Relationships between forest structure, composition, site, and spruce beetle occurrence in the Intermountain West

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Abstract: Engelmann spruce forests are structurally and compositionally diverse, occur across a wide range of physiographic conditions, and are the result of varying disturbance histories such as fire, wind and spruce beetle. The spruce beetle is a natural disturbance agent of spruce forests and has population levels that fluctuate from endemic to epidemic. Conceptually, structural and compositional diversity of Engelmann spruce forests are thought to provide resistance to spruce beetle activity, and have traditionally been used to assess stand risk to the beetle. We used FIA data from nine states in the Intermountain West to test the effect of stand structure, composition, and site attributes on the occurrence of spruce beetle. A suite of independent variables from FIA data were used to predict the presence or absence of spruce beetle. Results suggested structural variables such as trees per acre and stand density index ratio were influential in the model. Similarly, compositional variables such as percent stand density index of aspen, lodgepole pine, Douglas-fir, and subalpine fir were also influential. Co-occurrence of multiple species with Engelmann spruce helped explain some of the patterns of spruce beetle occurrence. Ubiquitously occurring species such as subalpine fir and Douglas-fir explained less of the variation in model predictions. Elevation and latitude were significant predictors of spruce beetle occurrence; however, co-variation made direct interpretation of these independent variables difficult. Although statistically weak, the model results were ecologically interpretable and provided a range-wide context in explaining spruce beetle activity at some sites in the Intermountain West.

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**Introduction**

Engelmann spruce (*Picea engelmannii* Parry es. Engelm.) forests are widespread in the Intermountain West at higher elevations and are effectively southern extensions of the boreal forest. They occur from approximately 105° to 118° west in longitude and from approximately 33° to 50° north in latitude and range in elevation from less than 3,000 ft in northern Idaho to almost 12,000 ft on the Colorado Plateau. These forests occur across a wide range of physiographic conditions and are typically structurally and compositionally diverse (Peet 2000). Structurally, Engelmann spruce forests are commonly multi-aged, exhibiting a wide range of tree sizes (Aplet and others 1988). Compositionally, many other species co-occur with spruce, its most common associates are subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Douglas-fir (*Pseudotsuga menziesii* var. glauca (Beissn.) Franco), and more regionally common species such as aspen (*Populus tremuloides* Michx.), limber pine (*Pinus flexilis* James), whitebark pine (*Pinus albicaulis* Engelm.), and lodgepole pine (*Pinus contorta* Dougl. ex. Loud.) (see Figure 1).

Both low- and high-severity disturbances influence the structure and composition of Engelmann spruce forests (Veblen and others 1994). Windthrow, root and butt rots, and endemic spruce beetle (*Dendoctronus rufipennis* Kirby) all act locally to create low-severity canopy gaps in spruce forests. In contrast, crown fires, wind storms, and spruce beetle outbreaks, while infrequent, are high-severity disturbances that occur at much larger scales.

The spruce beetle is a host-specific bark beetle native to Engelmann spruce forests across the Intermountain West (Holsten and others 1999). Endemic populations of the beetle can build to epidemic (outbreak) levels in recently downed material such as logging slash, wind throw, or avalanche debris (Schmid 1981). Transition from endemic to epidemic population levels can be facilitated by warmer-than-average summer temperatures allowing univoltine beetles to reproduce successfully (Hansen and others 2001a) and, in combination with semivoltine beetles, overwhelm their host.

It is commonly though that composition and structure of Engelmann spruce-dominated stands influence the potential for spruce beetle activity. For example, a commonly used stand-level spruce beetle risk-rating (Schmid and Frye 1976) suggests dense (high basal area), pure (greater than 65 percent Engelmann spruce), old (large diameter) stands on well-drained creek bottoms (high site productivity potential) are most likely to be attacked by the spruce beetle. The Schmid and Frye (1976) risk-rating in effect quantifies the view that
compositionally and structurally diverse stands have less potential for spruce beetle activity, including the shift from endemic to epidemic population-levels.

We use FIA data to explore the relationships between stand structure, composition, site attributes, and spruce beetle occurrence in Engelmann spruce forests across the Intermountain West. We examine the putative relationship between compositional and structural diversity and spruce beetle occurrence and explore whether stand and site variables in fact have potential for use in the construction of predictive models of spruce stands susceptible to the spruce beetle.

