcutting activities between 1875 and 1885 (Murphy and Knopp 2000). Almost all trees on the site naturally regenerated post-harvest, and stands were dominated by trees 100–120 years of age. No known pathogenic tree disease such as western dwarf mistletoe *Arceuthobium campylopodum* Engelm.), black stain root disease (caused by *Leptographium wageneri* Harrington), or annosus root disease [caused by *Heterobasidion irregular* (Underw.) Otrosina & Garbelotto] infected vegetation during the outbreak.

Data collection

In the fall of 1994, survey crews established 149 anchor points with geospatial coordinates to stem map all attacked Jeffrey pines within the study area. Anchor points were monumented and geospatial location was recorded for each point with a global positioning system unit (Trimble Navigation, Inc.). Slope-adjusted distances, using a Criterion 400® slope-adjusted survey laser (Laser Technology, Inc.), as well as azimuth and diameter at 1.37 m in height (DBH) to the nearest 2.5 cm were collected for every Jeffrey pine that was mass-attacked by JPBs since the outbreak began in 1991. Attack status and mortality agent

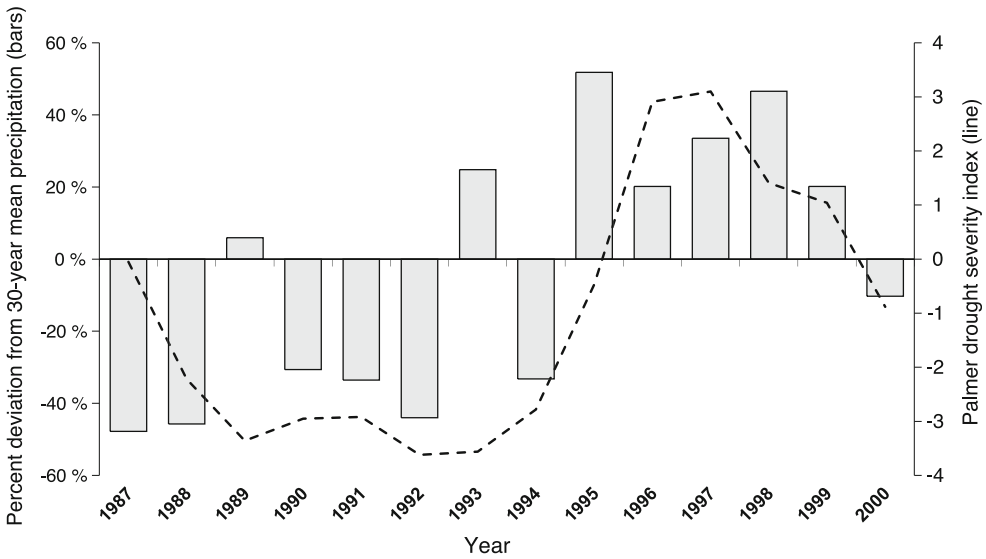

Fig. 1 Deviation from mean annual precipitation and Palmer Drought Severity Index within the Lake Tahoe Basin from 1987 to 2000. Precipitation data refers to water year from October to September with the latter year depicted in chart for Marlette Lake SNOTEL station (NRCS 2015). Palmer drought severity index is depicted as 2-year revolving average for Nevada Climatic Division 1 (NCDC 2015)

were determined by evaluating pitch tubes, boring dust, and/or inner-bark galleries on the bole of each Jeffrey pine (Goheen and Willhite 2006). Year of attack was determined for trees with faded crowns attacked from 1991 to 1993 based on crown coloration as well as needle and fine branch retention criteria. Surveys were duplicated in this manner in 1995 and 1996 and mortality was verified for mass-attacked trees. In 1996, surveys indicated few mass-attacked trees and it was apparent that the JPB outbreak declined substantially. During this year crews created 172 additional anchor points and surveyed all live, non-attacked stems within the study unit. Crews recorded species and DBH as well as azimuth and slope-adjusted distance to nearest anchor point as described for dead trees. Observations in 1997 indicated no mass-attacked trees and the JPB populations returned to endemic levels within the study unit.

Live and JPB-attacked annual tree data were rendered into a two-dimensional, geospatial environment from distance and azimuth parameters to each anchor point with ArcGIS v9.3 (ESRI 2008). As data were collected at each anchor point, instrumental precision bias for individual tree locations was minimized. Rendered coordinates were validated to be in correct locations through comparisons with aerial detection photos, orthoquad imagery, and ground surveys. In total, a comprehensive geospatial dataset was created to represent the species, DBH, and annual JPB-attack status for 10,721 trees within the study area during the outbreak period from 1991 to 1996 (Fig. 2).

Data calculations

Forest characteristics were reconstructed from measured stand conditions to baseline values when the outbreak originated in 1991 by aggregating the JPB mass-attacked and live tree data collected. Live tree data were obtained in 1996; thus, there is an assumption of limited radial stem growth between 1991 and 1996 for reconstructed trees. This assumption is reasonable as (1) the study time period took place during the latter portion of a severe drought period that likely limited radial growth and (2) diameter data were collected to the nearest 2.5 cm which exceeds expected growth over the 6 year study period (Uzoh et al. 1998). Coordinates were obtained for every tree in the study area and topographic position was assigned to each tree. An inter-tree distance matrix with 10,721 × 10,720 values was created by calculating each possible distance between the study trees. These data were used to calculate tree-level, nearest neighborhood distances for every Jeffrey pine in the study area and for each year of the outbreak. Spatial data were obtained for four circular neighborhoods with radii of 17.9 m (0.1 ha sample area), 25.4 m (0.2 ha), 35.9 m (0.4 ha), and 44.0 m (0.6 ha). Forest attributes were calculated for each neighborhood size with common methods to determine species composition, quadratic mean diameter, and basal area. Stand Density Index (SDI) was calculated by summing individual tree SDI values derived from Reineke (1933) equations through the individual tree summation method described in Stage (1968) to remain consistent with Forest Vegetation Simulator program results typically used by forest managers (Keyser 2008).

JPBs have a 1-year life cycle in the Lake Tahoe Basin wherein trees are mass-attacked for brood reproduction in a given year and become a source of emerging beetle populations the following year (hereafter called brood trees) when tree mortality occurs (Smith et al. 2009). Variables describing proximity to brood trees and a proxy for beetle population pressure were derived for every Jeffrey pine tree in the study area and for each year of the study period from 1991 to 1996. Brood tree proximity was calculated by obtaining the minimum, linear distance to nearest tree attacked in the prior year. The proxy for beetle population pressure was calculated within each neighborhood size by summing the basal area of all trees infested by JPBs in the previous year.

Data analysis

The phase of the outbreak was designated to each outbreak year by (1) assessing whether mortality increased or decreased relative to the prior year and (2) the level of clustering within mass-attacked trees within a given year. Bark beetle outbreak phases have been characterized into four unique categories of endemic, incipient, epidemic, and post-epidemic (Safranyik and Carroll 2006; Schmid et al. 2007). The endemic phase is characterized by having an individual-tree spatial pattern of attack with no clustering, epidemics have clusters $\geq$5 trees per attacked group, and the incipient phase is between these thresholds (Sartwell and Stevens 1975). Years that had an increasing rate of mortality relative to the prior year were designated into either incipient or epidemic outbreak phase based on whether the spatial pattern for the majority of attack occurrences observed was $\geq$5 trees per group. Years with declining rate of mortality based on the prior year were designated as post-epidemic. These phases represent a continuum of behavioral changes rather than discrete categories; thus, a transition designator was applied where the phase changed relative to the prior year.

The spatial pattern of JPB infestations was evaluated for each outbreak year. An infestation is defined as having either a clustered or individual-tree attack pattern. Infestations were first assessed through two automated, model-based cluster delineation techniques (Fraley et al. 2012; F. Murtagh and P. Legendre, unpublished data); however, each procedure was found insufficient to capture the

