

**Stand and landscape level effects of a major outbreak of spruce beetles on forest
vegetation in the Copper River Basin, Alaska**

(submitted to Forest Ecology and Management)

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Abstract

From 1989–2003, a widespread outbreak of spruce beetles (*Dendroctonus rufipennis*) in the Copper River Basin, Alaska, infested approximately 240,000 ha of forests in the region. During 1997 and 1998, we measured forest vegetation structure and composition on 136 20-m x 20-m plots to assess both the immediate stand and landscape level effects of the spruce beetle infestation. A photo-interpreted vegetation and infestation map was produced using color-infrared aerial photography at a scale of 1:40,000. We used linear regression to quantify the effects of the outbreak on forest structure and composition. White spruce (*Picea glauca*) canopy cover and basal area of medium-to-large trees [≥ 15 cm diameter-at-breast height (1.3 m, dbh)] were reduced linearly as the number of trees attacked by spruce beetles increased. Black spruce (*Picea mariana*) and small diameter white spruce (< 15 cm dbh) were infrequently attacked and killed by spruce beetles. This selective attack of mature white spruce reduced structural complexity of stands to earlier stages of succession and caused mixed tree species stands to lose their white spruce and become more homogeneous in overstory composition. Using the resulting regressions, we developed a transition matrix to describe changes in vegetation types under varying levels of spruce beetle infestations, and applied the model to the vegetation map. Prior to the outbreak, our study area was composed primarily by stands of mixed white and black spruce (29% of area) and pure white spruce (25%). However, the selective attack on white spruce caused many areas to transition to black spruce dominated stands (73% increase in area) or shrublands (26% increase in area); the post-infestation landscape was thereby composed by more even distributions of shrubland and white, black, and mixed spruce communities (17–22% of study area). Changes in the

cover and composition of understory vegetation were less evident in this study. However, stands with the highest mortality due to spruce beetles had the lowest densities of white spruce seedlings suggesting a longer forest regeneration time without an increase in seedling germination, growth, or survival.

Keywords: Alaska, *Dendroctonus rufipennis*, Forest disturbance, Landscape-level changes, Spruce beetle, Vegetation change, White spruce.

1. Introduction

Natural disturbances are a major factor governing the distribution and diversity of plant communities across landscapes (White and Pickett, 1985). In the boreal forests of south-central Alaska, such disturbances include floods, fire, disease, and insect outbreaks. Spruce beetles are endemic to south-central Alaska and are usually present in small numbers in spruce (*Picea* spp.) stands (Werner and Holsten, 1985; Holsten et al., 1991). Occasionally large-scale outbreaks arise in response to warm temperatures (Werner and Holsten, 1985; Berg et al., this issue), large numbers of spruce suitable for breeding (Werner and Holsten, 1985), or other disturbances such as windthrow or logging (Dyer and Taylor, 1971). In 1989, a widespread epidemic of spruce beetles began in the Copper River Basin, Alaska and infested over 240,000 hectares of forest (U.S. Forest Service, 2004). The last major outbreak in the Copper River Basin occurred in the late 1910s and early 1920s, during which an estimated 81,000 ha of forest were infested (Moffit, 1922; Holsten, 1990). Major outbreaks of spruce beetles influence not only

stand structure (Hard et al., 1983; Veblen et al., 1991; Doak, 2004), but also the composition of understory plant communities and fuels available to fires (Holsten et al., 1995; Schulz, 1995). At a landscape scale, the size, distribution, and diversity of vegetation patches should be altered substantially by large outbreaks of spruce beetles, however, such effects have not been evaluated in Alaska.

Spruce beetles change forest stand structure by attacking the slower growing, larger diameter spruce, thereby lowering the average diameter and height of trees in forest stands (Hard et al., 1983; Veblen et al., 1991; Doak, 2004). The death of the larger dominant and co-dominant conifers from bark beetle (*Dendroctonus* spp.) outbreaks may release both smaller suppressed trees (Veblen et al., 1991) and understory vegetation plants from competition for light and nutrients (Kovacic et al., 1985; Holsten et al., 1995; Stone and Wolfe, 1996). For example, several studies in temperate forests have reported increased understory biomass and plant productivity following various bark beetle epidemics in lodgepole pine (*Pinus contorta*; Stone and Wolfe, 1996), ponderosa pine (*Pinus ponderosa*; Kovacic et al., 1985), and spruce-fir stands (*Picea engelmannii*-*Abies lasiocarpa*; Yeager and Riordan, 1953). Yet, boreal forests with their characteristic permafrost, thick mats of organic matter, and low species diversity, may respond differently than temperate forests to insect disturbance.

