

The relative importance of tree and stand properties in susceptibility to spruce beetle outbreak in the mid-20th century

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Abstract. Tree susceptibility to potentially lethal agents is determined not only by attributes of individual trees, but also by neighborhood effects at a range of scales. For example, effects of disturbances on individual trees are often contingent on the size, configuration, and other properties of neighboring trees. Wildfires can modify postfire properties of individual trees as well as of entire forest stands, both of which can affect subsequent ecological processes, including subsequent disturbances. In recent years, much has been learned about how disturbances interact, but numerous questions concerning underlying mechanisms remain unresolved. For example, the relative importance of forest properties at different spatial scales in determining how fires affect forest susceptibility to subsequent disturbances is not well understood. This study explicitly compares the relative importance of tree vs. fine-scale neighborhood effects (e.g., stand properties at <7 m radii), on susceptibility to a 1940s' spruce beetle outbreak. Attributes of individual trees and of stand structure were spatially reconstructed at five 250-m² sites that were partly burned in the late 19th century and then affected by spruce beetle outbreak in the 1940s. Random Forest models and classification trees were used to compare the relative importance of variables for susceptibility to spruce beetle attack. Individual tree properties (diameter at breast height and age) were the most important predictors of susceptibility to the outbreak across all sites combined and at each of the sites individually. In contrast, neighborhood effects were poor predictors of susceptibility. This study suggests wildfires reduce susceptibility to outbreaks primarily by reducing the size of postfire live trees and only secondarily by modifying stand structure. One implication of this is that management strategies that aim to modify stand structure over large areas in order to reduce susceptibility to spruce beetle outbreaks may be unnecessarily intensive.

Key words: *Abies lasiocarpa*; *Dendroctonus rufipennis*; disturbance interactions; linked disturbances; *Picea engelmannii*; subalpine forests.

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INTRODUCTION

Tree susceptibility to potentially lethal agents is determined not only by attributes of individual trees, but also by neighborhood effects at a range of spatial scales (Das et al. 2008). Even the effect of natural disturbances on individual trees is often contingent on the size, configuration, and other properties of neighboring trees. For

example, the likelihood of a tree being killed by a fire depends in part on the flammability of surrounding vegetation (Bond and Midgley 1995). During windstorms, trees may be killed by the fall of neighboring trees, as well as the direct force of wind (Das et al. 2008). Likewise, susceptibility to insect attack can be a function of not only the properties of the target tree, but also of its neighborhood (Schmid and Frye 1976, Schenk

et al. 1977, 1980). One of the most important disturbances in western North America is wildfire, which can affect subsequent disturbances by modifying postfire properties of individual trees as well postfire stand structure. Here, we examine the relative importance of tree vs. neighborhood stand attributes in mediating interactions between severe fires and subsequent outbreaks of spruce beetle (*Dendroctonus rufipennis*) in Colorado.

The most important disturbances in the subalpine forests of Colorado include fire, insect, and wind disturbances (Baker and Veblen 1990, Peet 2000). These forests are dominated by Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa* Hook. Nutt.), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), and quaking aspen (*Populus tremuloides* Michx.) (Peet 2000, Veblen 2000). Fires are primarily large, infrequent, and severe, and generally occur during extremely dry years (Rebertus et al. 1992, Peet 2000, Veblen 2000). As a result, the subalpine landscape is a mosaic of stands of varying ages and compositions, with the precise structure of each stand depending on its particular disturbance history and biophysical setting. Recently burned stands tend to be even aged, and become more heterogeneous over decades to centuries (Veblen 1986). While low-severity surface fires can occur in these forest ecosystems, they are rare and have a relatively minor effect on composition and structure (Kipfmüller and Baker 2000, Sibold et al. 2006). Outbreaks of spruce beetle have been important in shaping these forests for centuries or longer and significantly change tree size, structure, density, and species composition (Baker and Veblen 1990, Veblen et al. 1991a). For example, a severe and extensive outbreak in the late 1940s killed >50% of the large Engelmann spruce in Grand Mesa National Forest and >90% in White River National Forest in northwestern Colorado (Schmid and Hinds 1974). This outbreak was most severe in the Flat Tops Wilderness of White River National Forest in northwestern Colorado where an estimated 99% of the overstory spruce were killed over an area of 2700 km² (Cahill 1951).

Outbreaks of bark beetles are affected by patterns and processes that span biological levels and broad spatiotemporal scales, from the scale of phloem to individual trees, small patches (<7 m), forest stands (> few hectares), and landscapes

(100s or 1000s of hectares) (Powers et al. 1999; Raffa et al. 2008). The latter two scales may be important in allowing large populations of beetles to develop and maintain a sustained high beetle pressure (Raffa et al. 2008), whereas the former may be important in determining fine-scale patterns of outbreaks (Jenkins et al. 2014).

Previous studies have shown coarse-resolution spatial associations that highlighted how stand-replacing fires reduced susceptibility to spruce beetle outbreaks at stand and landscape scales during the 19th (Kulakowski and Veblen 2006) and 20th centuries (Veblen et al. 1994, Bebi et al. 2003, Kulakowski et al. 2003). In contrast, stand-replacing fires that occurred >100 yr ago did not strongly influence stand structural traits that determined susceptibility to outbreak in the early 21st century (Hart et al. 2014b). This apparent decoupling may be due to a threshold in stand age, beyond which stand structure no longer determines susceptibility to outbreak. Or, it may be due to climatically driven increases in intensity of outbreaks that may diminish the importance of tree and stand attributes in determining susceptibility (Hart et al. 2014b). Warm and dry conditions promote larger beetle populations (Bentz et al. 2010) and also decrease tree resistance to beetle attack (Mattson and Haack 1987, Hart et al. 2014a), which together can relax constraints on beetle outbreaks. This possibility is consistent with the observation that numerous small-diameter trees were affected by spruce beetle in the early 21st century outbreak prior to any eventual host saturation, suggesting that tree-level constraints were not as important as in previous outbreaks (Hart et al. 2014b).

The mechanisms by which forest structure can affect susceptibility to outbreaks can be related to properties of individual trees (e.g., size) as well as neighborhood effects (e.g., basal area, stem density, or species composition immediately surrounding the target tree; Schmid and Frye 1977). At the scale of the individual tree, spruce beetles preferentially attack large-diameter trees because thicker bark provides protection for beetle larvae from cold winter temperatures and larger trees provide a higher volume of nutritional phloem, which increases survival rates of the beetle larvae (McCambridge and Knight 1972, Dymerski et al. 2001, Hart et al. 2014b). Slow growth due to stress resulting from limited resources is also

likely to increase an individual tree's susceptibility to attack (Hard 1985).

Stand-scale characteristics, including structural heterogeneity and basal area, also affect susceptibility to spruce beetle outbreaks (Schmid and Frye 1977, Fettig et al. 2007). For instance, a higher total stand basal area has been interpreted to be an indicator of higher competition and tree stress (Schmid and Frye 1977, Hodgkinson et al. 2015), which may contribute to an increased susceptibility to attack as SB preferentially attack stressed trees. Despite the importance of spatial variability of stand structure as a potential influence on outbreak dynamics, within-patch variability of the severity of outbreaks is rarely reconstructed or studied, especially for larger outbreaks where remotely sensed data of the perimeters of outbreaks (e.g., aerial detection surveys) are commonly used.

