Forest-landscape structure mediates effects of a spruce bark beetle 
*(Dendroctonus rufipennis)* outbreak on subsequent likelihood of burning 
in Alaskan boreal forest

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**Abstract**

Characterizing how variation in forest landscape structure shapes patterns of natural disturbances and mediates interactions between multiple disturbances is critical for anticipating ecological consequences of climate change in high-latitude forest ecosystems. During the 1990s, a massive spruce bark beetle (*Dendroctonus rufipennis*) outbreak took place in boreal spruce forest on the Kenai Peninsula, Alaska allowing us to ask (1) *How did the extent and duration of bark beetle outbreak differ between a homogenous landscape dominated by white spruce (*Picea glauca*), and a landscape in which white spruce and black spruce (*Picea mariana*) were intermixed?* (2) *How has the occurrence and duration of bark beetle outbreak influenced the likelihood of subsequent burning in these two landscapes?* Forest landscape structure had a substantial effect on disturbance patterns and interactions between disturbances in this study. The spruce bark beetle outbreak was smaller in extent and duration where white spruce, the beetle’s primary host tree, was intermixed with more beetle-resistant black spruce. However, likelihood of subsequent burning increased where outbreak did occur. Surface fuel loads increased substantially in this landscape following the outbreak, potentially increasing the flammability of white spruce where they once served as fire breaks. In contrast, the outbreak was larger and lasted longer in the landscape with homogeneous stands of white spruce, but was not related to likelihood of subsequent burning, which is consistent with the fire history. Our results suggest that bark beetle outbreaks may have different effects on subsequent patterns of burning than in other systems, such as the Rocky Mountains. These results could inform more effective and targeted management strategies to ameliorate fire risk in beetle-killed stands of Alaska and may help us anticipate the dynamics and consequences of future boreal bark beetle outbreaks as climate warms at high latitudes.

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1. Introduction

Evaluating how variation in forest-landscape structure shapes natural disturbance patterns and mediates interactions between multiple disturbances is critical for understanding ecological consequences of climate change (Turner, 2010; Johnstone et al., 2011). Warming and drying are causing pronounced increases in the frequency, size, and severity of natural disturbances (Millar and Stephenson, 2015; Trumbore et al., 2015). In western North America, annual area burned by wildfire is now nearly 6.5 times the 1970–1986 average (Westerling et al., 2006), and bark beetle outbreaks have become substantially more prevalent in recent decades (Bentz et al., 2010). Concern persists that bark-beetle-driven tree mortality could further increase the risk of subsequent fire frequency, size, and severity (Hicke et al., 2012), a concept known as linked disturbance interactions (Simard et al., 2011). However, landscape structure may mediate climate-change effects on disturbances (Turner and Romme, 1994; Duffy et al., 2007). Variation in tree-species distributions across landscapes can influence patterns of burning (Schoennagel et al., 2004; Kelly et al., 2013) and determines forest vulnerability to bark beetle outbreak (Hart et al., 2015a; Temperli et al., 2015). Accounting for the role of forest-landscape structure could yield powerful insights into changing disturbance regimes in the 21st century and the nature and
magnitude of their interactions. This could help us anticipate when and where forests may be vulnerable to bark beetle outbreaks and whether such outbreaks may influence subsequent patterns of burning.

Few places on Earth are experiencing as rapid climate change as the Alaskan boreal forest, warming at twice the rate of the global average during the 20th century (Wolken et al., 2011). Annual area burned in boreal Canada and Alaska is expected to increase 74–118% by 2100 (Balshi et al., 2008; Flannigan et al., 2005). In white spruce (Picea glauca) stands of the western Kenai Peninsula in south-central Alaska, recent climate warming also led to a massive spruce bark beetle (SBB) (Dendroctonus rufipennis) outbreak that extended over almost 1.2 million ha during the 1990s (Berg et al., 2006). An estimated 30 million trees were killed per year between 1990 and 1996, when the outbreak peaked (Werner et al., 2006). The distribution of tree species varied markedly in SBB-affected landscapes. This variation may have mediated outbreak dynamics (Seidl et al., 2015; Temperli et al., 2015) and subsequent ecological consequences. White spruce, the beetle’s primary host tree in Alaska, dominated the southern portion of the outbreak extent, forming homogenous stands of susceptible mature forest (Berg and Anderson, 2006). In the northern portion of the outbreak, white spruce trees were intermixed with black spruce (Picea mariana) (Devolder, 1999), which are not vulnerable to SBB (Werner et al., 2006).