The majority of research on spruce beetles in Alaska has taken place on the Kenai Peninsula (e.g., Hard et al., 1983; Hard, 1985; Werner and Holsten, 1985; Reynolds and Hard, 1991; Holsten et al., 1995; Schulz, 1995), with only a few studies from the Copper River Basin (Loso, 1998; Matsuoka et al., 2001; Doak, 2004). The Kenai Peninsula is coastal, farther south, and has a more temperate climate in comparison to the Copper

River Basin, which is interior with a continental climate, lower precipitation, and lower and higher temperatures in the winter and summer, respectively. Thus the effects of spruce beetle outbreaks on stand structure and understory plant communities in the Copper River Basin may be quite different than those reported from the Kenai Peninsula. Land managers within the region, specifically Wrangell-St. Elias National Park and Preserve, were interested in the spatial extent and impacts of spruce beetles on forest vegetation and wildlife habitats in the region (Wesser and Allen, 1999; Matsuoka et al., 2001). More recently, subsistence use of beetle-killed spruce and concerns over potential fires hazards in infested stands have both increased (D. Sharp, National Park Service, personal communication).

In this study, we examined the stand and landscape level effects of a spruce beetle outbreak on forest vegetation structure and composition in the Copper River Basin, Alaska. Our objectives were to 1) determine the immediate effects of spruce beetle infestations on forest structure and composition at the stand level; 2) map vegetation cover and the location of beetle infestations; and 3) determine short-term effects of spruce beetle infestations on the total area, number patches, and average patch size of different vegetation types at the landscape level.

2. Methods

2.1. Study area

We conducted our study from 1997–1999 in the Copper River Basin, in south-central Alaska. The study area was approximately 257,000 ha in size and within the administrative boundaries of Wrangell-St. Elias National Park and Preserve (Fig. 1). Elevation ranged from 190–1900 m, with the majority of the study area below tree-line (approximately 900 m). The study area was composed of a heterogeneous complex of vegetation types resulting from spatial variation in topography, soils, drainage, temperature, and disturbances including fire and insect outbreaks. Coniferous forests dominated by white spruce and mixed forests of white spruce and quaking aspen (*Populus tremuloides*) or balsam poplar (*Populus balsamifera*) were common on well-drained sites and along streams and flood plains. Black spruce forests occupied low lying, poorly drained sites.

2.2. Vegetation and infestation mapping

We mapped the distribution of vegetation types and spruce beetle infestation levels (Table 1) in the study area using manual photo-interpretation of color-infrared aerial photography (Lillesand and Kiefer, 1987) at a scale of 1:40,000 with a minimum mapping unit of 2 ha. Aerial photography for the study area was acquired in August 1997. To train the interpreters and assist in map classifications, we flew over and inspected from the ground 113 patches that represented the range of photo-signatures within the study area. We also used an additional 286 ground truth sites from a previous project in the area (M.B. Cook, National Park Service, unpublished data) to refine map

classification of vegetation communities. Photo-interpreted polygons and their attributes were entered into a geographic information system (GIS) as vector data.

We classified the structure and composition of each mapped polygon using a modification of a vegetation classification developed for the region by Loveland (1984). Each vegetation class was defined by the dominant overstory species, a canopy cover class, tree diameter size class (if forested), the subordinate understory shrub type if visible, and infestation level. We coded the vegetation classes using an alpha-numeric system (Table 1). In areas with infestations we mapped the pre-infested tree species, cover, and size class, which was possible because a majority of the study area was infested just 1–4 years prior to the 1997 photography (U.S. Forest Service, 1998).

Canopy cover of infested stands was evident because most beetle-killed spruce were still standing and dying spruce, lacking chlorophyll, were discernable by a distinct bluish hue on the color-infrared photography. Based on photo-interpretation and analysis of field data, we did not assign infestation levels to polygons that did not contain white spruce.