While both tree and stand characteristics have been shown to affect susceptibility to outbreaks, the relative importance of variability at these two spatial scales is not well understood. A recent study by Hart et al. (2014b) showed that the spruce beetle outbreak in the early 2000s in Grand Mesa National Forest in Colorado was influenced by characteristics of individual trees, but not by topographic variables or stand structure. However, these relationships have not been considered in the context of previous outbreaks, including the 1940s' extreme outbreak in northwestern Colorado on which we focus in this study. Furthermore, to date no study has explicitly quantified fine-scale spatial variability of tree and neighborhood attributes to reveal the mechanisms that may explain tree susceptibility to spruce beetle attack. Understanding these relationships is important not only for better understanding how fires mediate susceptibility to outbreaks, but also for improved management in the face of future spruce beetle outbreaks.

Management strategies associated with bark beetle outbreaks typically aim to increase either resilience (increasing the ability of a stand to regenerate following a disturbance) or resistance (decreasing the susceptibility of a stand to a disturbance; DeRose and Long 2014). Strategies aimed at increasing stand resistance to beetle attacks through manipulating stand composition and structure often utilize partial cuts or forest thinning (Alexander 1986, Fettig et al. 2007,

Jenkins et al. 2008, DeRose and Long 2014; Temperli et al. 2014), in part to increase spruce vigor (Fettig et al. 2007). However, as trees continue to grow, these strategies only prolong the time at which the stand becomes susceptible to an outbreak and may not be effective during extreme outbreaks during which most trees are killed by beetles (Fettig et al. 2007, DeRose and Long 2014). Alternatively, management strategies may aim to promote stand resilience by facilitating postoutbreak establishment of spruce, especially in stands with high hazard ratings (Schmid and Frye 1977; DeRose and Long 2014). Underlying management strategies of increasing both resistance and resilience are questions of whether tree or stand attributes are most important in determining susceptibility to outbreaks.

The goal of this study was to explicitly compare the relative importance of tree vs. neighborhood effects (e.g., stand properties at <7 m radii from potential host trees), as determined by fire history, in determining susceptibility to a 1940s' spruce beetle outbreak. Specific objectives were to: (1) reconstruct fine-scale variability of severity of the 1940s' spruce beetle outbreak, (2) investigate the relationships between fine-scale spatial variability of vegetation (which was partly shaped by preoutbreak fire history) and susceptibility to the 1940s' outbreak, and (3) determine the relative importance of tree and neighborhood effects in predicting susceptibility to future spruce beetle outbreaks.

METHODS

Study area

The study area (107°15' W, 40°00' N; Fig. 1) is located in White River National Forest in northwestern Colorado. Sampled sites range in elevation from 2600 to 3200 m above sea level and are dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) with some lodgepole pine (*Pinus contorta*). The closest climate station with data extending back to the period of the 1940s' outbreak is in Meeker, Colorado, and is located at 1902 m a.s.l. Mean January temperature was -6.8°C, mean July temperature was 19.1°C, and mean total annual precipitation was 416 mm between 1941 and 1950. This area was affected by stand-replacing fires in the early 18th century (Kulakowski et al. 2003)

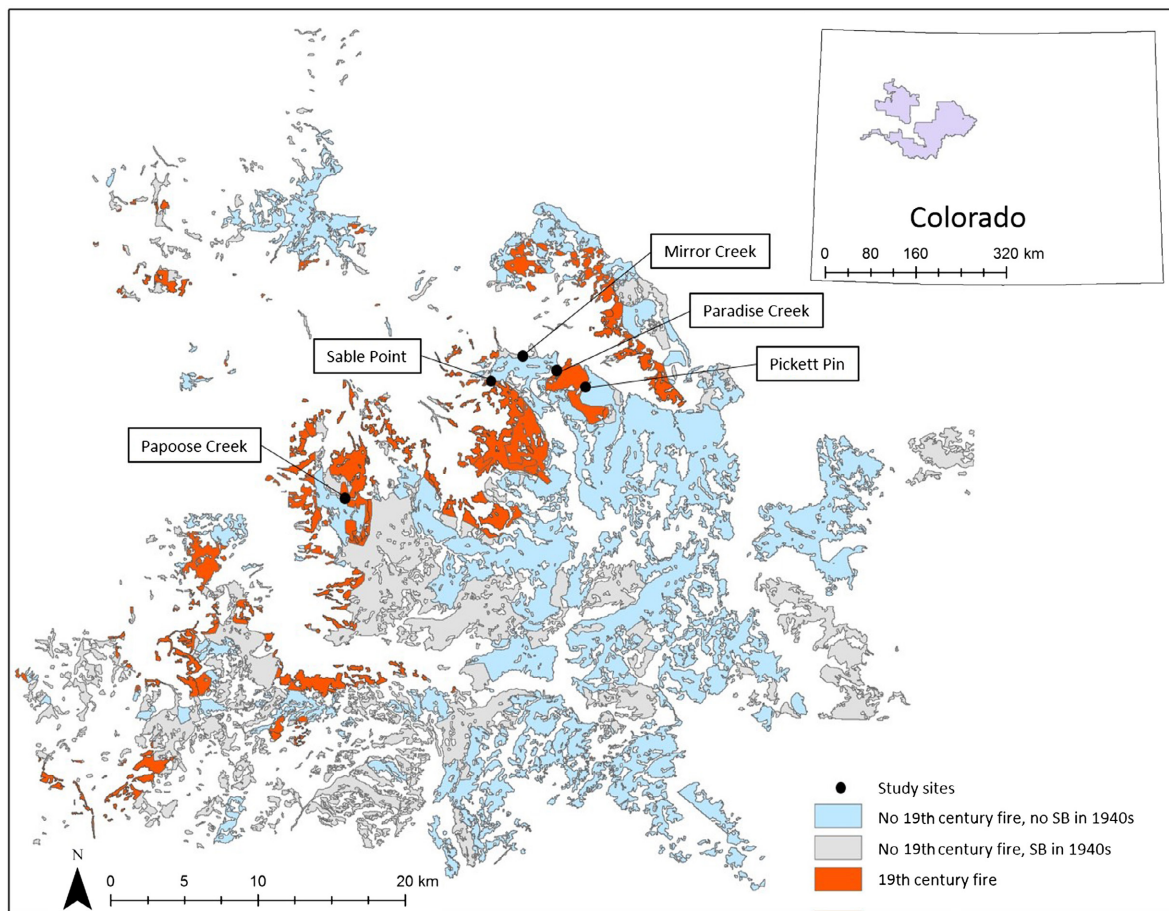


Fig. 1. Location of study sites and extent of 19th century fires and 1940s' outbreak based on Kulakowski et al. (2003) and Bebi et al. (2003).

and then by patchy, severe fires in the late 19th century (Bebi et al. 2003, Kulakowski et al. 2003). In the 1940s, this area was affected by a severe spruce beetle (*D. rufipennis*) outbreak that overlapped with previously mapped fires (Bebi et al. 2003, Kulakowski et al. 2003).