Methods

Forest Inventory and Analysis (FIA) data from nine Intermountain West states: Arizona, Colorado, Idaho, Montana, Nevada, New Mexico, Utah, eastern Washington, and Wyoming (Table 1) were used to explore the relationship between structure, composition, site attributes, and spruce beetle occurrence. The nationwide hexagonal sampling strategy implemented in 2000 provided most of the data for this analysis while the remaining data came from previous periodic plots. Each hexagon is 5937 acres or, 1 plot per approximately 6000 acres, national sampling precision. Each plot will be visited on a 5 (east) or 10 (west) year return interval. (FIA Fact Sheet Series, online http://fia.fs.fed.us/library/fact-sheets/default.asp). Because the FIA data is unbiased and systematically collected it is appropriate for analyzing spruce beetle occurrence patterns in the Intermountain West.

Data preparation

Phase 2 data (inventory data) from plots which had the presence of Engelmann spruce were used in this analysis. Data indicating the occurrence of spruce beetle in FIA came from two sources: the tree table and the condition table. If spruce beetle was found on a measurement tree the recorder assigned that tree an Agent Code of 10. Similarly, if spruce beetle activity was found on or near the FIA plot, Disturbance Code = 10 was designated in the conditions table (USDA 2007). Therefore reference to spruce beetle activity or occurrence in this paper is interpreted as Engelmann spruce activity and/or mortality as a result of the spruce beetle. For the analysis we assumed both designations indicated beetle activity and collectively analyzed them as spruce beetle affected stands. Final data preparation included filtering so that re-measurement plots were only represented once (most recent) and only plots with Condition Proportion = 1.0.

A suite of independent variables characterizing structural, compositional, and site-level attributes for each plot (Table 2) were calculated from the filtered data. Although a total of 41 species co-occurred with Engelmann spruce across the
Intermountain West we limited calculation of compositional variables to the 13 species that shared at least 100 plots with spruce (Figure 1). As an example, individual species contribution to total stand basal area and stand density index as a percent were calculated to describe stand composition. To characterize structural attributes we calculated trees per acre, quadratic mean diameter, basal area, and the stand density index ratio (SDIr). SDIr is the ratio of stand density index calculated using the summation method (Shaw 2000) to stand density index calculated using the average method (Reineke 1933). SDIr is interpreted as an index of structural diversity from least (greater than 0.9) to most diverse (less than 0.78) (Shaw and Long 2007). With the exception of aspect value (Roberts and cooper 1989), site variables were taken straight from the FIA data.

Data analysis

The presence/absence nature of the dependent variable, spruce beetle occurrence, lent itself to the logistic regression approach to model fitting. We initially predicted the presence/absence of spruce beetle in Engelmann spruce stands using compositional, structural, and site-level variables individually and their interactions (Table 2). To accurately reflect pre-beetle conditions reconstruction of stand attributes was done for plots that had beetle-caused mortality. One shortcoming with the binary nature of the dependent variable (spruce beetle occurrence) was that it could indicate either endemic or epidemic beetle populations. Therefore the results are interpreted as spruce beetle activity or occurrence in Engelmann spruce stands, and differentiation between population levels was not made. Models were evaluated for goodness-of-fit using pseudo-$R^2$, or deviance ($D^2$). Pearson’s correlations ($r^2$) were used to further evaluate the significant independent variables.

Results

Both Engelmann spruce plots and plots with spruce beetle were wide ranging across the Intermountain West (Figure 2). Therefore it was not surprising that generally the logistic models explained very little of the overall variance in spruce beetle occurrence, with a range of $D^2$ from 6 percent to 19 percent. However, the models did indicate independent variables with statistical significance and we evaluated these further.

Of the 13 species that co-occurred with Engelmann spruce, four were influential in predicting spruce beetle activity: basal area of aspen, basal area of lodgepole pine, and percent stand density index of aspen, lodgepole pine, Douglas-fir, and subalpine fir. Aspen and lodgepole pine basal areas were negatively related to spruce beetle occurrence, whereas aspen and lodgepole percent stand density index were positively related. The contradiction in signs was difficult to explain; however, the fact that both these species perform the same
role ecologically, although primarily at different latitudes, suggested this pattern was not spurious. Both Douglas-fir and subalpine fir had a positive relationship with spruce beetle occurrence, occurred nearly ubiquitously with Engelmann spruce across the Intermountain West, and were weakly inter-correlated \( (r^2 = 0.23) \). Subalpine fir, because of its near complementary relationship with corkbark fir, was weakly correlated with latitude \( (r^2 = 0.28) \) which likely drove its significance in the model.