We conducted an accuracy assessment of the resulting vegetation map by verifying the composition and structure of 109 polygons by helicopter and 116 polygons from ground sampling. Specifically we made ocular estimates of the percent of spruce infested by spruce beetles, percent canopy cover of dominant tree and shrub species, and the dominant size class of trees, and assigned a vegetation map class for each polygon. We assessed the accuracy of the map in differentiating spruce species, canopy cover, size classes, and infestation levels by comparing map and ground classifications of same polygons.

2.3. Forest sampling methods

We collected detailed information on forest structure, composition, and understory plant communities at 136 vegetation plots in spruce forests during July–August 1997 and 1998 (Fig. 1). We used a stratified random sampling design to select stands (mapped polygons) based on 12 forest types and the presence or absence of beetle infestations (Table 2). We used stratification to ensure that our sampling was representative of the various types of white spruce forests, with and without spruce beetle infestations in the study area. For each of the 12 forest types, 4–5 polygons were randomly selected for both infested and non-infested stands. In 1997 we selected stands using the Loveland (1984) map in combination with the U.S. Forest Service aerial maps of spruce beetle outbreaks (U.S. Forest Service, 1997). In 1998 we selected stands using the vegetation map developed in this study; in addition we increased our sampling in stands of large diameter white spruce to increase the number of plots with higher levels of infestation. Plots were assigned a vegetation class at the plot level, which did not always match the vegetation map class. Consequently, distribution of the samples within the vegetation classes and infestation classes varied from the intended sampling regime (Table 2).

Within each selected polygon, we randomly selected a single point where we established a 20-m x 20-m macroplot (0.04 ha) to measure vegetation structure and floristics of the stand. For all trees ≥ 2.5 cm diameter-at-breast height (dbh), we recorded the species; dbh (cm); crown radius (cm); and evidence of disease, insect attacks, and other damage. Crown radii were estimated for beetle- and other recently killed trees by

measuring from the tree bole to outermost end of the dead branches. Trees ≥ 15.0 cm dbh were measured on the full macroplot; trees 2.5–14.9 cm dbh were measured on a 20-m x 10-m subplot within the macroplot. A one-meter belt transect around the inside perimeter of the macroplot (0.007 ha) was used to count the number of tree seedlings/saplings (< 2.5 cm dbh) by species.

Within each macroplot we sampled cover and structure of vegetation overstory, understory, and ground cover using a height-stratified, point-intercept technique (Cooper et al., 1987). We recorded the presence (intercept) or absence of plants by species in each of four height strata (0–20 cm, 20 cm–1.5 m, 1.5–3.0 m, and > 3.0 m above the ground) at 60 points spaced every meter along three parallel 20-m transects. The sample size of 60 sampling points per plot was determined from the asymptote of a species accumulation curve developed from sample plots in similar vegetation types with 120 points (J. Allen, National Park Service, unpublished data). The number of intercepts in each height class was divided by the number of sample points to provide an estimate of percent coverage by height strata for each species or substrate. For each species we used the height classes with the greatest overall cover in analyses of vegetation cover. Only 126 of the 136 plots had point-intercept data collected, due to time constraints in the field.

2.4. Data analysis

2.4.1. Stand level changes in vegetation

For each vegetation plot we summed the number of species of vascular plants, lichens, and bryophytes detected from point-intercept sampling. We compared the average number of species among the four levels of infestation by spruce beetles using a one-way analysis of variance (ANOVA). We calculated levels of infestation as the percent of the spruce on the plot that were either attacked or killed by spruce beetles. Only plots where white spruce were dominant or co-dominant were included in this and the following two analyses ($n = 101$ plots).

For each of 18 common understory plants we tested for differences in mean cover by infestation level using a Kruskal-Wallis one-way ANOVA. We restricted our analysis to species that occurred on ≥ 30 plots because we had low statistical power to detect differences for the many species that were infrequently sampled. We used a non-parametric test because of unequal variances and non-normal distributions. For each tree species we used a Kruskal-Wallis one-way ANOVA to test for differences in the density of seedlings by level of infestation. The frequency of spruce with and without spruce beetles was compared among species and size classes of spruce trees using a chi-square analysis.