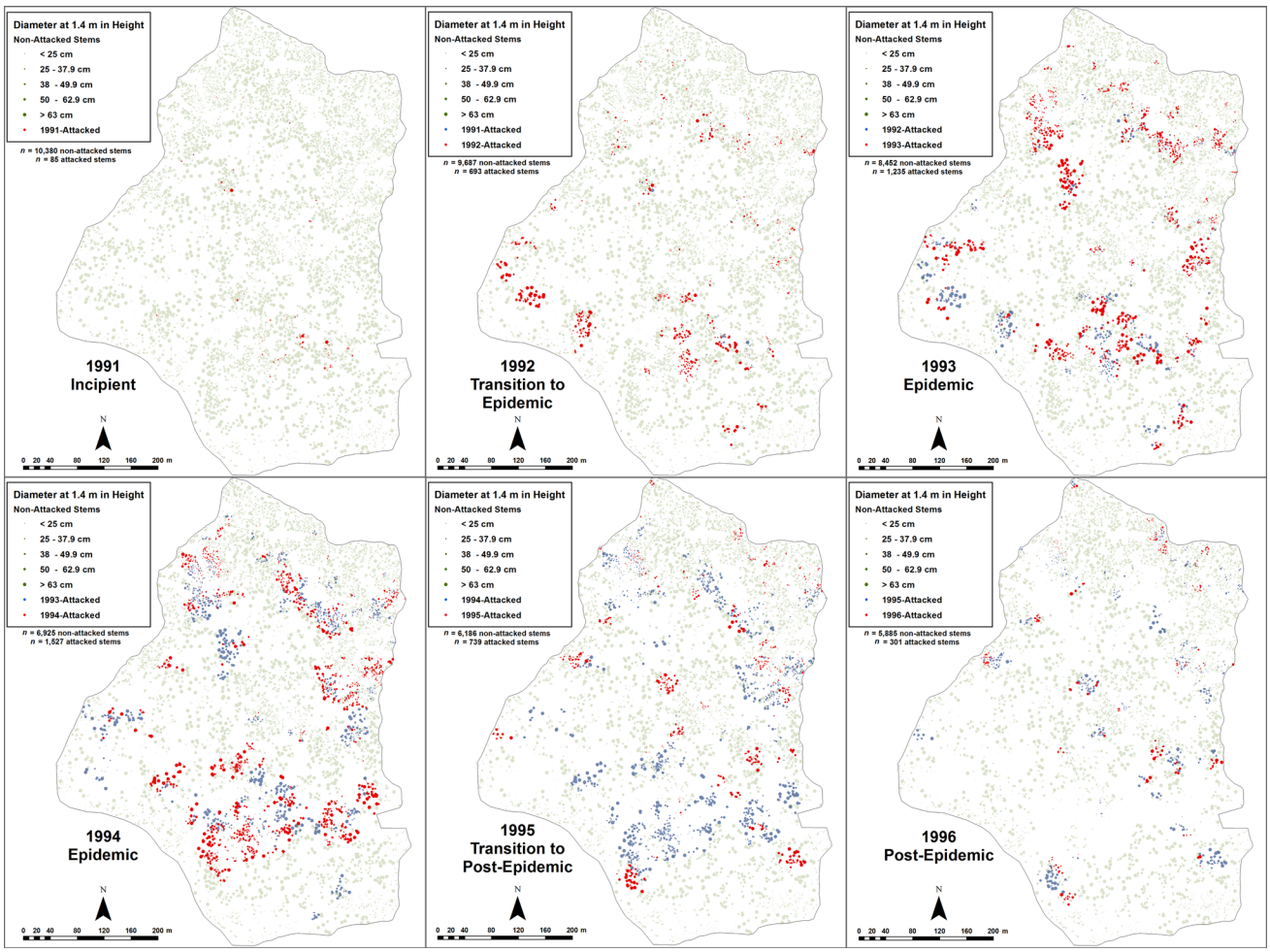

Fig. 2 Spatial location of JPB mass-attacked trees and brood trees by diameter from 1991 to 1996 within the Lake Tahoe Basin

variation in infestations and could not delineate attack patterns. Thus, every JPB-attacked tree was evaluated within each year of attack to determine the infestation's spatial pattern with a modified version of single linkage clustering (Florek et al. 1951). Spatially aggregated patterns were identified by starting with an attacked tree, then iteratively adding any additional candidate trees to form a cluster if they met two criteria. First, each candidate attacked tree had to be within 15 m from another attacked tree within a cluster. This distance was chosen as (1) the natural spatial distribution of trees within the study area indicated 99.96 % of all trees had at least one other tree within a 15 m spatial distance; (2) pheromone concentrations that facilitate bark beetle aggregations diminish substantially after 10 m from infested tree sources source and by 30 m their concentration is minimal (Thistle et al. 2011); and (3) 30 m distances or grid cells often used in landscape-scale studies (Powell and Bentz 2014) were considered too coarse to investigate the fine-scale group dynamics within our study area. Second, each attacked candidate tree could not have more than one non-attacked Jeffrey pine between it and the nearest attacked tree that was within a given cluster. Any attacked trees that did not meet the previous criteria for cluster incorporation were labeled as having an individual-tree infestation pattern. Subsequently, stems per cluster and spatial extent values were calculated. Infestation expansion and new spot infestation formation was determined by assessing whether each infestation of a given year had any infestations from the previous year that met the spatial criteria identified previously for tree-level cluster formation. Expansion was defined as those infestations that grew spatially the subsequent year while new spots are those infestations that did not result from expansion of any infestations from the prior year. Finally, stems per infestation values were compared for (1) infestations that expanded the subsequent year vs. those that did not and (2) infestations that were new spots vs. those that were not with Student's t test statistics for each year of the outbreak.

Inferential probit regression modeling was used to assess the relationship between tree-level probability of successful JPB mass-attack (P_{JPB}) and individual variables representing site, neighborhood and forest attributes, as well as neighborhood JPB population pressure and distance to nearest brood tree spatial attributes for each year of the outbreak. Species composition and quadratic mean diameter (QMD) were not used due to limited variation in the study area and confounding issues. The study area was nearly pure Jeffrey pine composition which led to substantial temporal autocorrelation when mortality reduced Jeffrey pines present within neighborhoods. Similarly, QMD values were not used as they were collinear with forest density attributes and diameter information was incorporated at the individual tree-level. Site, forest, and tree-level variables were, respectively modeled as individual predictors against the JPB mass-attack status response for each year of the outbreak. Due to multiple comparison errors and the substantial number of trees modeled within the dataset, a conservative $\alpha = 0.01$ was used to confirm significance for each variable. For the variables with multiple neighborhood sizes, Akaike information criterion (AIC) was used to identify which neighborhood size generally preformed best at predicting JPB-attacks for all years and those with the lowest AIC values were displayed within figures (Akaike 1974). Variables that did not contain a spatial component (i.e., stem diameter and basal area) were verified to ensure spatial variables, or the degree of bark beetle population pressure, did not confound relationships identified.

Probit regressions assume a linear relationship between quantitative predictors and the probit-transformed probability of a binary response variable, referring to JPB-attacked and non-attack status in this study (Bliss 1934). This assumption was validated through exploratory analysis plots and descriptive data summaries to identify any non-linear relationships or quantitative thresholds. For most variables, the assumption was satisfied; however, one variable had clear evidence of a curvilinear relationship and evaluation of two variables indicated a potential threshold-effect where the relationship with probability of mortality changed above a certain point. This was verified by modeling the potential threshold with a categorical dummy variable that partitioned data above and below the threshold. Where incorporating this dummy variable changed the sign of the relationship or had significantly different slope or intercept parameters, the threshold was validated and retained in models.

The relative importance of individual predictor variables for predicting JPB-attack for each phase of the outbreak was compared with an adjusted Brier skill score that indicates how well each variable improves a forecast relative to a reference condition (Brier 1950). The reference condition used was the base P_{JPB} for a tree within a given year without incorporating any explanatory variables. These Brier skill scores, along with the reference condition used, also indicated whether any variables substantially contributed to JPB-attack predictions and alluded to whether such predictions are advisable for a given outbreak phase.

Results

Outbreak phases

Outbreak phases were identified based on the degree of spatial clustering within mass-attacked trees and the annual trend of mortality rates. Incipient phase was designated for 1991, epidemic for 1992–1994, and post-epidemic for 1995–1996. Transition years were identified for 1992 and 1995 as these years had distinct changes in the rate of attacked trees relative to the prior year.

Forest and mortality characteristics

Forested characteristics that promoted JPB mass-attack were high stem densities when the outbreak originated, an abundance of susceptible stem diameters, and a composition of nearly pure Jeffrey pine (Table 1). Stocking and QMD variables varied slightly by topographic slope position. QMD variables remained similar pre- and post-outbreak while JPB mass-attacks caused mortality that reduced stocking levels (Table 1).

In total, 4580 of the 10,465 (43.8 %) Jeffrey pine stems available within the study site sustained tree mortality caused by JPB mass-attack during this outbreak (Fig. 3). Annual mortality varied, with the highest values occurring in 1993 and 1994. The rate of attacked trees increased substantially from 1991 to 1992, continued to increase at a reduced rate in 1993 and 1994, and then declined substantially each year in 1995 and 1996. This decline was associated with a 60 % above average increase in precipitation during the 1995–1996 water year that ended the multi-year drought period (Fig. 1).

Spatial pattern of infestations

The spatial pattern of attacked trees changed throughout the course of the outbreak (Table 2; Fig. 2). In 1991, the majority of stems (80 %) were infested within an individual-tree or small cluster ($\leq$4 stems per cluster) attern of spatial aggregation. The distribution of attacks within individual-trees and small clusters declined for the remainder of the outbreak as the degree of spatial aggregation increased (Table 2; Fig. 2). In 1993 and 1994, the

Table 1 Characteristics for individual Jeffrey pines within 0.4 ha neighborhoods from 1991 to 1996, Lake Tahoe Basin