Field sampling was conducted in June and July of 2001 at five study sites near the border of the late 19th century fires and within the area of the 1940s' outbreak based on previous mapping of disturbances (Fig. 1; Kulakowski et al. 2003, Bebi et al. 2003). At each site, one 50 m × 50 m plot was established in a restricted random location that, based on field reconnaissance, appeared to cross the border of 19th century fires and the 1940s' outbreak. The purpose of selecting sites in this manner was to capture variation in the effects of fires that would allow us to examine how stand

structure, as shaped by previous fires, affected susceptibility to outbreaks at fine spatial scales. In each plot, we recorded the following data for all stems ≥ 4 cm dbh (diameter at breast height): location within each plot (x , y coordinate), species, dbh, and status (live or dead). Dendroecological methods followed other studies that have successfully reconstructed tree mortality dates (Mast and Veblen 1994) and outbreaks of spruce beetles in this region (Veblen et al. 1991b, 1994, Kulakowski et al. 2003). Increment cores were systematically collected from every third tree in each plot, resulting in a total of 145–263 cores per plot to determine dates of establishment, mortality, and growth releases. Cores were extracted as close to the ground and the pith as was possible from trees that were alive and dead, standing, and fallen. If a tree was too decomposed to yield

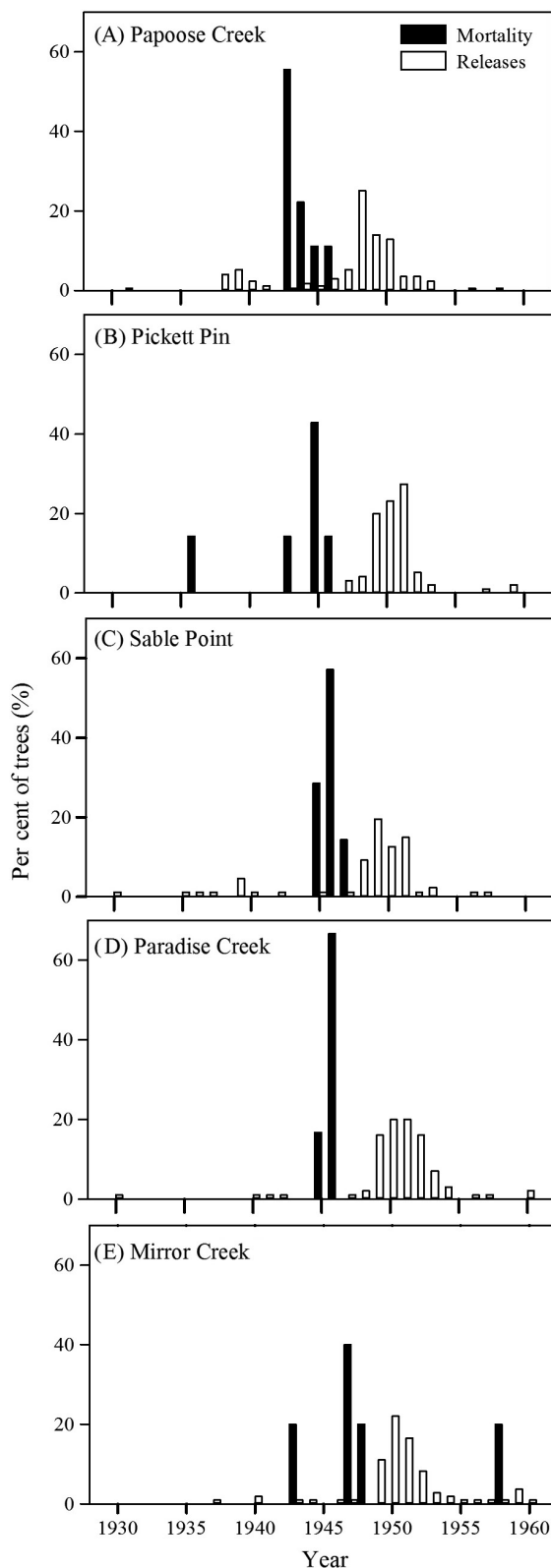


Fig. 2. Proportion of tree mortality (black bars) and growth releases defined as an abrupt increase in ring width (white bars) of sampled cores for each corresponding site. Peak outbreak year is represented by each largest sample percentage of mortality year. (A) Peak 1943, $N_{\text{mortality}} = 9$, $N_{\text{release}} = 171$; (B) Peak 1945, $N_{\text{mortality}} = 7$, $N_{\text{release}} = 95$; (C) Peak 1946, $N_{\text{mortality}} = 7$, $N_{\text{release}} = 6$; (D) Peak 1946, $N_{\text{mortality}} = 5$, $N_{\text{release}} = 100$; (E) Peak 1947, $N_{\text{mortality}} = 5$, $N_{\text{release}} = 109$.

a sound core sample, then a core was collected from the closest neighboring tree which was of the same status (live or dead), same species, and similar diameter. All cores were processed, measured, and cross-dated using standard dendroecological methods (Stokes and Smiley 1968, Grissino-Mayer 2001). In the event that the increment core sample missed the pith, a simple geometric model was used to estimate the number of rings to the pith (Duncan, 1989). This method was used to estimate up to a maximum of 20 missing years to the pith. Cores that missed the pith by >20 yr were counted as minimum ages. Tree age is reported as age at coring height and is interpreted to be an approximation of year of establishment. Because increment cores were taken near the ground, it is unlikely that the discrepancy between actual tree age and its age at coring height would be a large (e.g., <20 yr) source of error (Veblen et al. 1991b, Kulakowski and Veblen 2002). Dates of mortality are based on the last complete year of growth. Growth releases were defined as >200% increase in ring width sustained for >10 yr.

Individual tree attributes

For each stand, the peak year of spruce beetle attack was based on the mode year of mortality of Engelmann spruce as determined from cores taken at each site (Fig. 2). For live trees from which increment cores were collected, dbh during the peak of the outbreak was estimated by:

$$\text{dbh}_{\text{op}} = \text{dbh}_{2001} - 2(r_{2001} - r_{\text{op}})$$

where dbh_{op} is dbh at the outbreak peak, dbh_{2001} is dbh in 2001, and $(r_{2001} - r_{\text{op}})$ is the difference in radial growth, as determined by increment core samples, between 2001 and the year of the outbreak peak. Bark thickness was assumed to have

remained constant. Within each site, the relationship between dbh in 2001 and the change in dbh between the peak outbreak year and 2001 was determined using linear regression. Linear regression equations for the host species, Engelmann spruce, were calculated separately from nonhost species (subalpine fir and lodgepole pine) at each site separately. Using the resulting regression equations, dbh in the year of peak attack was estimated for each live tree from which increment cores were not collected.

The sample size for cores from live trees ≥ 35 cm dbh was low due to a scarcity of live trees > 35 cm dbh at the time of sampling, which was due to the extensive mortality of large trees during the 1940s' SB outbreak. In order to address this, a data set from similar forests located in the Flat Tops Wilderness of White River National Forest (Kulakowski et al. 2003) was used to estimate dbh of trees ≥ 35 cm in the mid-1940s. From that data set, collected in 2000, ring widths of 50 cores from randomly selected Engelmann spruce and subalpine fir ≥ 35 cm dbh were measured between the peak year of outbreak across sites and 2000. This ring-width measurement represents the change in tree radius and was used to represent the change in tree dbh. These average changes were then applied to all live trees ≥ 35 cm dbh in each site to estimate dbh at the time of the outbreak.