Next we quantified structural changes in trees by species and size class in relation to infestations of spruce beetles using linear regression where reductions in canopy cover and tree basal area were treated as response variables and the proportion of spruce attacked or killed by spruce beetles was treated as the independent variable. We calculated reduction in basal area for each plot by summing the basal area per ha of all trees killed by spruce beetles. Similarly, we calculated reduction in canopy cover for

each plot by summing the tree canopy area calculated from the radii among all trees killed by spruce beetles.

2.4.2. Landscape level changes in vegetation

To assess landscape level effects of the outbreak, we used plot data from forest types with ≥ 2 plots (Table 2) and developed a vegetation transition matrix to apply to the vegetation map. We combined live and beetle-killed tree data to calculate the average pre-infestation values for basal area by species and size class, and canopy cover by species for each forest type. For each combination of forest type and infestation level we used the regression models described above to estimate mean reductions in canopy cover, basal area of medium and large white spruce, and total basal area of white spruce, using the midpoint of each infestation level (trace = 5%, low = 20%, moderate = 45%, high = 80%) in the regression models. We subtracted these mean reductions from the average pre-infestation values to calculate the post-infestation forest structure for each forest type under each infestation level. We then developed a transition matrix of pre-infestation forest types and the post-infestation forest types that were predicted by our model.

We applied the transition matrix and the mapped infestation levels to the polygon based landcover map of vegetation types to estimate the post-infestation landscape. We compared the pre- and post-infestation landscapes using Fragstats*arc (McGarigal and Marks, 1995) to assess changes in the distribution, extent, and configurations of vegetation types across the study area. We aggregated the map vegetation classes for both maps into seven general classes to reduce data volume and complexity for

Fragstats*arc analyses (McGarigal and Marks, 1995). These classes include black spruce, white spruce, mixed spruce, white spruce–deciduous, deciduous, shrub, and other. We used five landscape metrics to describe the distribution, density, shape, and size of each generalized vegetation class across the study: total area (ha), number of patches, density of patches (per km²), mean patch size (ha), and mean shape index (MSI) which measures the average perimeter-to-area ratio.

We used SPSS statistical package (SPSS, 2004) for all analyses. Significance level of statistical tests was set at $P < 0.05$; means are presented $\pm$ SE.

3. Results

3.1. Vegetation and infestation map

The total amount of forested area prior to the infestation was estimated at 181,228 ha within the 256,975 ha study area. Stands with white spruce (pure and mixed) made up 58% of the study area. The remaining pre-infestation landscape consisted of 43,524 ha of shrublands (17% of the study area), 25,716 ha of pure black spruce forest (10%), 6,954 ha pure deciduous forest (3%), 4,228 ha of harvested forests (2%), and 27,896 ha of other land cover (11%) prior to the infestation. Of the forest types containing white spruce, 73,346 ha had greater than 10% of its white spruce killed by spruce beetles; this constituted 29% of the study area and 49% of the white spruce forest types.

Based on error matrices (Wesser and Allen, 1999), we found that overall accuracy of the map varied from 61–74%, depending on the map attribute. Overall, our

classification of beetle infestation levels was 74% accurate. Errors typically occurred from underestimating infestation levels for stands with dense canopies and overestimating infestation levels in mature black or mixed spruce stands. We had 64% correct classification of major species. Correct classification was highest for white spruce, while mixed spruce types were overestimated in the map. The overall correct classification for canopy cover and size classes was 71% and 61%, respectively. Open canopy classes and small diameter classes had the highest map accuracy.

3.1. Stand level changes in vegetation

We identified a total of 209 species of plants on 126 macroplots including 5 tree, 31 shrub, 8 dwarf shrub, 45 forb, 5 lower vascular plant, 15 grass and sedge, 48 lichen, and 51 bryophyte species. There was no difference in the mean number of species per macroplot among the four infestation levels ($F_{3,97} = 1.4$, $P = 0.25$): Trace = 23.6 ± 0.7 , Low = 21.8 ± 0.9 , Moderate = 20.5 ± 1.6 , High = 23.2 ± 2.2 . We did not detect a difference in cover among the four infestation levels for any of the 18 understory species (Table 3).