Structural variables significant in the prediction of spruce beetle occurrence were: trees per acre, stand basal area, stand density index, and SDIr. Trees per acre and basal area were positively related to beetle occurrence whereas stand density index and SDIr had negative relationships. Trees per acre and basal area were highly correlated \( (r^2 = 0.60) \) and probably co-varied in the model. However, the difference in sign between trees per acre and stand density index was suspect since they were strongly positively correlated \( (r^2 = 0.74) \).

Site-level variables significant in the prediction of spruce beetle occurrence were elevation and latitude. Unfortunately latitude, longitude, and elevation were highly inter-correlated (range of \( r^2 = 0.79 – 0.81 \)) in this study so isolating the effect of one from the other was difficult. Model results indicated either latitude or elevation was significant individually, but not simultaneously. Furthermore, although they appeared to proxy one another their signs differed. The difference in sign between these two variables in the model (elevation was positive, latitude was negative) can be explained by the inherent negative relationship between latitude and elevation. Individually, their patterns with spruce beetle occurrence were ecologically explainable. The number of spruce beetle plots decreased with decreasing latitude (Figure 3) but did not occur disproportionately to the total number of spruce plots (data not shown). In contrast, the number of spruce beetle plots generally increased with increasing elevation but for the 9,000 – 11,000 foot elevation range spruce beetle plots occurred disproportionately more than the number of spruce plots (Figure 4).

**Discussion**

The large variation in compositional, structural, and site-level attributes for Engelmann spruce forests across the Intermountain West proved only marginally useful in predicting the occurrence of spruce beetle activity. Regardless, ecologically meaningful patterns between the independent variables and observed spruce beetle activity were revealed by the data. The weakness in statistical results generally provides support for the complex, non-linear nature of spruce beetle populations which exhibit shifts from endemic to epidemic levels that are catalyzed by specific events and therefore not reliably predictable. The geographically unbiased FIA data revealed the spruce beetle generally occurred across the entire range of Engelmann spruce (Figure 2), suggesting it is a normal
part of spruce forests but also complicated efforts to identify useful predictors of future outbreaks.

Understanding the relationships between co-occurring species and spruce beetle in Engelmann spruce forests is important because mixed stands are much more common than pure stands. For example, when the FIA data were filtered for nearly pure Engelmann spruce composition (greater than 80 percent stand density index), approximately 13 percent of the spruce plots met the criteria. All significant composition variables were early successional species with the exception of subalpine fir. Perhaps more interesting was that the stocking of all four species was positively related to spruce beetle occurrence. This is counterintuitive to our expectation that compositionally simple stands of relatively pure spruce are more susceptible to beetle activity. The biogeographical patterns of aspen, lodgepole, and subalpine fir were interesting and somewhat predictable, for example, corkbark fir gave way to subalpine fir at approximately 38° latitude. Similarly, aspen shifts from common to rare at approximately 44° latitude where lodgepole pine becomes common and remains so to the Canadian border (Figure 2). This is consistent with the observations along the Colorado Front Range made by Peet (1978) who suggested aspen yielded to lodgepole as the early successional player in spruce stands as one moved north in latitude. Biogeographical patterns for the other common species that co-occurred with spruce such as limber pine, whitebark pine, and grand fir (Figure 1) were also predictable from site and structural variables but were not influential in the spruce beetle models.