The Kenai Peninsula is one of the most densely populated areas in Alaska, and following the outbreak, there has been substantial concern about increases in the subsequent risk of wildfire. A number of wildfires have burned on the Kenai Peninsula since the outbreak. Warming trends suggest that future outbreaks and increased interaction with fire may occur in Alaska (ACIA, 2005; Berg et al., 2006; Raffa et al., 2008; Sherriff et al., 2011; Werner and Holsten, 1985; Werner et al., 2006). However, it remains poorly resolved when and where Alaskan boreal forests may be vulnerable to future outbreaks and whether future outbreaks could influence subsequent patterns of burning.

In montane to subalpine Rocky-Mountain conifer forests, bark beetle outbreaks can alter fire behavior (Hicke et al., 2012) and compromise fire-fighter safety (Jenkins et al., 2012). For example, active crown fire potential may increase 1–4 years post outbreak, before declining, as needles are shed from beetle-killed trees (Hicke et al., 2012). However, outbreaks appear to have modest or little effect on post-outbreak fuel profiles (Simard et al., 2011; Donato et al., 2013; Schoennagle et al., 2012; Harvey et al., 2014a), wildfire probability (Kulakowski et al., 2003; Lynch et al., 2006; Kulakowski and Veblen, 2007; Kulakowski and Jarvis, 2011), area burned (Hart et al., 2015b), and fire severity (Bigler et al., 2005; Harvey et al., 2013, 2014b; Andrus et al., 2015). On the Kenai Peninsula, surface-fuel loads of nearly all size classes increased following the outbreak. Duff and moss depth, an indicator of fuel moisture, also decreased (Schulz, 1995, 2003). This suggests that post-outbreak changes in forest structure may differ between boreal and Rocky-Mountain forests in ways that could lead to divergent consequences for subsequent patterns of burning.

The SBB outbreak on the Kenai Peninsula offers a tremendous opportunity to evaluate linked disturbance interactions in the boreal forest and the mediating role of forest-landscape structure. In this paper, we ask: (1) How did the extent and duration of the 1990s SBB outbreak differ between a homogenous landscape dominated by white spruce and a landscape in which white spruce and black spruce were intermixed? (2) How has the occurrence and duration of SBB outbreak influenced the likelihood of subsequent burning in these two landscapes, as compared to other factors? We hypothesized that the SBB outbreak was not as spatially extensive and of shorter duration in the north where white spruce and black spruce were intermixed. Conversely, we expected the outbreak to be substantially more extensive in the south where white spruce dominated. Despite different outbreak extents and durations, we hypothesized that increased surface fuels would lead to higher probabilities of subsequent burning in both regions.

2. Materials and methods

2.1. Study area

The Kenai Peninsula of south-central Alaska sits south of Anchorage (Fig. 1) and is an ecological transition zone. West of the Kenai Mountains, much of the peninsula is a relatively flat, topographically homogenous plain that lies at the southwestern extent of the physical and ecological conditions characterizing Alaskan boreal forest (Morton et al., 2006). This is where the majority of the SBB outbreak occurred in the 1990s (Fig. 2). On the western Kenai Peninsula, mean annual precipitation varies from 369 mm in the north to 650 mm in the south (1971–2000) (Western Regional Climate Center, 2012). Average annual temperature is approximately 1 °C. The Kenai Peninsula is also one of the most densely populated areas of Alaska, and people increase numbers of ignitions and decrease area burned by suppressing fires in proximity to roads (Calef et al., 2008). To try to minimize confounding influences of people, we limited our analyses of bark-beetle effects on fire to include only forested areas more than 20 km away from the nearest major road. Tree-species composition varies markedly. Interior stands on the Kenai Peninsula are comprised of white spruce with some resin birch (Betula neoalaskana) in the south. Black spruce stands dominate the north of the peninsula, with a transition zone in the middle, where black spruce and white spruce are intermixed (Berg and Anderson, 2006). Landscape structure of black spruce and white spruce strongly influence the fire regime. Black-spruce stands are highly flammable with a historical fire return interval of 60–80 years (Devolder, 1999). White spruce forests have burned much less frequently (fire return intervals of 400–600 years) (Berg et al., 2006). Thus, we stratified our study area by tree species distributions and identified two separate study regions; one north of Tustumena Lake (97,000 ha), where black spruce and white spruce are intermixed, and one south of the lake (133,500 ha), dominated by white spruce (Fig. 1) (Berg et al., 2006).