Variable	1991 Incipient	1992 Transition to epidemic	1993 Epidemic	1994 Epidemic	1995 Transition to post-epidemic	1996 Post-epidemic	Post-outbreak
All study area: number of live Jeffrey pine stems [#]	10,465	10,380	9687	8452	6925	6186	5885
All study area: mean Jeffrey pine composition [%] (SD)	96.9 (4.8)	90.4 (11.2)	80.2 (17.9)	69.9 (25.2)	68.4 (20.4)	66.1 (19.9)	66.5 (20.0)
All study area: mean quadratic mean diameter [cm] (SD)	35.3 (6.9)	35.3 (7.0)	35.3 (7.2)	35.1 (7.2)	34.8 (7.4)	35.2 (7.3)	35.3 (7.3)
All study area: mean basal area [m^2 ha^{-1}] (SD)	52.9 (15.5)	52.6 (15.4)	49.8 (14.9)	43.8 (13.9)	38.7 (14.9)	35.5 (14.7)	35.5 (14.8)
All study area: mean stand density index (SD)[a]	357.3 (109.2)	356.9 (109.4)	339.1 (108.4)	299.3 (103.1)	300.9 (108.1)	263.4 (110.1)	261.6 (111.1)
Toeslope[b]: number of live Jeffrey pine stems [#]	3349	3293	2841	2443	1742	1596	1529
Toeslope[b]: mean Jeffrey pine composition [%] (SD)	94.6 (5.6)	81.2 (14.2)	72.5 (20.8)	56.4 (30.1)	61.8 (25.8)	61.4 (25.5)	62.0 (25.6)
Toeslope[b]: mean quadratic mean diameter [cm] (SD)	39.9 (5.6)	40.1 (5.7)	40.6 (5.8)	40.0 (6.3)	39.6 (7.1)	39.1 (7.2)	39.2 (7.2)
Toeslope[b]: mean basal area [m^2 ha^{-1}] (SD)	45.9 (18.1)	45.0 (17.6)	38.6 (15.1)	32.0 (13.3)	22.5 (10.0)	19.5 (7.4)	19.4 (7.4)
Toeslope[b]: mean stand density index (SD)[a]	288.7 (114.7)	286.8 (114.6)	243.9 (96.8)	202.9 (84.7)	181.8 (82.6)	137.2 (57.1)	133.8 (55.2)
Midslope[b]: number of live Jeffrey pine stems [#]	3128	3109	2992	2524	2056	1736	1646
Midslope[b]: mean Jeffrey pine composition [%] (SD)	97.5 (4.8)	93.7 (6.1)	79.4 (17.3)	70.0 (22.1)	64.0 (18.6)	61.0 (18.9)	61.2 (19.0)
Midslope[b]: mean quadratic mean diameter [cm] (SD)	36.1 (7.3)	36.2 (7.3)	36.4 (7.5)	36.5 (7.4)	37.5 (7.4)	38.9 (7.5)	38.8 (7.5)
Midslope[b]: mean basal area [m^2 ha^{-1}] (SD)	52.7 (10.8)	52.5 (10.7)	50.9 (10.1)	44.0 (9.2)	39.1 (10.3)	34.4 (8.9)	34.2 (8.9)
Midslope[b]: mean stand density index (SD)[a]	352.5 (78.9)	352.4 (79.0)	341.6 (75.5)	294.9 (70.5)	292.6 (70.3)	251.6 (69.7)	249.8 (69.6)
Shoulder slope[b]: number of live Jeffrey pine stems [#]	3988	3978	3854	3485	3127	2854	2710
Shoulder slope[b]: mean Jeffrey pine composition [%] (SD)	98.5 (3.0)	95.5 (5.3)	86.5 (13.2)	79.3 (18.1)	74.9 (15.7)	71.9 (14.7)	72.2 (14.7)
Shoulder slope[b]: mean quadratic mean diameter [cm] (SD)	30.7 (4.1)	30.7 (4.1)	30.7 (4.1)	30.6 (4.4)	30.4 (4.5)	30.8 (4.3)	30.9 (4.3)
Shoulder slope[b]: mean basal area [m^2 ha^{-1}] (SD)	59 (13.6)	58.9 (13.5)	57.2 (12.7)	51.9 (11.0)	47.4 (11.9)	45.1 (12.4)	45.3 (12.5)
Shoulder slope[b]: mean stand density index (SD)[a]	418.7 (87.3)	418.5 (87.3)	407.3 (82.9)	369.9 (74.9)	372.6 (75.6)	341.1 (80.3)	341.0 (80.7)

Characteristics refer to stand conditions at beginning of each respective year prior to JPB emergence and tree-attack

[a] Stand density index calculated with individual tree summation method detailed in Stage (1968)

[b] Topograhpic position categories ranged by elevation. Toeslope was from 2093 to 2144 m, midslope was 2145—2195 m, and shoulder slope was 2196–2247 m

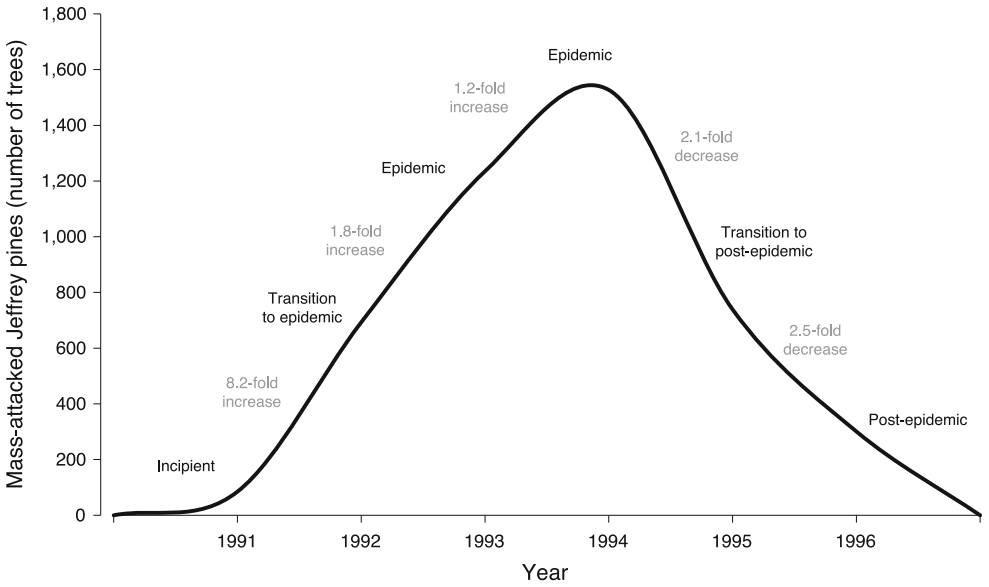

Fig. 3 Frequency count of JPB mass-attacked trees by year of attack from 1991 to 1996 within the Lake Tahoe Basin

Table 2 Spatial parameters for individual-tree and clustered JPB infestations from 1991 to 1996, Lake Tahoe Basin

Variables	1991 Incipient	1992 Transition to epidemic	1993 Epidemic	1994 Epidemic	1995 Transition to post-epidemic	1996 Post-epidemic
Mean ± SEM stems per infestation[A]	1.8 ± 0.3	7.3 ± 1.4	24.2 ± 5.7	36.4 ± 15.0	11.9 ± 2.0	8.1 ± 1.3
Mean ± SEM spatial extent per infestation (m^2)	6.3 ± 2.3	83.2 ± 21.5	362.9 ± 99.5	1051.1 ± 593.2	137.6 ± 28.0	69.3 ± 13.5
Percent of all attacked stems infested as individual trees (number of stems)	34.1 % (29)	5.5 % (38)	0.6 % (7)	1.0 % (15)	1.9 % (14)	2.3 % (7)
Percent of all attacked stems infested within small clusters (number of stems)[B]	44.7 % (38)	8.5 % (59)	2.8 % (34)	2.0 % (31)	6.1 % (45)	10.3 % (31)
Percent of all attacked stems infested within moderate clusters (number of stems)[B]	21.2 % (18)	41.4 % (287)	22.9 % (283)	6.5 % (99)	31.5 % (233)	87.4 % (263)
Percent of all attacked stems infested within large clusters of (number of stems)[B]	0.0 % (0)	44.6 % (309)	73.8 % (911)	90.5 % (1382)	60.5 % (447)	0.0 % (0)
Maximum number of stems within a clustered aggregation	11	85	203	528	53	29
Percent of infestations that expanded the subsequent year (number of infestations)	76.1 % (46)	80.0 % (95)	84.3 % (51)	45.2 % (42)	50.0 % (61)	n/a (0)
Mean ± SEM stems per infestation that expanded (number of infestations)	2.0 ± 0.3 (35)[a]	8.6 ± 1.7 (76)[a]	27.0 ± 6.7 (43)[a]	74.1 ± 31.2 (19)[a]	19.1 ± 3.4 (31)[a]	n/a (0)
Mean ± SEM stems per infestation that failed to expand (number of infestations)	1.4 ± 0.2 (11)[a]	2.3 ± 0.5 (19)[b]	9.4 ± 2.6 (8)[b]	5.2 ± 1.9 (23)[b]	4.7 ± 0.9 (31)[b]	n/a (0)
Percent of all infestations that were new spots (number of infestations)	100.0 % (46)	73.7 % (95)	37.3 % (51)	23.8 % (42)	40.3 % (62)	21.6 % (37)
Mean ± SEM stems per infestation that were new spots (number of infestations)	1.8 ± 0.3 (46)	5.3 ± 1.1 (70)[a]	6.2 ± 2.4 (19)[a]	2.2 ± 0.5 (10)[a]	10.7 ± 3.0 (25)[a]	4.5 ± 2.0 (8)[a]
Mean ± SEM stems per infestation that were not new spots (number of infestations)	n/a (0)	12.9 ± 4.2 (25)[a]	34.9 ± 8.4 (32)[b]	47.0 ± 19.3 (32)[b]	12.7 ± 2.7 (37)[b]	9.1 ± 1.5 (29)[a]

[A] Infestations refers to either an individual-trees or clustered spatial pattern of JPB-attack

[B] Small clusters defined as 2–4 stems, moderate as 5–29 stems, and large clusters as ≥30 stems per group

[ab] Refers to significant difference comparing mean stems with Student's t test at $\alpha = 0.05$

vast majority of JPB-attacks occurred within large aggregations (≥30 stems per cluster) while only minimal infestations (≤1 %) had an individual-tree spatial pattern of attack. In 1995 and 1996, the amount of JPB-attacks within large clusters decreased gradually while attacks with the individual-tree pattern of attack increased slightly. Cluster growth from 1 year to the next indicates a radial spread of beetle populations into adjacent stems. Clusters that grew had significantly greater stems per cluster values compared with clusters that did not grow during all outbreak years except for 1991 (Table 2; Fig. 2). New spot infestations that did not have adjacent mortality the prior year indicate beetle dispersal to novel locations. High levels of spot infestations, and thus beetle dispersal, occurred in 1991 during the first year of the outbreak as well as in the 1992 and 1995 transition years. New spots had significantly fewer stems per cluster relative to infestations that grew from the prior year from 1993 to 1995. New spots had lower mean stems per cluster values in 1992 and 1996 but were not significantly different from infestations that grew (Table 2; Fig. 2).

Stem diameter

The relationship between stem diameter and P_{JPB} changed throughout the course of this outbreak (Fig. 4; Table 3). Rates of mortality are presented to document actual mortality occurrence in small-diameter (<38.0 cm), mid-sized (38.0–75.9 cm), and large-diameter stems (≥76.0 cm) categories (Table 4). In 1991, there was a significant negative relationship where P_{JPB} decreased with increased stem DBH values. During this year, the majority of mortality occurred in small-diameter stems (<38.0 cm) while no mortality occurred in large-diameter stems (≥76.0 cm) (Table 4). Stem DBH had a quadratic association that was not significant in 1992 ($P = 0.011$) as the relationship with JPB-attack appeared to be transitioning. In 1993 and 1994, there was a significant quadratic relationship where P_{JPB} increased with increasing smaller diameter stems, peaked in mid-sized stems ranging from 50.0–60.0 cm, then declined with increasing stem diameters (Fig. 4). In 1995 and 1996, the effect transitioned to a negative linear relationship where P_{JPB} decreased with increasing stem diameter. Thus, P_{JPB} varied for trees <51.0 cm from a negative orientation in 1991, to positive from 1993 to 1994, then back to negative from 1995 to 1996. Conversely, larger stems ≥51.0 cm had a constant negative relationship for all years including 1992 when there was a negative trend but the effect was not significant (Table 3; Fig. 4). Overall, rates of cumulative mortality (adjusted for host available within diameter class) for all outbreak years was limited in stems ≥76.0 cm (Table 4).