For all dead spruce trees in each plot (dbh 4–75 cm), dbh in 2001 was interpreted to be dbh at the time of attack as previous work has found that during the 1940s' outbreak $> 90\%$ of canopy size Engelmann spruce were killed (Hinds et al. 1965, Schmid and Hinds 1974) and that in our study region of White River National Forest an estimated 99% of the overstory spruce were killed (Cahill 1951). Cross-dating of the outermost ring on dead trees in this study indicates that the smallest Engelmann spruce killed during the 1940s' outbreak was 11 cm dbh. As a result, dead Engelmann spruce < 11 cm dbh were considered to have died due to causes other than spruce beetle (not spruce beetle killed; NSBK) for the remainder of the analysis. Finally, for each individual tree, basal area was calculated using the estimated dbh at the time of attack peak. For all live trees from which cores were collected, age at peak outbreak was calculated by subtracting the difference between 2001 and outbreak year. For all dead trees from which cores were collected,

approximate age was determined by subtracting cross-dated innermost year (i.e., approximate date of establishment) from outermost year (i.e., approximate year of mortality).

Vegetation attributes of patches (<7 m radius)

For each site separately, neighborhood properties within a 3, 5, and 7 m radii surrounding each Engelmann spruce tree were calculated using ArcGIS 10.1 (ESRI, 2011): stem density, sum of surrounding tree dbh, average surrounding tree dbh, sum of surrounding tree basal area, and average of surrounding tree basal area. These properties did not include the target tree itself. Each variable was calculated for just the surrounding host species (Engelmann spruce) and also for all surrounding trees (both host and nonhost species). Edge effects were accounted for using an area-based edge effect correction, by which the potential number of observations outside of the study plot but within a circle around a point in the study area is statistically determined using a ratio of the number of observations within the circle to the area of the circle contained within the study area (Getis and Franklin 1987, Dale and Powell 2001). This method maintains a larger sample size by making full use of the recorded data. As very few spruce trees died in the years prior to the outbreak and no evidence of any large wind disturbance (e.g., uprooted logs oriented in the same direction) was observed in the field, fallen logs were not used as an independent variable in the present research design.

Statistical analysis

Outbreak severity was calculated for each individual site and for all sites collectively at two thresholds: (1) the percentage of Engelmann spruce ≥ 11 cm dbh killed and (2) the dbh above which 100% of spruce trees were killed in the outbreak. A threshold of ≥ 11 cm dbh was chosen because cross-dating results from this study indicate that the smallest Engelmann spruce killed during the 1940s' outbreak was 11 cm dbh.

A Welch's *t* test was used to compare tree and neighborhood properties between spruce that had and had not been killed during the outbreak. Because many variables were highly correlated (Appendix S1: Table S1), to avoid redundancy only dbh and age of the target tree,

and local vegetation properties within 3 m were used in the paired-samples *t* test. Additionally, to assess the relative importance of individual tree attribute and neighborhood variables on the susceptibility of Engelmann spruce to spruce beetle attack, we used a two-step combination of Random Forest (RF) models and subsequent classification trees based on RF output. These methods are effective in revealing hierarchical and nonlinear relationships among variables, deal well with highly correlated variables, and do not require assumptions of normal distribution (Breiman et al. 1984, De'ath and Fabricius 2000, Maindonald and Braun 2010). Random Forest models use a large number of potential trees to provide a list ranking the importance of explanatory variables, and are a valuable tool in combination with classical classification trees, which make complex relationships among variables easier to interpret (Maindonald and Braun 2010). However, RF models cannot be used on data sets with missing data (Breiman et al. 1984).

Random Forest models were built by including (1) all predictor variables (excluding tree age) for all sites, (2) all predictor variables (excluding tree age) for each individual site, (3) only neighborhood variables for all sites, and (4) only neighborhood variables for each individual site. Age data were only available for about one in five spruce trees because cores were only collected from a subset of the trees and because we were not able to effectively estimate age for dead spruce due to insignificant relationships between dbh and age. Consequently, a separate full RF model was built by including all predictor variables for all sites but only for the subset of individuals for which age data were available. Ten runs of 1000 trees were independently grown using RF. The increase in mean square error for exclusion and the mean decrease in gini of each variable were averaged across runs, providing a rank list of variable importance. For the three RF runs based on data from all sites collectively, the top 10 variables that improved model fit were added to the full classification trees. Classification trees were then trimmed to avoid overfitting, minimizing cross-validated error by removing splits exceeding the complexity parameter (Maindonald and Braun 2010). All statistical analyses were performed in R (R Core Team, 2014).

RESULTS

All five study sites were characterized by age structures consistent with stands that established several hundred years ago and that were partially burned in severe fires in the late 19th century (Fig. 3). Patchy vs. diffuse spatial distributions of similarly aged trees suggest that in some cases the fires of the 19th century severely burned part of the plot, but in other cases, the fires may have had a more diffuse effect across a larger area. Both patterns can be expected at the perimeters of high severity fires. The oldest trees at each site established in the 1600s or 1700s. Pulses of establishment during the late 19th century, which were likely the result of widespread fires in this area, ranged in intensity and timing across the five study sites (Fig. 3). Cross-dated dates of mortality for spruce ($n = 42$) ranged from 1900 to 1960. The majority (57.1%) of spruce died in the 1940s, and very few (4.8%) died after the outbreak. Peak mortality in the five study sites ranged between 1943 and 1947 (Fig. 2). Growth releases corresponding to the peak outbreak years occurred between two and seven years after peak tree mortality (Fig. 2). Duration of outbreak as determined by tree mortality and release dates varied among stands and lasted between two and four years (Fig. 4). Outbreak severity, measured as Engelmann spruce ≥ 11 cm that were killed across all sites, was 93%, and ranged from 86% to 99% across individual sites (Table 1). The dbh threshold above which 100% of spruce trees were killed in the outbreak was 26 cm for all sites collectively and ranged from 14 to 26 cm across individual sites (Table 1).

Stem density and total BA (basal area) varied across the three neighborhood scales analyzed (i.e., 3, 5, and 7 m; Appendix S1: Table S2). Mean dbh and age were significantly smaller in trees that survived the attack ($P < 0.01$, Table 2). Mean dbh and basal area of surrounding trees were significantly smaller around trees that survived the outbreak ($P < 0.01$, Table 2). Stem density was significantly higher surrounding trees that survived the attack and lower surrounding dead trees for all radii ($P < 0.01$, Table 2).