2.2. Approach and data

To determine how forest-landscape structure mediated SBB outbreak extent and duration and to evaluate effects of SBB outbreak on the likelihood of subsequent burning, we assembled gridded geo-spatial datasets of fire perimeters (2001–2014), occurrence/duration of SBB outbreak (1989–2000), previous fire history (1946–2000), mean decadal (2001–2010) fire-season potential aridity (2001–2009), and information on forest structure (Table 1). All data were resampled using nearest neighbor to ~1 km² resolution (chosen because it was the resolution of our coarsest dataset; climate). This yielded 1276 pixels and 1890 pixels in the northern and southern study regions, respectively, that served as observations in analyses.

Fire perimeters between 2001 and 2014 and previous fire history were derived from Alaska Fire Service’s Fire History Database (Alaska Fire Service, 2014). Perimeter maps are developed using field and aerial surveys and satellite imagery (Kasischke et al., 2002). The database includes all fires >405 ha since 1946 and all fires >40.5 ha since 1988 (Calef et al., 2015). SBB outbreak and duration between 1989 and 2000 were measured in our study regions using aerial detection surveys from The U.S. Forest Service and Alaska Department of Natural Resource’s Alaska Forest Health
Protection Program (Fig. 2) (United States Forest Service and Alaska Department of Natural Resources, 2012). The number of years that outbreak was recorded in any given pixel varied substantially. To explore whether outbreak duration was important, we conducted all analyses using several different duration thresholds to define whether or not outbreak occurred in a given pixel (e.g., varying whether we consider outbreak to have occurred by if it lasted ≥1 year, ≥2 years, ≥3 years, or ≥4 years).

We used the 2001 National Land Cover Database (NLCD) to map vegetation type and % forest canopy cover (Homer et al., 2004). In our study area, these data categorize pixels based on the dominant canopy tree type (e.g., conifer, mixed conifer-deciduous, deciduous) taller than five meters in forested areas. Other categories included shrub, human development, barren land, water, etc. In the boreal forest, conifers can grow quite slowly. Thus, early to mid-succession forests may be misclassified as shrub in the NLCD. Eighty-two percent of pixels were classified as coniferous forest or shrub and only five percent as deciduous or mixed forest in our study regions. Because fire is most prevalent in conifer stands and to ensure that we had sufficient observations in each forest-type category to conduct robust statistical analyses, we only included pixels classified as conifer or shrub. We defined vegetation type as either late-successional conifer forest (conifer in NLCD) or early-successional conifer/shrub (shrub in NLCD).

Decadal (2001–2010) fire season (May–August) potential aridity, measured as precipitation minus potential evapotranspiration (P-PET), was calculated using gridded historical CRU TS 3.1 temperature data and CRU TS 3.1.01 precipitation data (Jones and Harris, 2008; Mitchell and Jones, 2005). Scenarios Network for Alaska and Arctic Planning downscaled climate data to a 1 km² resolution following the delta methodology and calculated PET using the Hamon equation (SNAP, 2012). P-PET incorporates precipitation with evaporative demand, driven by temperature, to provide an estimate of landscape aridity. A lower P-PET value (increased potential aridity) means dryer conditions.

2.3. Analysis

We developed regressions to predict likelihood of burning between 2001 and 2014 as a function of SBB outbreak occurrence and duration, while controlling for other factors. Aspect and past fires between 1941 and 2000, which occurred in 1.6% of pixels,
were not correlated with fire occurrence in earlier univariate analyses and thus were excluded from final regressions. Collinearity was evaluated using a variance inflation factor cutoff of four. Analyses were conducted separately for north and south study regions, and multiple regressions were run in each region using different duration thresholds (outbreak occurred for $\leq 1$ year, $\geq 2$ years, $\geq 3$ years, or $\geq 4$ years) to define SBB outbreak occurrence. Our response variable, whether a pixel burned or not, is binary (a value of one if fire burned; zero if not), which is conducive to logistic regression. However, we identified spatial autocorrelation in logistic-regression residuals. Spatial autocorrelation often leads to biased standard error estimates. Thus, we used General Linear Mixed Models using Penalized Quasi Likelihood (GLMMPLQ), which are widely applied to account for spatial dependence in binary regressions (Dormann et al., 2007). GLMMs combine linear mixed models, which account for correlated residual variance, with generalized linear models that can handle non-normal data (i.e. binary dependent variables) (Bolker et al., 2009).