Forest density

Forest density variables assessed were SDI, basal area, and original basal area reconstructed to 1991 when the outbreak originated. The basal area attributes were better predictors than the stand density index predictors based on AIC comparisons; thus, SDI was not utilized further as it was highly collinear with basal area. Pre-outbreak basal area was used as the primary forest density attribute as it was a slightly better predictor for all years based on AIC criteria. Pre-outbreak basal area values had significant, positive linear relationships with P_{JPB} for all years of this outbreak (Fig. 5). However, the best pre-outbreak basal area neighborhood size varied by year (Table 3). In 1991, the largest neighborhood sizes at 0.4 and 0.6 ha were the best

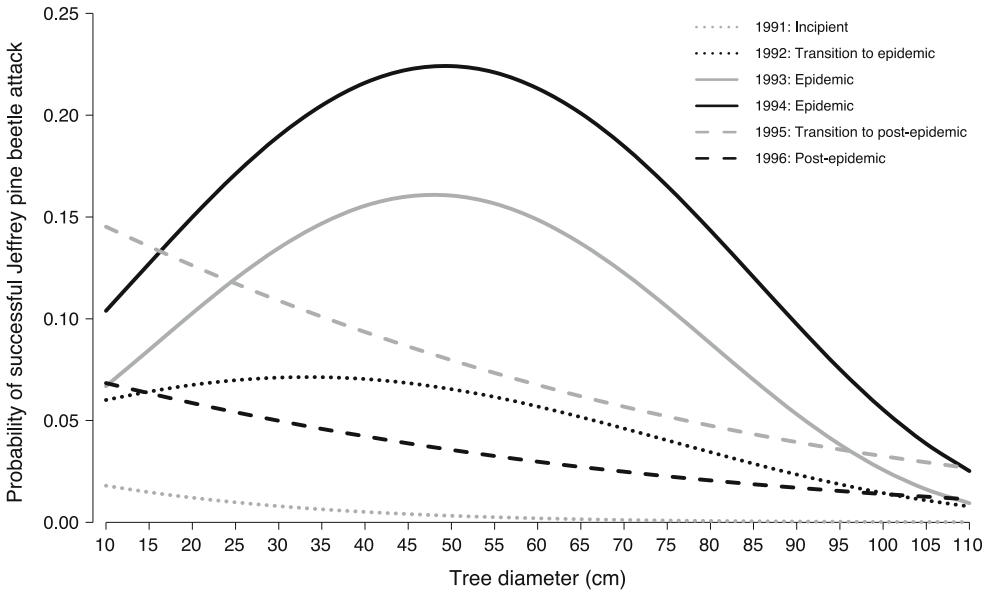

Fig. 4 Probability of successful JPB mass-attack by tree diameter from 1991 to 1996, near Spooner Junction within the Lake Tahoe Basin. Stem diameter had a significant relationship with the P_{JPB} in all years except for 1992

Table 3 Relationship between JPB mass-attack and influential predictor variables depicted with slope parameters from 1991 to 1996, Lake Tahoe Basin

	1991	1992	1993	1994	1995	1996
Variable	Incipient	Transition to epidemic	Epidemic	Epidemic	Transition to post-epidemic	Post-epidemic
Stem diameter linear coefficient (AIC)	−0.016 (967)	–	–	–	−0.009 (4667)	−0.008 (2393)
Stem diameter quadratic coefficient (AIC)[a]	–	*0.011 (5087)*	0.034 (7332)	0.032 (7925)	–	–
Stem diameter^2 quadratic coefficient (AIC)[a]	–	*−0.000 (5087)*	−0.000 (7332)	−0.000 (7925)	–	–
Pre-outbreak basal area coefficient in 0.1 ha neighborhood (AIC)	0.076 (973)	0.103 (4947)	0.141 (7048)	0.184 (7932)	0.108 (4579)	0.125 (2316)
Pre-outbreak basal area coefficient in 0.2 ha neighborhood (AIC)	0.068 (958)	0.057 (4983)	0.097 (6978)	0.110 (7451)	0.064 (4588)	0.044 (2377)
Pre-outbreak basal area coefficient in 0.4 ha neighborhood (AIC)	0.061 (931)	0.031 (5005)	0.061 (6963)	0.060 (7568)	0.032 (4626)	*0.009 (2406)*
Pre-outbreak basal area coefficient in 0.6 ha neighborhood (AIC)	0.054 (910)	0.019 (5025)	0.040 (7046)	0.0339 (7644)	0.017 (4659)	*0.002 (2411)*
Minimum distance to nearest brood tree (AIC)[b]	–	−0.020 (2793)	−0.045 (6297)	−0.036 (7188)	−0.012 (4639)	−0.080 (1889)
Fixed P_{JPB} for stems ≥50 m from nearest brood tree	–	0.0322	0.0043	0.0181	0.055	0
P_{JPB} with no beetle pressure in 0.1 ha neighborhood	–	0.0426	0.0402	0.0736	0.0777	0.0028
Beetle pressure coefficient in 0.1 ha neighborhood (AIC)[c]	–	1.308 (4703)	0.192 (6519)	0.226 (7152)	0.099 (4629)	0.277 (1983)
Beetle pressure coefficient in 0.2 ha neighborhood (AIC)[c]	–	0.902 (4772)	0.208 (6603)	0.211 (7067)	0.111 (4603)	0.253 (2043)
Beetle pressure coefficient in 0.4 ha neighborhood (AIC)[c]	–	0.538 (4862)	0.150 (6745)	0.166 (7061)	0.080 (4586)	0.207 (2131)
Beetle pressure coefficient in 0.6 ha neighborhood (AIC)[c]	–	0.406 (4925)	0.115 (6913)	0.128 (7093)	0.049 (4580)	0.166 (2195)
Topographic slope position categorical variable (AIC)[d]	n/a (947)	n/a (4741)	n/a (7336)	n/a (7662)	n/a (4640)	*n/a (2411)*

Italics indicate single variable effects within probit model were not significant at $\alpha = 0.01$

[a] Best-fit model for stem diameter at breast height incorporated a linear effect for 1991 and 1996 and a quadratic curvilinear relationship for 1992–1995

[b] Minimum distance to nearest brood tree probability model incorporated linear effect within 50 m of brood tree due to identified threshold

[c] Beetle population pressure coefficient refers to relationship when infested basal area from prior year exceeds 0 m^2 ha^{-1} within neighborhood

[d] Parameter estimates for categorical variables are relative to a designated category; thus, only AIC values are presented

Table 4 Mortality rates for successful JPB mass-attacked trees by diameter and distance to nearest brood tree classifications from 1991 to 1996, Lake Tahoe Basin

Variable	1991 Incipient	1992 Transition to epidemic	1993 Epidemic	1994 Epidemic	1995 Transition to post-epidemic	1996 Post-epidemic	1991–1996 Total for all years
Percent of all stems attacked (total stems)	0.8 % (10,465)	6.7 % (10,380)	12.7 % (9687)	18.1 % (8452)	10.7 % (6925)	4.9 % (6186)	43.8 % (10,465)
Percent of all <38.0 cm stems attacked (total stems)	1.1 % (6951)	6.9 % (6874)	11.8 % (6403)	16.7 % (5645)	11.6 % (4700)	5.4 % (4156)	44.2 % (6951)
Percent of all 38.0–75.9 cm stems attacked (total stems)	0.2 % (3368)	6.5 % (3360)	14.8 % (3140)	20.9 % (2675)	9.0 % (2116)	3.9 % (1925)	45.1 % (3368)
Percent of all ≥76.0 cm stems attacked (total stems)	0.0 % (146)	1.4 % (146)	8.3 % (144)	17.4 % (132)	3.7 % (109)	0.0 % (105)	28.1 % (146)
Percent of all <50 m stems attacked (total stems)	0.0 % (n/a)[a]	8.3 % (5910)	14.1 % (8759)	19.2 % (7845)	11.5 % (6284)	5.5 % (5456)	40.1 % (10,465)[b]
Percent of all ≥50 m stems attacked (total stems)	0.8 % (10,465)[a]	4.6 % (4470)	0.0 % (928)	3.1 % (607)	2.4 % (641)	0.0 % (730)	3.1 % (10,465)[b]

[a] No trees were attacked within study area in 1990; thus distance to nearest brood tree exceeded 50 m for all stems attacked in 1991

[b] Refers to percent of all stems that were attacked when nearest brood tree was within or exceeding 50 m threshold during year of attack

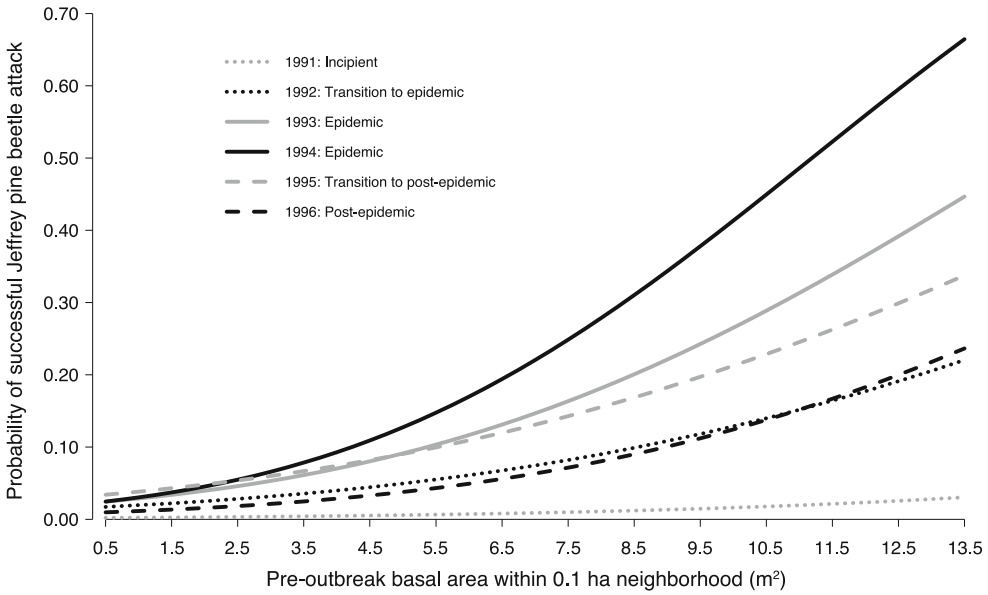

Fig. 5 Probability of successful JPB mass-attack by pre-outbreak basal area within 0.1 ha neighborhoods from 1991 to 1996 within the Lake Tahoe Basin

predictors of P_{JPB}. This transitioned over time as the smaller 0.1 and 0.2 ha neighborhoods were the best predictors for the remainder of the outbreak.