Structural variables such as spruce basal area and spruce mean diameter greater than 10 inches are commonly used to interpret stand risk to a beetle outbreak. However, only stand-level variables that ignored the spruce component were indicated in our analysis. Based on previous research the positive relationship between basal area and spruce beetle occurrence was expected (Schmid and Frye 1977). What was less intuitive was the significance of tree density on beetle occurrence, except that it likely co-varied with basal area. One explanation is that stand basal area was highly correlated with spruce basal area ($r^2 = 0.53$) but only weakly correlated with trees per acre ($r^2 = 0.19$). Furthermore, to reconcile the difference in signs between stand density index and trees per acre it helps to understand stand density index and spruce basal area were correlated ($r^2 = 0.48$). An index of structural diversity, SDIr, did not co-vary with any of the other structural indices. Lower SDIr indicates stands that are irregular in structure, for instance, stands with an index of greater than 0.9 have a unimodal diameter distribution, stands of approximately 0.75 exhibit a reverse-J distribution, and stands with an index below 0.7 exhibit increasingly bimodal or irregular structures. The negative relationship of SDIr with spruce beetle occurrence found here is counterintuitive to our expectation that stands of simple structure would have more beetle activity. This result is likely driven by the non-linear nature of the distribution of SDIr across the Intermountain West range of spruce and the
possible effects of elevation on the relationship due to the correlation between these variables on the spruce beetle plots ($r^2 = 0.28$, see below).

Other variables such as stand age and site quality (xeric versus mesic) have traditionally been used in combination with composition and structure to predict the risk of spruce beetle populations shifting from endemic to epidemic (Schmid and Frye 1976). While some compositional and structural variables were significant in predicting spruce beetle occurrence in this study, the strongest pattern that emerged was the disproportionate number of spruce beetle plots at high elevation (Figure 4). Generally the proportion of spruce beetle plots increased with increasing elevation with the exception of the 11,000 – 12,000 foot elevation bin (Figure 4). This increasing relationship can be partially explained by the relatively strong relationship between elevation and Engelmann spruce stand density index ($r^2 = 0.41$) which is not inconsistent with the idea that increasing spruce composition increases spruce beetle activity. However, this does not fully explain the spike in spruce beetle observations in the 9,000 – 11,000 foot elevation range. As for the 11,000 – 12,000 foot elevation range perhaps the spruce that occur here are very small, for example krumholz stands, and climatic extremes are such that it is relatively inhospitable for spruce beetle populations.

Climatic and weather variables have been found to exert a heavy influence on insect populations including the family Scolytidae (Logan and Bentz 1999; Hansen and others 2001b). If changes in climate were manifest at varying levels across an elevation gradient we would have reason to suspect the higher than expected numbers of spruce beetle in the 9,000 – 11,000 foot range would be influenced. We suggest the unpredictability of spruce beetle activity from structural and compositional attributes in this study is likely due to the influence of an overriding factor, climate. Indeed, climate, and specifically temperature, has surfaced as the controlling factor in spruce beetle populations in Alaska (Berg and others 2006) and the recent explosive mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado (Kulakowski and Veblen, unpublished paper). Since temperature controls insect populations, we hypothesize climatically sensitive areas, such as those found at high elevations, will exhibit the most pronounced response to spruce beetle activity. Compounding this problem is the observation that strong temperature-precipitation interactions control the range limit for Engelmann spruce, and climate modeling under various global climate change scenarios revealed the bioclimatic window for spruce is likely to close for populations at high elevations and lower latitudes (Rehfeldt and others 2006). Since both beetle populations and the realized niche for Engelmann spruce are controlled by temperature, perhaps increased spruce beetle activity at higher elevations is exacerbating the predicted shift in spruce range limits.

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Disturbance regime and disturbance interactions in a Rocky Mountain subalpine
# Table 1: Forest Inventory and Analysis data from Engelmann spruce plots by state.