3. Results

3.1. Bark beetle outbreak extent and duration

SBB outbreak was recorded by aerial detection surveys between 1989 and 2000 in approximately 35% of the northern study region, where black spruce and white spruce were intermixed (Table 1). Recorded outbreak duration ranged from one to seven years (Fig. 3). In 40% of pixels, outbreak was recorded as lasting a single year, and an outbreak duration of $\geq$ four years was recorded in only

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Table 1

<table>
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<tr>
<th>Region</th>
<th>Total Area (ha)</th>
<th>Mean</th>
<th>SE</th>
<th>Min</th>
<th>Max</th>
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<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
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<td>SBB outbreak (ha)</td>
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<td>1</td>
</tr>
<tr>
<td>SBB outbreak duration (yrs)</td>
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<td>0.10</td>
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<td>7</td>
<td></td>
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<td>Fire (ha)</td>
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<td>10,206</td>
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<td>–</td>
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<tr>
<td>Potential aridity (mm)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>Canopy cover (%)</td>
<td>–</td>
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<td>1.0</td>
<td>0</td>
<td>94</td>
</tr>
</tbody>
</table>

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![Map of the Kenai Peninsula depicting (A) the extent of the 1990s spruce bark beetle outbreak and (B) wildfires that burned between 2001 and 2014.](image)
Fig. 3. Top panel: Log transformed extent of SBB outbreak (ha) in each study region by year. Bottom panel: Proportions of SBB outbreak in each study region binned by outbreak duration (Year).

Fig. 4. Influence of SBB outbreak occurrence and duration (regression coefficients, $\beta$) on likelihood of burning between 2001 and 2014. Asterisk denote significant relationships.
In the north, three fires occurred between 2001 and 2014, burning nearly 30% (30,600 ha) of the region (Table 1). Fire was less prevalent in the south. Five fires burned 15% (19,500 ha) of the study region. Likelihood of burning in the northern study region increased with occurrence of SBB outbreak, if outbreak duration in a pixel was ≥2 or ≥3 years (Fig. 4). Likelihood of burning also increased in pixels classified as late-succession conifer forest and where percent canopy cover was higher. In the southern study region, likelihood of burning was unrelated to occurrence and duration of SBB outbreak as well as whether or not an observation was classified as late-successional conifer forest (Table 2, Fig. 4). However, likelihood of burning did increase with percent canopy cover. In both study regions, likelihood of burning was unrelated to potential aridity (Table 2).

### 4. Discussion

Our study illustrates how variation in forest landscape structure can shape SBB outbreak extent and duration and influences whether SBB outbreaks affect probability of subsequent burning in Alaska. On the Kenai Peninsula, SBB outbreak in the northern study area, where white and black spruce were intermixed, was not nearly as extensive and was often of shorter duration compared to the white-spruce dominated southern study area. Yet, likelihood of subsequent burning was higher when SBB outbreak occurred in the north, likely as a result of increased surface-fuel loads. In contrast, likelihood of burning was not altered by outbreak occurrence in the south, where fires have been historically rare. These results could inform more effective and targeted management strategies to ameliorate fire risk in beetle-killed stands of Alaska and may help us anticipate the dynamics and consequences of future boreal bark beetle outbreaks as climate warms at high latitudes.

SBBs generally do not target black spruce, instead preferring white spruce (Werner et al., 2006). Thus, suitable stands of host trees in the northern study region were less connected in their distribution, with black spruce intermixed, likely explaining smaller outbreak extent, shorter durations, and increased probability of subsequent burning, if outbreak duration was ≥2 or ≥3 years. Late-successional black spruce forests are highly flammable and have historically burned orders of magnitude more frequently than white-spruce-dominated stands on the Kenai Peninsula (DeVolder, 1999; Berg et al., 2006). Forest-structure changes related to the outbreak (e.g., larger and drier fuel loads) may have increased the flammability of white spruce stands when black spruce are intermixed, leading to increased burning in areas that once likely served as fire breaks (Werner et al., 2006; Wolken et al., 2011).