Proximity to nearest brood tree

The minimum linear distance to nearest adjacent brood tree was evaluated to determine common dispersal distances from brood source trees to JPB mass-attacked trees for each year of the outbreak. The majority of successfully mass-attacked trees were within close proximity to brood trees during all outbreak years (Figs. 2, 6). In 1992, 51 % of all attacks occurred within a 20 m distance of nearest brood trees. This was increased to >80 % of all attacks occurring within a 20 m distance of the nearest brood tree from 1993 to 1994. 1995 appeared to be a transition year and 69 % of all JPB-attacks were within a 20 m distance while 98 % of all attacks were within this distance the final year of the outbreak in 1996 (Fig. 6).

Minimum distance to nearest brood tree descriptive statistics and inferential models indicated a threshold effect at 50 m as all outbreak years had minimal JPB-attacks that exceeded this distance (Table 4). The relationship of this variable to P_{JPB} for stems <50 m was significant and had a negative orientation for all years where the closer proximity to nearest brood tree yielded a higher P_{JPB} (Table 3;

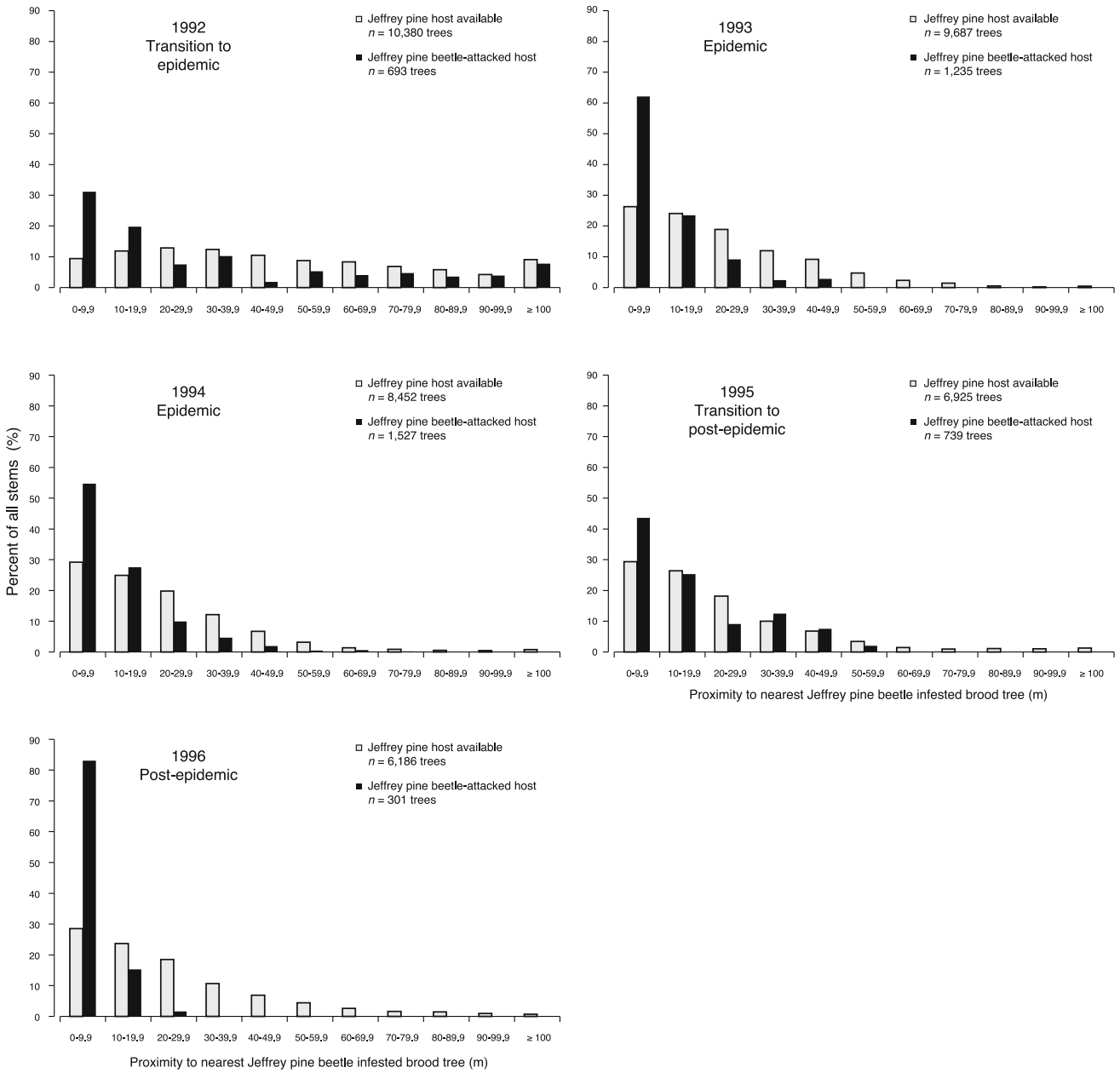

Fig. 6 Histogram of JPB mass-attacked trees and Jeffrey pine host available by distance to nearest brood tree from 1992 to 1996 within the Lake Tahoe Basin. Brood trees refer to Jeffrey pines successfully attacked by JPBs the prior year. The 1991 data is not depicted as brood trees were not detected in 1990

Fig. 7). For stems ≥the 50 m threshold, P_{JPB} was constant at <0.02 for 1993 to 1994 and 1996. This probability was slightly higher from 0.03 to 0.06 for 1992 and 1995 when greater dispersal occurred and a high percentage of infestations were attributed to being new spots (Table 5).

Bark beetle population pressure

A proxy to represent the degree of bark beetle population pressure exerted on a potential host tree was calculated from the amount of infested basal area attacked the prior year within the neighborhood sizes for each year of the outbreak. For this variable, a threshold was found based on whether or not a neighborhood had any JPB-infested basal area present. When there was no infested basal area present, the effect was modeled as constant. When there was infested basal area present, models for all years and neighborhood sizes indicated a significant positive, linear relationship between the P_{JPB} and degree of bark beetle population pressure (Table 3; Fig. 8).

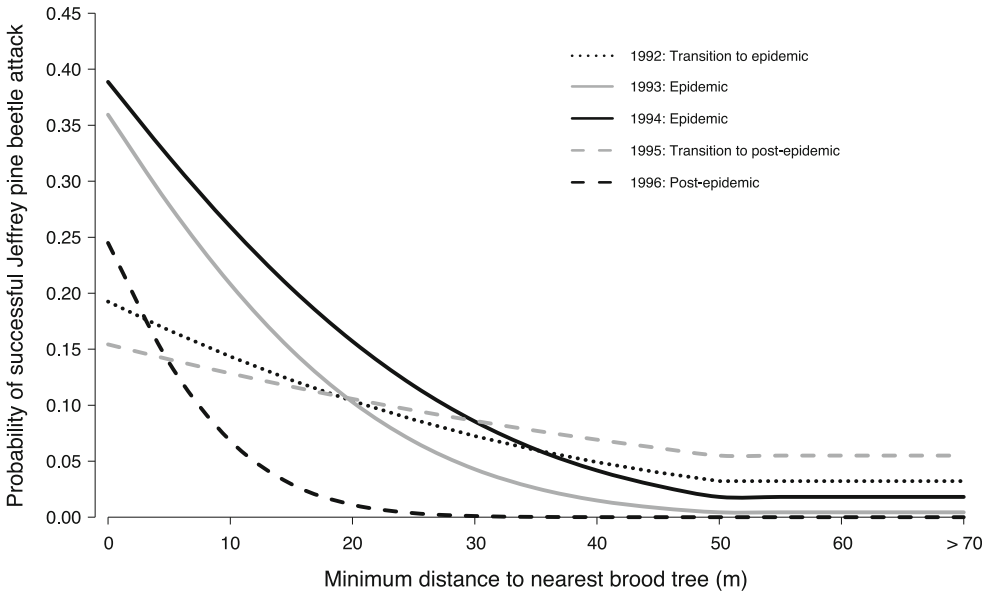

Fig. 7 Probability of successful JPB mass-attack by the minimum linear distance to nearest brood tree from 1992 to 1996 within the Lake Tahoe Basin

Table 5 JPB mass-attacked stems attacked and confidence intervals (CI) by topographic position from 1991 to 1996, Lake Tahoe Basin