<table>
<thead>
<tr>
<th>State</th>
<th># plots</th>
<th>Species present&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Trees per acre</th>
<th>Basal area (ft²)</th>
<th>Stand density index</th>
<th>Stand density index ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arizona</td>
<td>105</td>
<td>WF, CF, SF, LM, PP, DF, AS</td>
<td>36 – 705</td>
<td>54 – 338</td>
<td>54 – 575</td>
<td>0.39 – 0.98</td>
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<tr>
<td>Colorado</td>
<td>587</td>
<td>WF, CF, SF, LP, LM, PP, DF, AS</td>
<td>12 – 860</td>
<td>6 – 367</td>
<td>12 – 640</td>
<td>0.06 – 0.99</td>
</tr>
<tr>
<td>Idaho</td>
<td>548</td>
<td>GF, SF, WL, WBP, LP, LM, WWP, PP, DF, WRC, WH, AS</td>
<td>12 – 625</td>
<td>5 – 348</td>
<td>8 – 452</td>
<td>0.06 – 0.98</td>
</tr>
<tr>
<td>Montana</td>
<td>819</td>
<td>GF, SF, WL, WBP, LP, LM, WWP, PP, DF, WRC, WH, AS</td>
<td>3 – 821</td>
<td>7 – 327</td>
<td>10 – 528</td>
<td>0.04 – 1.0</td>
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<td>Nevada</td>
<td>4</td>
<td>WF, LM, DF, AS</td>
<td>88 – 412</td>
<td>63 – 223</td>
<td>99 – 346</td>
<td>0.25 – 0.55</td>
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<tr>
<td>New Mexico</td>
<td>101</td>
<td>WF, CF, SF, LM, PP, DF, AS</td>
<td>30 – 876</td>
<td>18 – 354</td>
<td>32 – 648</td>
<td>0.35 – 0.98</td>
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<td>Utah</td>
<td>345</td>
<td>WF, SF, LP, LM, PP, DF, AS</td>
<td>7 – 950</td>
<td>8 – 280</td>
<td>13 – 498</td>
<td>0.06 – 1.0</td>
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<td>Washington</td>
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<td>GF, SF, WL, LP, WWP, DF, WRC, WH</td>
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<td>Wyoming</td>
<td>388</td>
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<td>12 – 762</td>
<td>11 – 343</td>
<td>16 – 550</td>
<td>0.04 – 0.98</td>
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<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Description</th>
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<td><strong>Structural</strong></td>
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<tr>
<td>Trees per acre</td>
<td>Absolute density</td>
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<tr>
<td>Stand density index (summation)</td>
<td>Relative measure of stand density (Shaw 2000)</td>
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<tr>
<td>Stand density index ratio</td>
<td>Ratio of summation stand density index to Reineke stand density index (Long and Shaw 2005) density index (Reineke 1933), index of structural diversity</td>
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<tr>
<td>Stand basal area</td>
<td>Measure of stocking</td>
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<tr>
<td>Quadratic mean diameter</td>
<td>Geometric mean of stand diameter</td>
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<tr>
<td><strong>Compositional</strong></td>
<td></td>
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<td>Species basal area</td>
<td>Individual species basal area</td>
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<tr>
<td>Percent stand density index by species</td>
<td>Percent composition of each species present on the spruce plot</td>
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<tr>
<td>QMD of Engelmann spruce</td>
<td>Geometric mean diameter for spruce component only</td>
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<tr>
<td>QMD of Engelmann spruce greater than 10 inches</td>
<td>Mean of stand diameter for all Engelmann spruce greater than 10 inches</td>
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<tr>
<td><strong>Site</strong></td>
<td></td>
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<td>Elevation</td>
<td>Height above sea level</td>
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<tr>
<td>Site index</td>
<td>Measure of site potential productivity based on tree height and age</td>
</tr>
<tr>
<td>Aspect value</td>
<td>Moisture index</td>
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<td>Steepness of the plot</td>
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<td>Stand age</td>
<td>Age of the plot</td>
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<td>Latitude</td>
<td>North</td>
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<tr>
<td>Longitude</td>
<td>West</td>
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*Aspect value = [Cos((aspect-30)/180*3.14)+1]/2 (Roberts and Cooper 1989)*
Figure 1: Representation of species which co-occur with Engelmann spruce on at least 100 of the FIA spruce plots (total spruce plots, n = 2093). For species identification see Table 1.
Figure 2: Map of the distribution of Engelmann spruce in the Intermountain West based on FIA data (n = 2093). Plots with spruce beetle, aspen, and lodgepole pine are also shown.
Figure 3: Frequency distribution of Engelmann spruce plots (n = 2093) juxtaposed with Engelmann spruce plots that had spruce beetle (n = 175) over latitude.
Figure 4: Frequency distribution of Engelmann spruce plots (n = 2093) juxtaposed with Engelmann spruce plots that had spruce beetle (n = 175) over thousand foot elevation bins. Spruce beetle plots as a percent of total Engelmann spruce plots by elevation bin in red showing the disproportionate number of spruce beetle plots in the 9000 – 11000 elevation range.