Widespread post-outbreak increases in surface-fuel loads and heights on the western Kenai Peninsula were documented for 1-, 10-, 100-, and non-rotting 1000-h fuel classes (Schulz, 1995, 2003). This is in contrast with montane and subalpine Rocky-Mountain conifer forests where bark beetles appear to have modest effects on fuels (Simard et al., 2011; Donato et al., 2013; Schoennagel et al., 2012; Harvey et al., 2014a) and minimal influence on subsequent likelihood of burning or fire severity (Bigler et al., 2005; Kulakowski and Vebien, 2007; Kulakowski and Jarvis, 2011; Harvey et al., 2013, 2014b; Meigs et al., 2015). Surface fuels play a key role in the spread of boreal wildfires (Weber and Flannigan, 1997). Surface-fuel accumulation following outbreak on the Kenai Peninsula may explain why we saw increased likelihood of burning in boreal forests where black spruce were present, when similar effects of bark-beetle outbreaks on fire have not been documented in other systems.

Increased likelihood of burning in the northern study region may also have resulted from drying surface fuels following outbreak of longer duration. This is supported by observations of reduced moss and duff depth in post-outbreak stands (Schulz, 2003). Substantial uncertainty remains in how bark beetle outbreaks affect hydrologic and radiative fluxes in forest ecosystems (Pugh and Gordon, 2013; Brown et al., 2014; Bearup et al., 2014). However, bark beetle outbreaks can cause reduced evapotranspiration and increased sensible heat fluxes (Bearup et al., 2014). For example, summertime evapotranspiration was reduced 19% and sensible heat flux increased 8%, warming surface temperatures 1 °C, five years after a large bark beetle outbreak in British Columbia (Maness et al., 2013). Field-based measurements of air temperature in lodgepole pine stands of Yellowstone National Park varied with time since bark beetle outbreak. Initially, (0–4 years post outbreak) mean daily air temperature remained unchanged. By 30 years post outbreak, temperature was 1.3 °C warmer (Griffin et al., 2011).

It is not surprising that outbreaks were more extensive and generally lasted longer in the southern study area. Many pre-outbreak

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**Table 2**

Results of GLMM PQL regressions for (A) the northern study region and (B) the southern study region predicting likelihood of burning between 2001 and 2014. Coefficients (SE) are presented.

<table>
<thead>
<tr>
<th></th>
<th>Bark beetle outbreak duration</th>
<th>≥1 year</th>
<th>≥2 years</th>
<th>≥3 years</th>
<th>≥4 years</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. North Region</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SBB outbreak</td>
<td></td>
<td>0.11</td>
<td>0.15</td>
<td>0.27</td>
<td>0.1</td>
</tr>
<tr>
<td>Forested</td>
<td></td>
<td>0.02</td>
<td>0.22</td>
<td>0.21</td>
<td>0.23</td>
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<tr>
<td>Potential aridity</td>
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<td>-0.002</td>
<td>-0.003</td>
<td>-0.003</td>
<td>-0.002</td>
</tr>
<tr>
<td>% Canopy cover</td>
<td></td>
<td>0.002</td>
<td>0.002</td>
<td>0.002</td>
<td>0.23</td>
</tr>
<tr>
<td><strong>B. South region</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SBB Outbreak</td>
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<td>-0.06</td>
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<tr>
<td>Forested</td>
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<td>-0.01</td>
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<tr>
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<td>0.002</td>
<td>0.002</td>
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</tr>
</tbody>
</table>

* P < 0.1.
** P < 0.05.
*** P < 0.01.
stands in the south were dominated by even-aged, mature white spruce (Berg and Anderson, 2006), leading to more than 90% of trees killed and a 87% reduction in stand basal area (Werner et al., 2006; Wolken et al., 2011). Subsequently, calamagrostis, an early successional dominant grass, proliferated extensively throughout SBB-affected stands in the southern region (Boucher and Mead, 2006; Holsten et al., 1995; Lieffers et al., 1993; Schulz, 1995). The grass can form a thick mat of dead litter that can constrain spruce regeneration by reducing soil temperatures and out-competing tree seedlings for light and nutrients (Werner et al., 2006; Wolken et al., 2011). Though, inventories suggest sufficient regeneration has occurred to eventually restock most stands (Boucher and Mead, 2006).