Variable	1991 Incipient	1992 Transition to epidemic	1993 Epidemic	1994 Epidemic	1995 Transition to post-epidemic	1996 Post-epidemic	1991 - 1996 Total for all years
Percent toeslope stems attacked (total stems)[a]	1.7 % (3349)	13.7 % (3293)	14.0 % (2841)	28.7 % (2443)	8.4 % (1742)	4.2 % (1596)	54.3 % (3349)
Percent midslope stems attacked (total stems)[a]	0.6 % (3128)	3.8 % (3109)	15.6 % (2992)	18.5 % (2524)	15.6 % (2056)	5.2 % (1736)	47.4 % (3128)
Percent shoulder slope stems attacked (total stems)[a]	0.3 % (3988)	4.2 % (3978)	9.6 % (3854)	10.3 % (3485)	8.7 % (3127)	5.0 % (2854)	32.0 % (3988)
90 % CI for P_{JPB} in toeslope stems[a]	(0.013, 0.020)	(0.127, 0.147)	(0.129, 0.151)	(0.272, 0.302)	(0.073, 0.095)	(0.034, 0.050)	n/a
90 % CI for P_{JPB} in midslope stems[a]	(0.004, 0.008)	(0.032, 0.043)	(0.145, 0.167)	(0.173, 0.198)	(0.142, 0.169)	(0.043, 0.061)	n/a
90 % CI for P_{JPB} in shoulder slope stems[a]	(0.001, 0.004)	(0.027, 0.036)	(0.088, 0.104)	(0.094, 0.111)	(0.079, 0.096)	(0.044, 0.057)	n/a

[a] Topograhpic position categories ranged by elevation. Toeslope was from 2093–2144 m, midslope was 2145–2195 m, and shoulder slope was 2196–2247 m

Topographic position

JPB mass-attacked trees varied by topographic position during the course of the outbreak. During the early phases from 1991 to 1992, the vast majority of JPB activity was located within lower elevation toeslope locations (Table 5). Activity continued at this slope position from 1993 to 1994 while it also expanded to higher-elevation midslope and shoulder slope positions. During the 1995 transition year, mortality declined substantially in toeslope locations; however, it continued at a similar rate in the higher elevation midslope and shoulder slope locations. In 1996, mortality levels were further reduced across all topographic slope positions and occurred at low levels (Table 5).

Variable importance

The importance of each respective variable for predicting JPB-attack was compared with Brier skill scores representing each variable's contribution to reducing predictive error within respective single variable probit models. During the incipient phase of this outbreak, topographic slope position was the most important variable for determining P_{JPB} (Fig. 9). As the outbreak transitioned into, and progressed through, the epidemic phase the most important variables became those that described spatial parameters including proximity to nearest brood tree and beetle population pressure. When the outbreak transitioned to a post-epidemic phase, the forest basal area, topographic slope

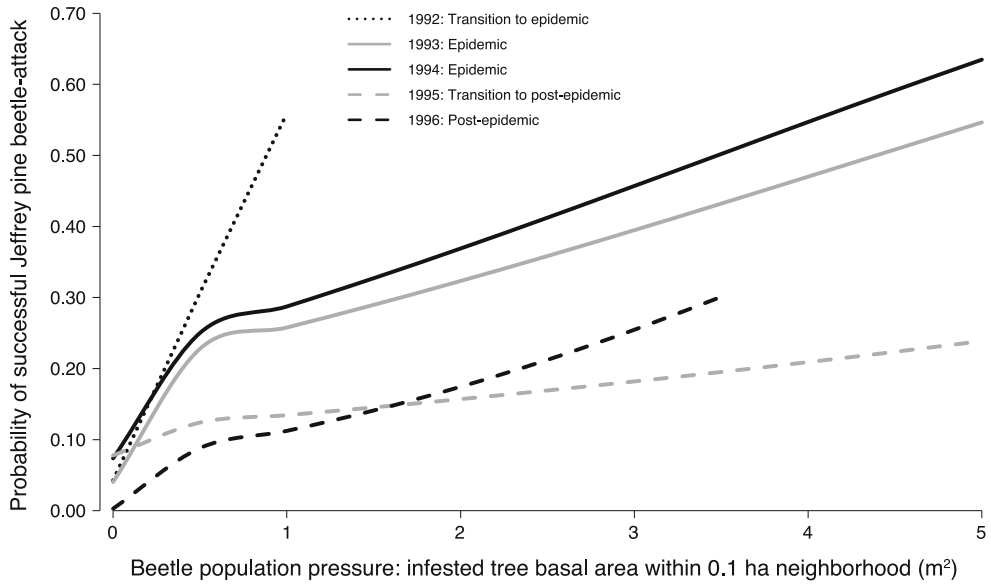

Fig. 8 Probability of successful JPB mass-attack by bark beetle population pressure within 0.1 ha neighborhood from 1992 to 1996 within the Lake Tahoe Basin

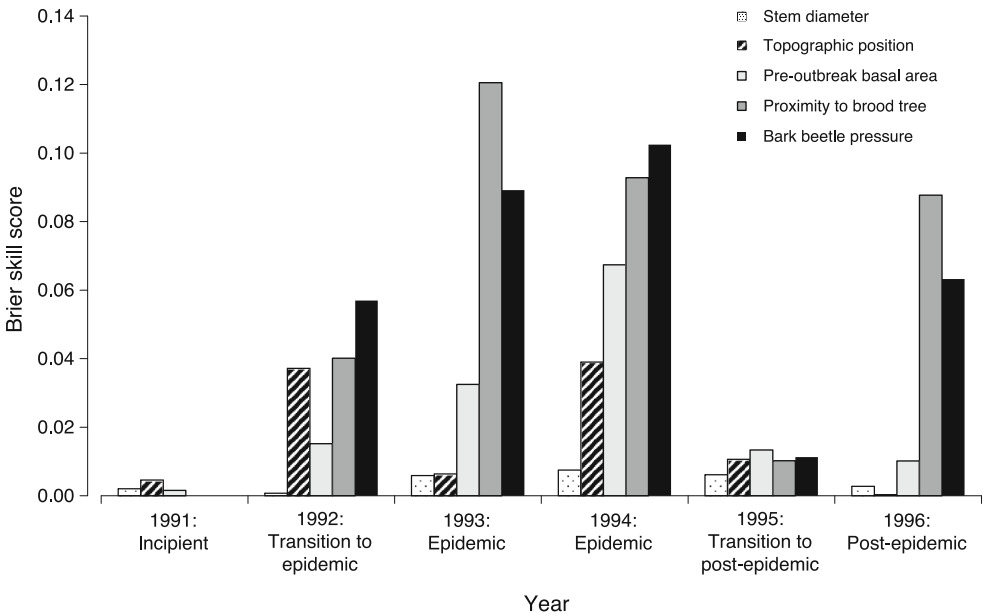

Fig. 9 Brier skill scores indicating variable importance by JPB outbreak phase from 1991 to 1996 within the Lake Tahoe Basin

position, and spatial parameters related to brood trees had similar importance although each contributed to only a small degree of model error reduction. Spatial parameters were the most important variables within 1996; however, it should be noted that very few trees were mass-attacked by JPBs during this final year of the outbreak. Overall, the most important variable within predictive models typically explained 20 times more variation in P_{JPB} within the epidemic phase models in 1993 and 1994 compared to the incipient phase models in 1991 (Fig. 9). This indicates tree-level mortality predictions are likely reasonable when JPBs are at epidemic levels but are not during the incipient and post-epidemic population phases.

Discussion

The relationships and trends documented in this study were evaluated in an exploratory context to derive mechanistic hypotheses and enhance baseline understanding of how JPBs interact with site and environmental conditions, at the individual-tree and group level, through the various phases

of an outbreak. This information is critical to support resource management decisions in Jeffrey pine forests. However, it should be noted that the JPB outbreak studied took place during the latter portion of a multi-year drought which had duration and severity characteristics that may be unique to the temporal period sampled. As such, findings are not provided to yield absolute or holistic predictions of tree mortality that will occur over the entire course of a future outbreak. Rather, these results characterize the progression of JPB-attack behavior through outbreak phases and patterns of mortality likely to be similar, for a specific phase, during future mortality events in locations with similar forest structure. The most important factors associated with JPB-attack behavior dynamics, and how these factors varied by phase, are discussed subsequently.

Drought and mortality trends

The drought conditions that occurred during the study period likely had substantial influence on the annual rate of JPB mass-attacked trees. This JPB outbreak started locally, rather than from migrating beetle populations in adjacent areas, following multiple years of below average precipitation that interacted with temperature to cause drought conditions (Fig. 1). During the incipient phase in 1991, less than 1 % of all Jeffrey pines were mass-attacked. There was a substantial increase in the rate of tree mortality in 1992 as the drought continued. This represents a 'boom' year when JPB populations erupted with an eightfold rate of increase and transitioned from an incipient to an epidemic phase. Interestingly, eightfold rates of MPB population increases have been identified as the greatest population amplification rate feasible due to brood mortality (Safranyik and Carroll 2006). Recent MPB outbreaks have had similar 'boom' years when increasing beetle populations were able to surpass an eruptive threshold (Raffa et al. 2008) leading to substantial increases in rates of tree mortality detected the year following an abnormally dry year occurring within a severe, multi-year drought period. These include MPB in lodgepole pine systems erupting within Colorado in 2002, western Canada in 2003, and within central Montana in 2007 (Gannon and Sontag 2009; Chapman et al. 2012; Walton 2012). Following the 'boom' year, JPB rates of tree mortality increased from one to twofold in magnitude during the epidemic years in 1993 and 1994. This is similar to common MPB epidemic phase expansion rates near twofold that have been documented when there are not 'boom' years in western Canada and throughout northern Idaho and Montana (Safranyik and Carroll 2006; Walton 2012; Egan et al. 2013; Egan 2014). The drought within the Lake Tahoe Basin ended in 1995 when JPB rates of mortality transitioned from epidemic to a post-epidemic phase and the rate of mortality declined twofold each year until the outbreak ended.