In the analysis considering only neighborhood properties of all sites combined, average BA of surrounding spruce trees within 5 m was the most important variable in predicting susceptibility to

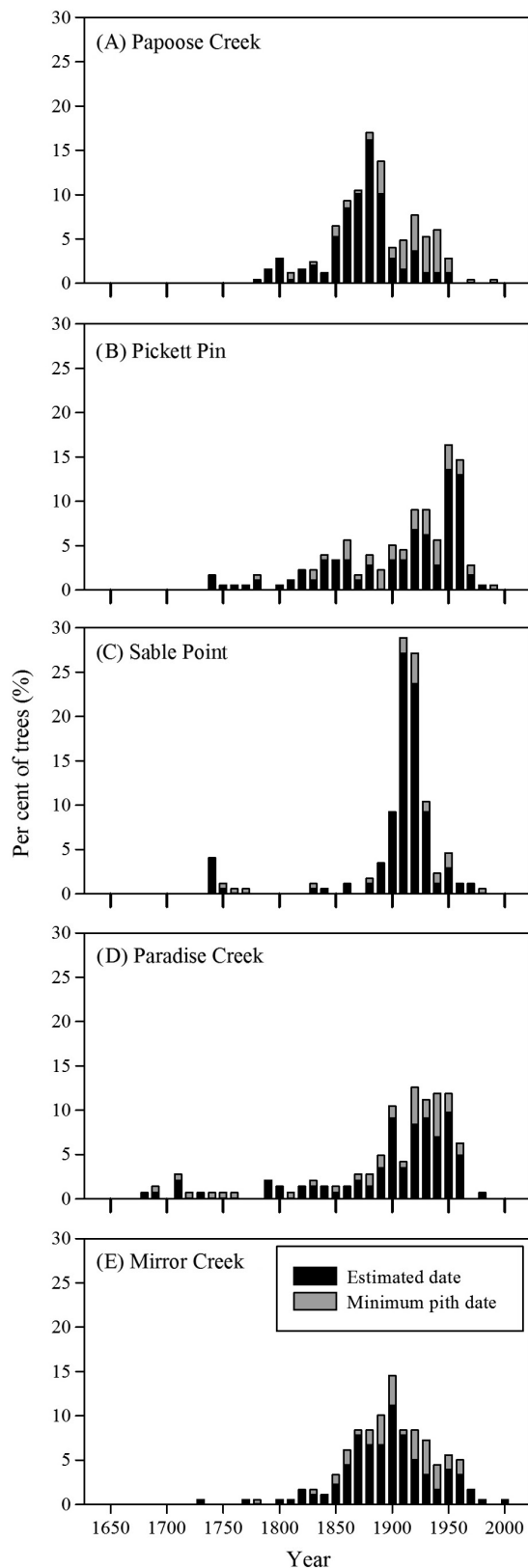


Fig. 3. Percentage of dates of establishment across each site of both live and dead trees. Pith and estimated establishment dates are represented by black bars; minimum pith dates (>20 rings to center) are represented by gray bars. Sample size ranged between sites (A) $N = 247$; (B) $N = 177$; (C) $N = 173$; (D) $N = 143$; (E) $N = 179$.

spruce beetle attack (Fig. 5B). Similarly, for each study site separately, average BA of surrounding spruce trees within 3–7 m was among the two highest ranked explanatory variable in four of five sites (Fig. 5D,F,J,L). However, these neighborhood properties, which included average BA, sum BA, and stem density (each calculated at 3, 5, and 7 m radii for only surrounding spruce trees and all surrounding trees), were poor predictors of susceptibility with RF out-of-bag error rates ranging from 17.1 ± 0.67 to 27 ± 1.25 (Fig. 5B,D,F,H,J,L).

Random Forest models that included individual tree and neighborhood attributes better differentiated spruce trees that survived the outbreak vs. dead trees (Appendix S1: Figs. S1 and S2). Individual tree dbh of target spruce was the most important predictor of susceptibility to beetle attack across all sites combined and for each of the sites individually (Fig. 5A,C,E,G,I,K). In the analysis in which age was included, both age and dbh were important predictors of susceptibility across all sites (Fig. 6), but dbh was more important than age (Figs. 6 and 7).

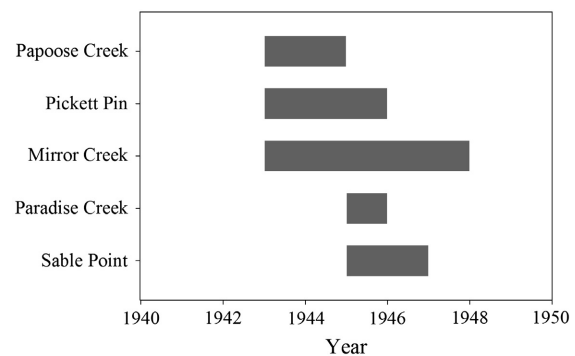


Fig. 4. Range of mortality years corresponding to spruce beetle outbreak for cores sampled at each site (Papoose Creek $n = 5$, Pickett Pin $n = 6$, Mirror Creek $n = 7$, Paradise Creek $n = 7$, Sable Point $n = 9$). Gray boxes encompass a minimum of 80% of samples.

Table 1. Comparison of spruce beetle outbreak severity across all sites collectively and for individual sites.

Site	11 cm (%)	100% (cm)	N
All	93	26	365
Papoose	86	20	56
Paradise	96	14	82
Mirror	93	16	57
Sable	86	26	73
Pickett Pin	99	14	97

Note: Severity was quantified using two measures: (1) percentage of spruce mortality above a 11 cm dbh threshold and (2) the dbh above which 100% spruce mortality occurred.

Out-of-bag error rates for RF models that included all predictor variables ranged from 1.00 ± 0.00 to 3.30 ± 0.51 (Figs. 5A,C,E,G,I,K and 6). Size of the target tree (dbh > 15 cm) was the most important variable predicting susceptibility in the classification tree that included properties of individual trees and neighborhood structure (Fig. 7A). The model misclassification rate based on including individual tree properties was 2.3% vs. the majority misclassification rate of 24.0%; thus, the model reduced misclassification by 21.7%.

Random Forest models that included only neighborhood attributes poorly differentiated spruce trees that survived the outbreak vs. dead trees (Appendix S1: Fig. S1). Average BA of spruce within a 3 m radius was the most important predictor of susceptibility in the classification tree based only on neighborhood variables. Spruce surrounded by other high BA spruce were more susceptible to beetle attack (Fig. 7B). Stem density of spruce within a 3 m radius was the second most important predictor such that

spruce surrounded within 3 m by a higher density of spruce were more susceptible to beetle attack. However, the model misclassification rate based only on neighborhood variables was 14.9% vs. the majority misclassification rate of 24.0%; thus, the model reduced misclassification by only 9.1%.

DISCUSSION

Understanding underlying mechanisms of tree mortality and disturbance interactions requires multiscale research approaches that highlight influences of variables acting at different scales. The unique approach of the present study, which explicitly compared the relative importance of tree vs. fine-scale neighborhood effects, shows that susceptibility to the extensive and severe spruce beetle outbreak in the 1940s was determined primarily by properties of individual trees, and only secondarily by vegetation attributes in radii of 3–7 m surrounding target trees. As the sites in this study were located at the edge of the severe fires of the late 19th century and these locations ranged in patchiness and severity of fire signal (Fig. 3), within-stand variation in tree size is likely the result of past fires. In this context, the current findings are consistent with previous studies that have found that stand-replacing fires reduce susceptibility to subsequent spruce beetle outbreak at stand and landscape scales for at least approximately 70 yr (Veblen et al. 1994, Bebi et al. 2003, Kulakowski et al. 2003, Kulakowski and Veblen 2006) and not longer than approximately 120 yr (Hart et al. 2014a). Our findings build on this previous work

Table 2. Comparison of (mean \pm SE) Engelmann spruce trees which survived the spruce beetle attack ($n = 1042$) and dead Engelmann spruce trees ($n = 339$) for selection of variables.