We found that SBB outbreak did not influence likelihood of subsequent burning in the southern study region. White spruce in this area have burned rarely during the Holocene, with a fire return interval of 400–600 years and some stands not burning for more than 1000 years (Berg and Anderson, 2006). It appears bark beetle outbreak has done little to alter the fire history of the region (Berg and Anderson, 2006), with one caveat. Our study was designed to minimize confounding effects of people on patterns of burning. Yet, some fire suppression still did occur, particularly in the southern study area. Although our finding that bark beetle outbreak has no effect of subsequent likelihood of burning in the south is consistent with past studies and the fire history (Berg and Anderson, 2006), it is impossible to completely rule out the potential influence of suppression on patterns of burning. Sufficient data were not available to statistically account for suppression activities that did occur.

Potential aridity was not related to likelihood of burning in either study region. Generally, climate is considered a key driver of boreal fire regimes at regional scales and strong linkages exist between annual area burned and climate trends over long time periods (e.g., Kelly et al., 2013) and broad spatial scales (e.g., Duffy et al., 2005). At finer scales, fire spread is primarily driven by fuels in combination with extreme weather conditions that occur for just a few days or even hours. Gridded spatially explicit data of weather patterns at fine temporal resolutions was unavailable for use in this analysis.

4.1. Management applications

Population density on the Kenai Peninsula is approximately three times greater than the average in Alaska (United States Census Bureau, 2010) and there is a pronounced wildland urban interface where homes are interspersed among natural forests (Hansen and Naughton, 2013). There has been substantial concern that SBB outbreak would increase the frequency, size, and severity of fires (Flint, 2006). Many fires have been suppressed since the 1990s outbreak as a result (Morton et al., 2006). While fire suppression can lead to short-term protection of people and property, excluding natural-caused wildfire will likely increase the extent of late-succession forest and could heighten the risk of large catastrophic wildfires (Chapin et al., 2003).

Significant federal and state resources have also been expended to develop community wildfire protection plans and reduce hazardous fuels in high-risk areas along the road network (Hansen, 2014). These efforts have had some success, and the approach is likely more promising than suppression for effectively protecting people and property over the long term. Results of this study could be used to direct application of fuel treatments on the western Kenai Peninsula and other areas of Alaska, if SBB outbreaks occur in the future. For example, managers could prioritize treatment in areas where white spruce are interspersed with more flammable black spruce.

5. Conclusion

We characterized how a massive SBB outbreak has influenced subsequent likelihood of burning in boreal forest of the Kenai Peninsula. Forest-landscape structure was a critical determining factor. Likelihood of burning increased in areas where flammable black spruce trees were intermixed with beetle-affected white spruce. We suspect that post-outbreak surface-fuel accumulation may increase the flammability of white spruce stands that would have once served as fire breaks and may also explain why our findings differ from many studies conducted in other systems (e.g., Rocky Mountains). Conversely, SBB outbreak had no effect on subsequent likelihood of burning in stands of uniform white spruce where fires have been historically rare (fire return interval of 400–600 years). Our results may help to anticipate the dynamics and consequences of future boreal bark beetle outbreaks, as climate warms at high latitudes. White spruce is widely distributed throughout interior Alaska (Calef et al., 2005) and interior white spruce burn substantially more frequently than white spruce on the Kenai Peninsula (Yarie, 1981). If beetle outbreaks begin to occur in interior Alaska, increased fuel loads may lead to a higher likelihood of subsequent burning, particularly when white spruce are intermixed with or adjacent to more flammable black spruce.

Acknowledgements

This paper is dedicated to the memory of Kipling Rand. A true sage of the mountains, his passion for conservation of wild places will never be forgotten. We thank J. Morton and E. Berg for valuable insight into social and ecological dynamics on the Kenai Peninsula, Alaska. We thank M. Turner, W. Romme, D. Donato, and B. Harvey for insightful feedback on earlier versions of this manuscript.

References