Stem diameter

During this outbreak, JPBs first successfully attacked small-diameter stems, then progressively colonized mid-sized and some large-diameter stems during the peak epidemic phase, and finally returned to attack small and mid-diameter stems in the post-epidemic phase. These results are mixed in comparison to studies of MPB outbreaks in respective ponderosa and lodgepole pine forest systems. For example, they are consistent with long-term studies within the Black Hills of South Dakota that indicated MPB-caused tree mortality initiated within small-diameter trees at an incipient outbreak phase then progressed into larger diameter stems (Schmid et al. 2007). They are also consistent with studies that reported drought-related MPB outbreaks led to mortality rates skewed away from the large-diameter ponderosa pines that exceeded 51.0 cm DBH within the Warner Mountains of California and Elkhorn Mountains of Montana (Egan et al. 2010; Randall et al. 2011).

The findings in our Jeffrey pine system differ with MPB activity within lodgepole pine systems that has been extensively studied. In this system, large-diameter lodgepole pine trees generally have greater defensive capacity relative to smaller trees (Boone et al. 2011). However, once MPBs reach the incipient phase of an outbreak, large-diameter trees can be overcome by high MPB population densities and are preferentially attacked (Boone et al. 2011). This leads to disproportionally higher mortality rates in large-diameter relative to smaller trees during incipient as well as the later phases of an outbreak (Safranyik and Carroll 2006). MPB research indicates physiologically stressed, small-diameter trees are attacked during an endemic phase while larger trees, that promote increased fecundity and energy reserves in reproducing brood, are preferentially during the incipient and epidemic phases of an outbreak (Elkin and Reid 2005; Safranyik and Carroll 2006). As such, MPB population density, typically approximated by tree mortality and outbreak phase, is the primary factor limiting mortality in large-diameter lodgepole pines. This paradigm is often extrapolated and used to describe other bark beetle species and host systems that haven't had rigorous study to-date.

Our findings conflict with the MPB paradigm as in our study large-diameter trees were attacked less and had reduced P_{JPB} during incipient and all other phases of the JPB outbreak. These results can be explained with four different hypotheses: (1) JPBs prefer smaller diameter trees. However, this is not supported by our data as the smallest trees in the study area (<38.0 cm) were attacked

disproportionally less, despite being the diameter class with the greatest component of the available trees during the peak epidemic years from 1993 to 1994. During this time period mid-sized stems (38.0–75.9 cm) had the greatest rates of mortality (see Table 3). (2) JPB population densities were not high enough to cause large-diameter tree mortality until they built up sufficiently in 1994. This is also not supported by our data as 1992 and 1993 had substantial population amplifications based on the proxy of substantial numbers of JPB mass-attacked trees which exceeded 700 and 1200 stems, respectively. Thus, populations were high and had the potential to focus attacks on greater numbers of high-quality large-diameter Jeffrey pine trees rather than avoiding them. (3) The surface area of large-diameter trees with infrequent spatial occurrences had reduced probability of being encountered by dispersing beetles looking for hosts to colonize (Byers 1996). This explanation is also not supported by our data as the P_{JPB} relationship with diameter was constant when bark beetle population pressure and distance to nearest brood tree variables were, respectively controlled for within P_{JPB} models to ensure large-diameter trees were challenged by JPBs. Similarly, attacked tree progression maps (Fig. 2) showcase high levels of beetle population pressure occurred within close proximity and challenged numerous large-diameter stems that were not mass-attacked. (4) The defensive capacity was greater in large-diameter Jeffrey pines relative to smaller trees and was a primary factor regulating the diameter distribution of JPB-attacked stems. This hypothesis is consistent with findings reported within our study.

The mechanisms regulating bark beetle mass-attacks in various sized stems appear to be more complex in a Jeffrey pine system relative to the lodgepole pine system. Our results strongly suggest that physiological stress within large-diameter Jeffrey pines had to reach a certain level to predispose them to mass-attack, even after the JPB outbreak reached the epidemic phase. Thus, large-diameter mortality was not only limited by high JPB populations but also by the degree of physiological stress and capacity for resistance within host trees. As the drought conditions manifested, small-diameter trees were impacted first while the larger trees that had more established root and crown systems were mass-attacked less as they likely had better physiological mechanisms that promoted drought avoidance and/or tolerance (McDowell et al. 2013). As the outbreak continued, interactions between high populations and aggregative physiological effects from multiple years of drought reduced defensive capacity of large-diameter trees and progressively enhanced susceptibility to successful JPB mass-attack. We anticipate that if the severe drought conditions persisted for additional years, a larger proportion of large-diameter stems would have been mass-attacked and killed by JPBs. Once the drought ended in 1995, JPBs immediately stopped attacking large-diameter trees and mass-attacks were limited to small and mid-sized stems. During this year, over 700 stems were attacked within the study area, indicating JPB populations remained high and could have distributed themselves into larger trees if defensive host capacity was not a substantial limiting factor.

Our study area had land-use history that promoted a consistent age class of mature stems (100–120 years or less) that established following extensive harvesting in the mid-1880s and no disease infection was known to occur within the study site (Murphy and Knopp 2000). Therefore, this study area was ideal for assessing drought interactions with different stem diameter sizes as confounding age-related decadence and disease infection factors were held constant. However, it should be noted that other locations may experience large-diameter tree mortality at earlier phases of a JPB outbreak if high levels of physiological stress occur due to disease infection, age-related decadence, inter-tree competition, mechanical damage, or severe drought.

Forest density

Stocking levels within locations that supported successful JPB-attacks were dense and averaged 357 SDI or 53 m^2 ha^{-1} of basal area across the study area. Pre-outbreak forest basal area calculated at the tree-level was an important variable for predicting JPB mass-attack during all phases of the outbreak; however, it was not the most important variable regarding mortality predictions during any outbreak phase. The positive relationship between JPB-attack and basal area grew progressively stronger through incipient and epidemic phases then waned during the post-epidemic portion of the outbreak. This relationship found within Jeffrey pine forest type is similar with those consistently found between bark beetle-caused mortality and stand density during outbreaks of MPB and western pine beetle (*D. brevicomis*) within ponderosa pine forest types (Oliver 1997; Cochran and Barrett 1998; Schmid et al. 2007; Egan et al. 2010). Dense forest stocking levels have been identified as beneficial habitat for a variety of bark beetle species as these characteristics promote tree competition for limited light and water resources and thus reduce individual tree vigor, while providing beneficial microclimate habitat that promote pheromone plume stability, shading to limit bark temperatures, reduced wind speeds, and other factors that have not received scientific evaluation to-date (Mitchell et al. 1983; Coops et al. 2006; Thistle et al. 2011). Conversely, stand density levels near or below 200 SDI or 14 m^2 ha^{-1} of basal area have shown resilience to high levels of bark beetle-caused mortality in

various geographic locations after being challenged by moderate or severe and widespread bark beetle outbreaks (Oliver 1997; Cochran and Barrett 1998; Schmid et al. 2007; Egan et al. 2010, 2011).

Interestingly, the forest density variable that incorporated living and dead trees estimated JPB mass-attacks better than those variables that adjusted for prior year mortality and were calculated using only living trees. Dead trees retain needles and fine branches for a few years post-mortality (Bull 1983); thus, they still impact fine-scale microclimatic factors such as bark temperature and pheromone plume stability while they do not transpire or uptake limited soil water resources as living trees do. This indicates there was not an immediate benefit to trees of having reduced transpiration and greater soil moisture due to adjacent, prior-year tree mortality within their neighborhood. Additionally, this suggests that microclimate may have been more important than tree vigor as a limiting factor for P_{JPB} when the severe drought conditions were ongoing during the epidemic phase. This could be because the residual trees with adjacent mortality needed more time and/or a sufficiently wet period to be able to respond to increased resources made available by adjacent tree mortality (Oliver and Larson 1990).

Topographic position

The JPB outbreak started and caused the greatest cumulative mortality within trees located in a low-elevation, toeslope topographic position. Jeffrey pines likely experienced physiological drought stress earlier than within toeslopes relative to higher elevation mid and shoulder slopes as soil water availability typically increases with elevation (Adams and Kolb 2004). Outbreak initiations for other bark beetles, such as the MPB, are similar and often start in relatively dry areas such as on south-facing slopes or within canyons, gullies, and valley bottoms that have high water table fluctuations (Safranyik and Carroll 2006; de la Giroday et al. 2011; Kaiser et al. 2013). After the incipient and transition to epidemic phase occurred from 1991 to 1992, JPBs spread out to attack trees within all topographic positions through the epidemic phase from 1993 to 1994. When the outbreak transitioned to a post-epidemic phase in 1995, mortality declined within toeslopes while mass-attacks continued at similar rates within mid and shoulder slopes. This is likely due to two factors: (1) majority of the small-diameter tree hosts, which were preferred throughout the post-epidemic phase, were exhausted within toeslope locations during the incipient and epidemic phases and (2) by 1995 toeslope stand density values were reduced below thresholds associated with ponderosa and Jeffrey pine stand resilience to beetle-attack that were discussed previously within the forest density section (see Table 1).

Proximity to nearest brood tree

The proximity to beetle source populations, gauged by the minimum linear distance to nearest brood tree, was one of the most important variables that influenced P_{JPB} during all phases of this outbreak. This variable was assessed as it approximates typical JPB dispersal distances. In 1992, two-thirds of JPB mass-attacked trees were located in close proximity to brood trees. During this year, beetles also dispersed to new locations as over one-third of all new attacks exceeded 50 m to the closest brood tree. Dispersal distances became progressively closer to brood trees during epidemic phase of the outbreak as self-focusing dynamics occurred. During this phase, dispersal was minimal as nearest neighbor to a brood tree were typically colonized and 92–96 % of all attacked trees were within 30 m of a brood tree. The gradual reduction in dispersal distances through time occurred as JPB-caused tree mortality increased and cumulative drought effects likely enhanced physiological stress to reduce the defensive capacity susceptibility of neighboring host trees, including those of mid and large-diameter stems discussed in the stem diameter section. Colonization of adjacent trees is beneficial to bark beetles as it minimizes search time in hostile environment while flight dispersal is a risky endeavor in which it is not uncommon for 75–85 % of searching adults to fail to find a suitable host tree for colonization and reproduction (Miller and Keen 1960; Byers 1996). When the outbreak transitioned to a post-epidemic phase, the drought period ended and dispersal increased slightly as only 80 % of attacked trees were within 30 m of a brood tree. This is likely because Jeffrey pines, especially large-diameter stems, had increased resilience to mass-attack and JPBs had to fly further to find the fewer patches of susceptible small and mid-diameter tree cohorts to colonize. Interestingly, during all outbreak years, there were consistently small percentages of attacked-trees that were not in close proximity to brood trees. This indicates a small degree of dispersal for a small segment of JPB populations occurred during all phases of this outbreak.