Variable	Radius (m)	Species included	Dead \bar{x} (\pm SE)	Survived \bar{x} (\pm SE)	Difference of means
dbh	n/a	PE	33.42 (0.58)	3.22 (0.10)	30.20** (0.58)
Age	n/a	PE	169.96 (6.77)	59.33 (2.13)	110.63** (5.72)
Stem density	3	All	0.28 (0.01)	0.34 (0.01)	-0.06** (0.01)
Sum dbh	3	All	65.85 (2.69)	59.56 (1.26)	6.30* (2.97)
Sum BA	3	All	0.13 (0.01)	0.09 (0.00)	0.03** (0.01)
Avg. dbh	3	All	9.35 (0.36)	6.89 (0.16)	2.46** (0.39)
Avg. BA	3	All	0.02 (0.00)	0.01 (0.00)	0.01** (0.00)

Notes: PE is Engelmann spruce (*Picea engelmannii*), All refers to both host and nonhost species combined, and BA is basal area. SEs are in parentheses. Asterisk denotes two-tailed significance to 95% confidence interval in paired-samples *t* test. Two asterisks denote significance to 99% confidence interval.

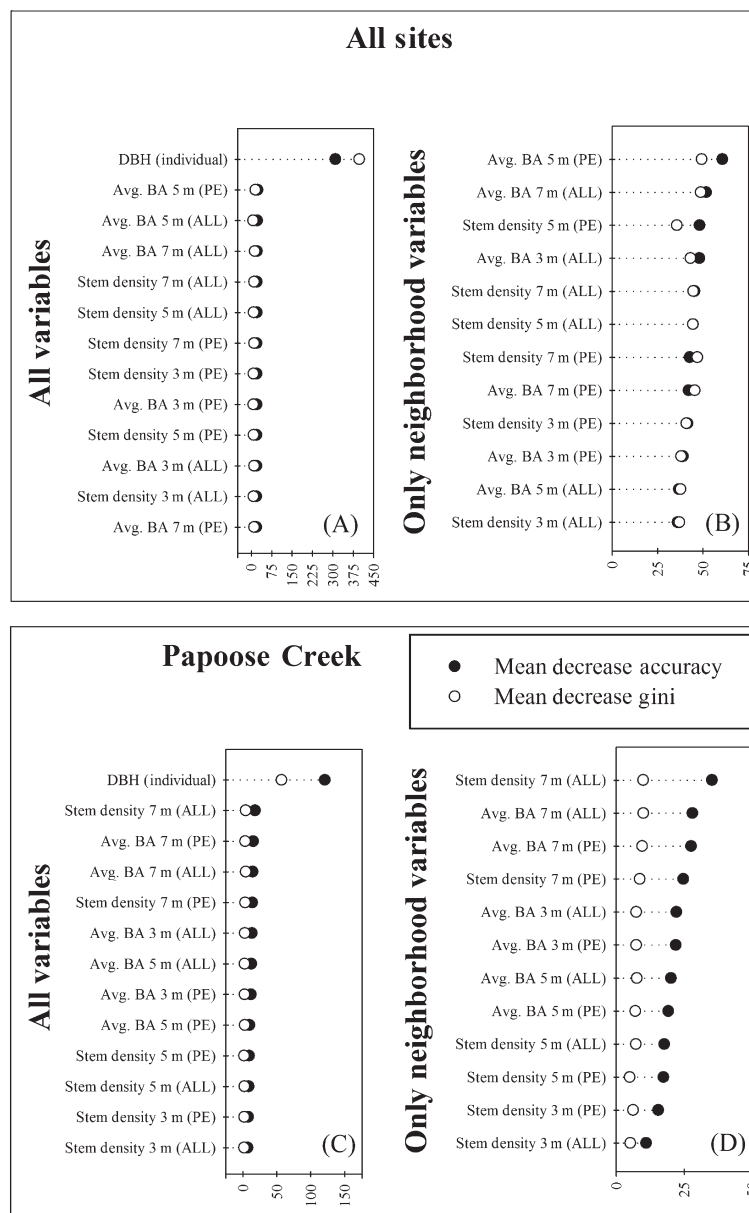


Fig. 5. Output from the classification analysis based on 10 Random Forest runs, indicating the most important variables across all study sites (A, B; $n = 1381$) and individual sites (C–L) for all variables, excluding age (A, C, E, G, I, K), and for only local stand property variables (B, D, F, H, J, L). Black dots represent mean decrease accuracy; white dots represent mean decrease in gini. Spruce trees were divided into two status categories (survived and dead) representing susceptibility to spruce beetle attack. PE is Engelmann spruce (*Picea engelmannii*), ALL refers to both host and nonhost species combined, and BA is basal area. For each of the 10 Random Forest runs, a different training data set was used and the number of potential variables to try at each node was adjusted to reduce each model out-of-bag (OOB) error. Average model OOB was as follows: (A) 2.7 ± 0.34 , (B) 22.3 ± 0.51 , (C) 3.3 ± 0.51 , (D) 17.1 ± 0.67 , (E) 1.0 ± 0 , (F) 25.6 ± 0.68 , (G) 1.3 ± 0 , (H) 22 ± 0.61 , (I) 1.5 ± 0.17 , (J) 27 ± 1.25 , (K) 1.5 ± 0 , (L) 18.7 ± 0.69 .

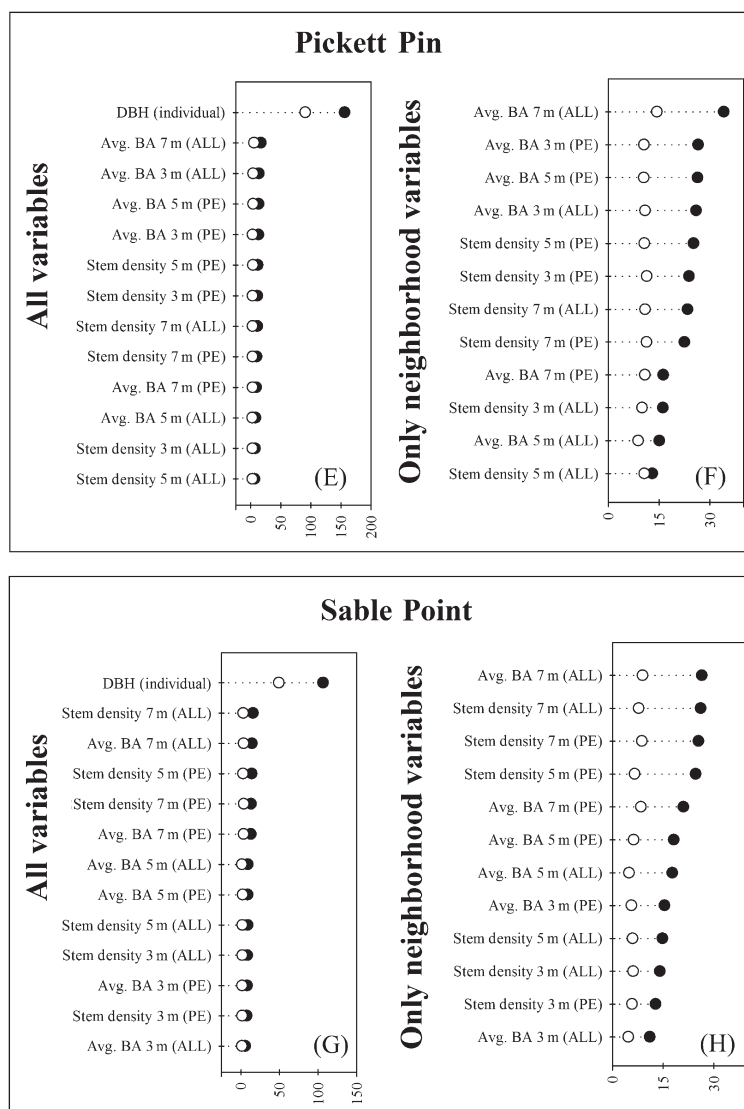


Fig. 5. Continued.

by showing that fire mediates susceptibility to outbreaks primarily by reducing the size of individual trees, and less so by changing stand structure at fine spatial scales.