In all phases of this outbreak, JPB mass-attacks were more likely as the distance from nearest brood tree decreased. A dispersal threshold indicated this negative relationship occurred within the nearest brood trees were within 50 m while beyond that distance proximity to brood trees had no discernible influence on JPB-attack. Similar dispersal distances have been reported in mature lodgepole pine forests during MPB epidemics where most beetle-attacked trees were within 50 m, and often less than 30 m, from brood trees (Safranyik et al. 1992; Robertson et al.

2007). Additionally, our results indicate that as this JPB outbreak progressed from incipient to epidemic phase, the spatial proximity of attacks to the nearest brood tree substantially decreased. Similar results were found comparing outbreak phases of an *Ips typographus* outbreak in Germany when spatial proximity between yearly attacks increased between distinct incipient and epidemic phases (Kautz et al. 2011).

Bark beetle population pressure

Bark beetle population pressure has long been identified as one of the most important variables influencing subsequent-year bark beetle mass-attack and tree mortality (Shore and Safranyik 1992). This statistic represents the magnitude of challenge exerted by beetle populations upon a host tree based on the amount of infested basal area within an immediate spatial neighborhood. JPB population pressure was one of the best predictors during all outbreak phases and the smaller neighborhoods, such as 0.1 ha, explained greater variation in P_{JPB} than larger neighborhoods for most outbreak years. A significant threshold effect was found that indicates neighborhoods with no JPB population pressure had consistently low P_{JPB} while the chances of mass-attack increased, in a linear fashion, based on the degree of beetle pressure. The influence of JPB population pressure on JPB-attack was greatest during the 'boom' year when the outbreak transitioned to an epidemic phase then declined slightly through the subsequent epidemic years. This relationship was significant, although the effect was weaker, when the outbreak transitioned into a post-epidemic phase as beetles dispersed further to find susceptible host trees.

Spatial pattern of infestations

Quantifications of the degree of clustering, along with information on whether mortality rates are increasing or decreasing, are important as they provided the best means of identifying the various phases of this JPB outbreak. JPB-attack aggregations led to tree mortality infestations that contained substantial more trees in the epidemic phase relative to the incipient and post-epidemic phases. Similar results have been documented with *I. acuminatus* (Gyllenhal) outbreak within Scots pine (*P. sylvestris*) forests in the southeastern Italian Alps where infestations were highly aggregated at populations levels during an epidemic phases and infestations were either weakly aggregated or randomly dispersed when populations were low or declining (i.e., incipient or post-epidemic phases) (Colombari et al. 2012). Infestation clustering by outbreak phase for other bark beetle species, at a tree-level spatial scale, is generally unstudied to-date.

The temporal dynamics of whether JPB infestations grew to have spatially adjacent trees mass-attacked the subsequent year yield important information on group dynamics over time. Following the incipient phase in 1991, smaller infestations tended to stop growing in the following year while larger infestations continued to get larger, and often grew together to coalesce, as a self-focusing occurred in conjunction with increases in JPB mass-attacked trees.

Smaller infestations failing to grow with mass-attacked adjacent stems the following year can be explained by three potential hypotheses: (1) beetle populations within the small infestations had a high degree of developing brood mortality due to environmental conditions associated with the small clusters and did not produce sufficient emerging beetles to attack adjacent stems. While possible, we find this explanation unlikely to produce consistent brood mortality across small infestations that were spatially widespread throughout the study area in a manner that was temporally robust through the various outbreak phases. (2) The more likely hypothesis is that beetles emerging from small infestations were drawn to high concentrations of aggregation pheromones and joined the emergent beetles near large clusters as adjacent host material was mass-attacked. Thus, creating a multi-temporal, positive feedback loop that enhanced cluster size as beetle populations amplified and self-focused in those locations where prior and current year's JPB populations were successful at finding and exploiting susceptible host material. The biological mechanism promoting this feedback loop is likely regulated by higher concentrations of aggregation pheromones (Strom et al. 2013) being eluded from large clusters mass-attacked by JPBs that, in turn, lure additional JPBs to that location. (3) Another possible mechanism, which is not in conflict with the second hypothesis, may also promote this self-focusing behavior and is related to the extended time period that can range up to 3 months in which JPB flight occurs after emergence from nurse trees (Strom et al. 2013). During this period, the larger clusters of mass-attacked trees, which have greater absolute numbers of emerging beetles, may have a greater amounts of pioneer beetles emerging earlier in the flight season when there are not any aggregation pheromone plumes to showcase the locations of susceptible trees that have previously been identified. Moreover, if beetles from large clusters emerge early to successfully find and colonize adjacent host trees, then their aggregation pheromones may draw in beetles from distant, smaller clusters where beetles emerge later in the season into an environment rich with pheromones providing information on susceptible tree locations.

Regardless of the underlying biological mechanism, large infestations that averaged 20 stems per cluster across all outbreak years typically expanded and those that

declined were generally small infestations that averaged five stems per cluster. This suggests that a multi-temporal, quorum group decision-making process occurred through all outbreak years in a manner similar to that which regulates facets of social insect community behavior (Deneubourg and Goss 1989). Other insect species that exhibit this behavior, albeit at a shorter time scale, include ants and honey bees foraging for food or choosing new colony locations (Franks 1989; Riley et al. 2005). Benefits of this multi-temporal quorum collective decision making process for JPBs includes enhancing successful host colonization by reducing search time for susceptible host material in a hostile environment while decreasing the possibility of unsuccessful host attacks and resulting beetle mortality. This represents a type of swarm intelligence, where lower-level biological mechanisms of individual JPBs interact to enhance higher-level group decisions and reproductive success by directing the spatial orientation of emergent beetle populations to locations where the likelihood of successfully finding and exploiting scarce host material is increased (Bonabeau et al. 1999).

The temporal dynamics of newly formed spot infestations that do not originate from spatial growth of prior year's infestations yield further information on JPB dispersal patterns. During all outbreak phases, even in 1994 at the height of the epidemic when self-focusing peaked, up to 20 % of all infestations occurred in new locations that were at least 50 m from the nearest brood trees. This indicates that while the quorum decision making process facilitated the multi-temporal spatial clustering of attacks and progressive self-focusing during all phases of the outbreak, a small proportion of beetles also dispersed to new areas to find susceptible host trees and create new spot infestations during all outbreak phases. This plasticity in dispersal behavior likely benefits the adaptive capacity to respond to environmental changes that influence host susceptibility, such as drought, and change during the course of an outbreak. This plasticity would also be especially beneficial in mixed-species forested environments where the spatial distance to potential Jeffrey pine hosts can vary substantially.

Summary

The driving factors that influenced P_{JPB} varied throughout the phases of this outbreak and were similar to those described previously for MPBs (White and Powell 1997). The incipient phase of the outbreak was characterized by an 'environmental determinism' during a drought period when topographic slope position, forest density, and location of small-diameter stems influenced P_{JPB}. Less than one percent of all trees within the study area were attacked during this phase and the most explanatory individual variables explained minimal amounts of model error. This raises doubts about the potential to accurately predict exactly which trees will have successful JPB-attacks during the incipient phase of an outbreak.

As numbers of JPB mass-attacked trees increased, the pattern of mortality progressively self-focused spatially during the epidemic phase. This phase was characterized by 'dynamic-determinism' in which beetle populations (represented by population pressure and proximity to brood tree variables) became the driving factors influencing P_{JPB}. These individual variables reduced model error to where tree-level mortality predictions appear reasonable. The variable that explained the most variation in P_{JPB} after the beetle-related variables was forest density. Interestingly, the spatial dynamics of JPB colonization switched to immediately adjacent stems during the epidemic phase when stem diameter, a reasonable proxy for tree vigor, had minimal importance in predicting P_{JPB}. This, along with the best variable that represented forest density incorporating both live and dead stems, suggests the reason forest density was important in influencing P_{JPB} progressively shifted from being associated with host defensive capacity during the incipient phase to a direct influence on microclimate and bark beetle habitat suitability during the epidemic phase when defensive capacity was reduced. This is an important result indicating fine-scale forest density management may reduce the probability of JPB or other bark beetle attack in western yellow pine systems during epidemic outbreak phases when majority of tree mortality occurs, even if host defensive capacity is limited.

During the post-epidemic phase, the driving factor for mortality transitioned back to 'environmental determinism' as JPBs dispersed further and mortality was limited by occurrence of susceptible, small and mid-sized diameter host trees that were located in densely forested neighborhoods. Individual predictor variables explained little variation in P_{JPB}, especially during 1995 when populations transitioned from an epidemic to post-epidemic phase. Thus, the potential for accurately modeling tree-level mortality is questionable during this post-epidemic phase as it was with the incipient phase.

To-date, no other studies have documented JPB, or other bark beetle, mortality patterns with precise tree-level spatial measurements through all temporal phases of an outbreak. However, similar findings have been reported with a remote-sensing derived landscape-scale assessment of MPB activity in lodgepole pine forests of northern Colorado (Walter and Platt 2013). Within this study area, the best mortality predictors changed throughout the outbreak from 'environmental determinism' during the incipient population phase, to 'dynamic determinism' driven by beetle pressure during peak epidemic years, and to host availability in post-epidemic years. Our findings are

consistent with the important factors identified for the lodgepole pine system during incipient and epidemic JPB population phases; however, we emphasize that host availability alone does not adequately describe post-epidemic conditions that occurred within this JPB outbreak. Rather, it was the availability of *susceptible* host trees, namely those that were small to mid-size in diameter and located in dense neighborhoods, which drove the location of JPB-caused mortality in post-epidemic years.

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