Relative importance of tree vs. stand properties on tree susceptibility

Previous studies have reported increased susceptibility to spruce beetle among larger Engelmann spruce (Massey and Wygant 1954, Schmid and Frye 1977, Dymerski et al. 2001, Doak 2004, Hart et al. 2014b). Likewise, we found that spruce >15 cm dbh were most susceptible to

the 1940s' outbreak but trees as small as 11 cm dbh were killed (Fig. 7A). The infestation of small-diameter trees during past outbreaks has been thought to occur because beetle populations increase substantially and suitable large-diameter hosts are depleted due to earlier mortality, resulting in relaxed constraints on beetle population's host preference (Raffa et al. 2008, DeRose and Long 2012, Hart et al. 2014a). The infestation of relatively small-diameter trees in the current study could suggest that the 1940s' outbreak had become host-limited due to its high intensity (Table 1).

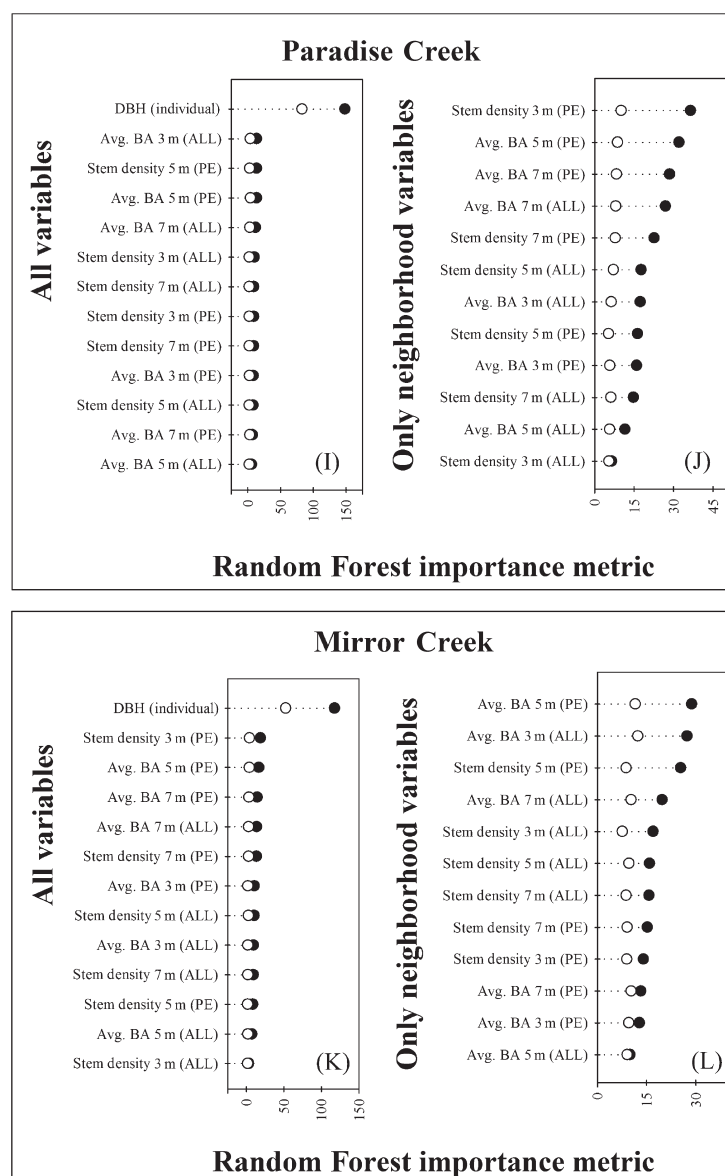


Fig. 5. Continued.

Individual tree size was the most important variable determining susceptibility to the 1940s' outbreak, but once this is taken into account, properties of surrounding spruce trees secondarily affected susceptibility to the outbreak (Fig. 5). The dominant effect of individual tree size was true overall and for all sites considered individually. Tree age was also an important predictor of susceptibility but was not as important as tree diameter (Fig. 6). Our data indicate that almost all (>90%) spruce that established prior

to the late 19th century fires and that were alive when the outbreak began were killed during the outbreak. It is not clear why a few of the older trees survived the outbreak, but it is likely they were in the diameter range in which most, but not all, spruce were killed (15–25 cm dbh). Our data indicate that no spruce >25 cm dbh survived the 1940s' outbreak.

Setting aside individual tree attributes, spruce that were surrounded by high basal area of spruce were more likely to have been killed by

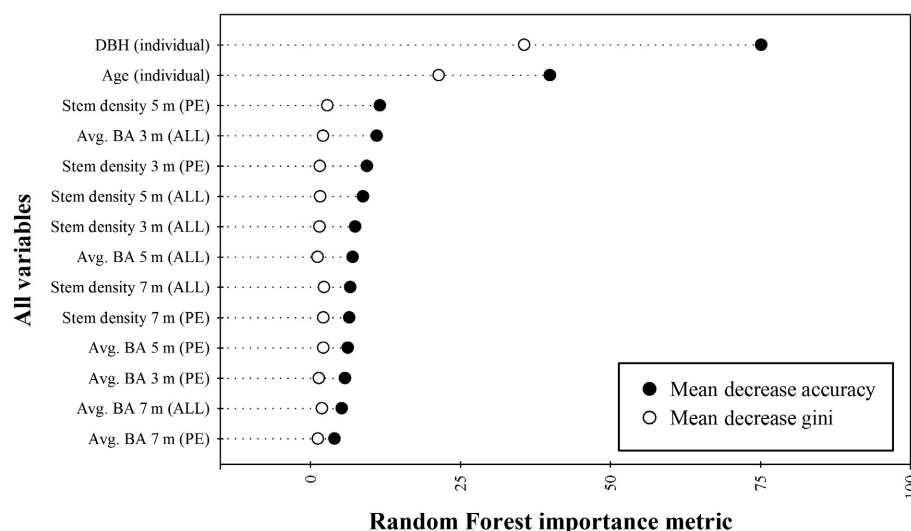


Fig. 6. Output from the classification analysis based on 10 Random Forest runs, indicating the most important variables across all study sites for all variables, including age. Only spruce trees for which age data were available ($n = 256$) were used in this analysis. Black dots represent mean decrease accuracy; white dots represent mean decrease in gini. Spruce trees were divided into two status categories (survived and dead) representing susceptibility to spruce beetle attack. PE is Engelmann spruce (*Picea engelmannii*), ALL refers to both host and nonhost species combined, and BA is basal area. For each of the 10 Random Forest runs, a different training data set was used and the number of potential variables to try at each node was adjusted to reduce each model out-of-bag (OOB) error. Average model OOB was 2.7 ± 0.34 .

spruce beetle (Figs. 5 and 7B). While this secondary influence is weak, it is consistent with the findings of Temperli et al. (2014) who reported an increased probability of infestation of large trees during a 1990s' outbreak, but only in patches of high spruce basal area. In the present study, these findings may reflect the location of sites at the edge of the severe late 19th century fires that resulted in larger trees being grouped together, which is relevant as spruce beetle prefer host material close to their origin of dispersal (Schmid 1970, Schmid and Frye 1977).

Spruce that were killed during the outbreak were surrounded by lower stem densities and larger dbh trees in comparison with spruce that survived. While these stand properties are related ecologically and collinear statistically, they are typical of late stages of stand development (Romme 1982, Veblen 1986). In contrast, patches around spruce that survived the attack were characterized by neighborhood stand properties consistent with early stages of development, such as higher stem densities and smaller surrounding trees (Table 2). Thus, while severe

fires may reduce susceptibility of stands to spruce beetle by reducing the number of large-diameter Engelmann spruce, the modification of stand structure toward earlier stages of development may further reduce susceptibility, although this effect is minor.

As in the present study, stand structure was also a poor predictor of spruce beetle infestation during the early phase of the 2002–2012 outbreak in western Colorado (Hart et al. 2014b). Tree susceptibility to this more recent outbreak was likely influenced by warm and dry conditions that can relax stand structure constraints on outbreaks. However, the present work shows that even under the relatively cooler and wetter conditions of the 1940s, neighborhood effects and local stand structure were also poor predictors of mortality during outbreak, which suggests a consistent relationship despite the different climatic conditions of the 1940s and early 2000s. Nevertheless, it is likely that these relationships will not remain stationary over time but will vary with beetle pressures and future climate (Bentz et al. 2010; DeRose et al. 2013). Furthermore, the current study has

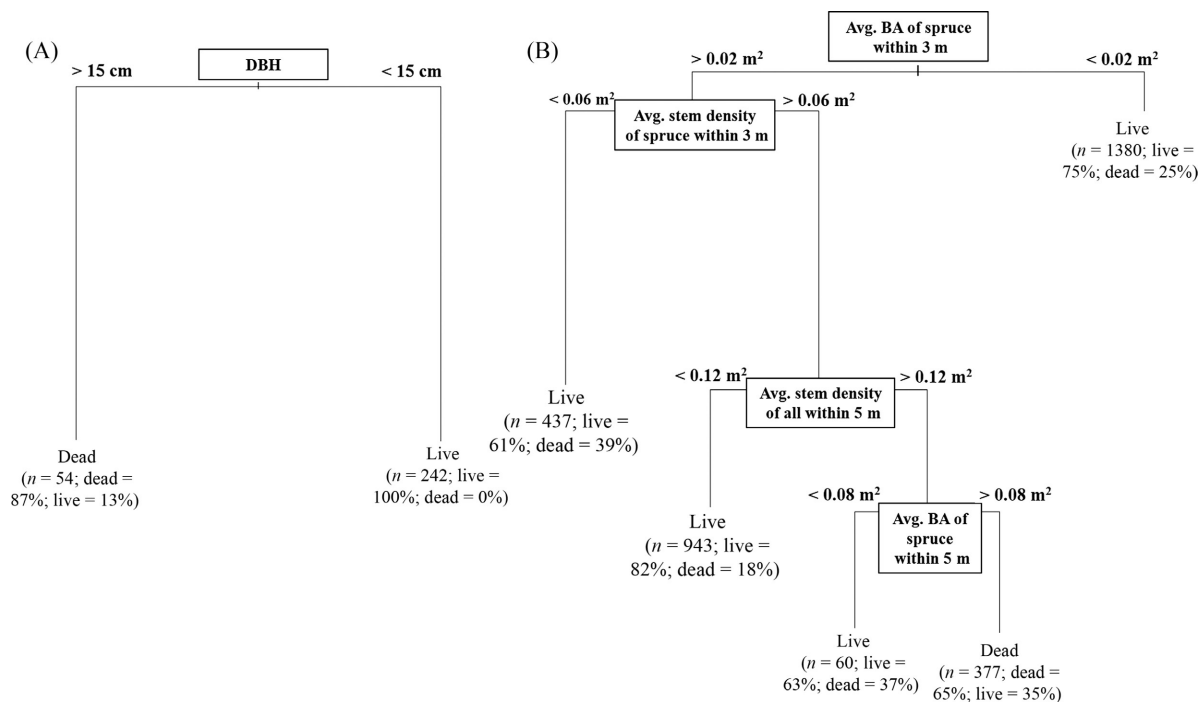


Fig. 7. Classification of all Engelmann spruce present during peak SB outbreak ($n = 1381$) as a function of (A) top 10 variables in Random Forest for all sites and all variables; (B) top 10 variables in Random Forest for all sites and only local stand property variables. The model misclassification rate was (A) 2.3% and (B) 14.9% vs. the majority rule misclassification rate of 24.0%. Each terminal node is labeled according to the predominant classification of tree susceptibility. Parenthetical numbers indicate the number of trees in that node and the percentage of observations in each node with given classifications. The figure depicts a tree model trimmed to (A) two and (B) five terminal nodes based on the cost-complexity measure. The complete model included (A) two and (B) eight terminal nodes.

focused on the relative importance of tree vs. fine-scale neighborhood effects and has not considered the effects of landscape structure, which affects stand susceptibility to spruce beetle outbreaks (Bebi et al. 2003) and which is also likely to change under future scenarios (Temperli et al. 2015).

Management implications

Current management strategies aim to either promote resistance to spruce beetle outbreak, often utilizing silvicultural practices such as thinning, to modify stand conditions favorable to insect and disease agents (Jenkins et al. 2008, Temperli et al. 2014), or aim to promote resilience by promoting regeneration of spruce following outbreaks (DeRose and Long 2014). The results of the current study suggest that modifying broad-scale stand structure may be unnecessarily intensive because susceptibility is primarily a

function of the size of live trees, and only secondarily of stand structure. In this context, severe wildfires, such as those that have been increasing across the western USA, appear to reduce susceptibility to subsequent outbreaks by creating conditions for the establishment of small-diameter trees that are not susceptible to outbreaks.

Conclusion

The current study suggests wildfires have reduced susceptibility to spruce beetle outbreaks primarily by reducing the size of available live host trees and only secondarily by modifying stand structure. These findings are consistent with those for spruce beetle outbreaks in the 21st century, which occurred under relatively warmer climatic conditions (Hart et al. 2014b). Thus, attributes of individual trees appear to be more important than attributes of stand structure

across a range of climatic conditions. Proposed management strategies that aim to modify stand structure over large areas in order to promote resistance to spruce beetle outbreaks may be unnecessarily intensive.

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