Among tree species, the average density of seedlings of white spruce and black spruce decreased under progressively higher infestation levels (Table 4). The number of trees attacked by spruce beetles varied with size class strongly for white spruce ($\chi^2 = 547.8$, $df = 2$, $P < 0.001$) and marginally for black spruce ($\chi^2 = 5.876$, $df = 2$, $P = 0.053$). Spruce beetles attacked 48% of 893 large white spruce (≥ 23 cm dbh), 25% of the 1150 medium white spruce (15–22.9 cm dbh), and only 5% of 1315 small white spruce

sampled (<15 cm dbh). Black spruce were less frequently attacked, but followed the same pattern relative to size classes with spruce beetles attacking 12% of 8 large, 3% of the 95 medium, and 2% of the 1383 small black spruce sampled.

Reduction of total basal area of stands increased with the proportion of spruce infested by spruce beetles ($\underline{E}_{[1,134]} = 666.1$, $\underline{P} < 0.001$, $\underline{r}^2 = 0.83$; Fig. 2) as did canopy reductions ($\underline{E}_{1,134} = 641.2$, $\underline{P} < 0.001$, $\underline{r}^2 = 0.83$; Fig. 3). Reductions of basal area were greater among white spruce ($\underline{E}_{1,134} = 647.2$, $\underline{P} < 0.001$, $\underline{r}^2 = 0.83$) than black spruce (Fig. 4). Reductions in basal area were also positively related to the proportion of spruce infested in each size class of white spruce but large spruce had the greatest reduction and best fit ($\underline{E}_{[1,134]} = 314.56$, $\underline{P} < 0.001$, $\underline{r}^2 = 0.70$), compared to medium ($\underline{E}_{[1,134]} = 98.39$, $\underline{P} < 0.001$, $\underline{r}^2 = 0.42$) and small spruce ($\underline{E}_{[1,134]} = 19.11$, $\underline{P} < 0.001$, $\underline{r}^2 = 0.12$) (Fig. 5).

3.2. Landscape level changes in vegetation

Our transition matrix of pre- and post-infestation vegetation predicted few changes in vegetation type and forest structure under trace and low levels of infestation (< 30% spruce mortality), with the exception of woodland stands, which were predicted to change to shrublands under low infestation levels. White spruce forests with open canopies changed to woodlands under moderate levels of infestation and to shrubs under high levels of infestation. Mixed spruce and white spruce-deciduous forests lost white spruce as a major overstory species at moderate levels of infestation. Most forest types were predicted to change to non-forested vegetation types under high levels of infestation (Table 5).

Projecting the transition matrix to the map of landcover and infestation levels, we detected few changes between pre- and post-infestation landscapes in terms of the overall number, size, and shape of the vegetation patches. Total number of patches increased only slightly by 3% with a corresponding small decrease in mean patch size. The patches in both the pre- and post-infestation landscape had irregular perimeters (MSI) and tended to be more linear in shape (Table 6). More landscape changes, however, were detected for individual generalized vegetation classes (Table 7; Fig. 6). Overall, there was a transition from a pre-infestation landscape dominated by mixed spruce (29% of study area) and white spruce (25%) to a post-infestation landscape with more even percentages of mixed spruce, black spruce, white spruce, and shrublands (17–22%). Forest types with white spruce decreased in total area in the post-infestation landscape, with mixed spruce forests declining by 25%, pure white spruce forests by 17%, and white spruce–deciduous forest by 9%. These decreases in area corresponded with decreases in patch size among mixed spruce (-32%) and white spruce stands (-13%); however patches of white spruce–deciduous forest increased slightly by 4%. Loss of white spruce also resulted in the elimination of 5% and 12% of the white spruce and white spruce–deciduous forest patches, respectively. However, the number of mixed spruce patches increased by 10% (Table 7).

Corresponding with these decreases in area was a substantial increase in area of black spruce (73%) and smaller increases in area of shrublands (26%) and deciduous forest (12%) in the post-infestation landscape. These increases in area were associated with increases in the projected number of shrubland (23%) and deciduous forest patches (16%) and a decrease in the number of black spruce stands (-12%) in the study area.

Finally, mean patch size increased substantially among black spruce stands (82%), increase slightly for shrublands (2%), and decrease slightly among deciduous forests stands (-3%; Table 7).

4. Discussion

The outbreak of spruce beetles in the Copper River Basin had a major influence on forest vegetation at both the stand and landscape level soon after the regional forest disturbance ended. However, the effects were somewhat different at the two spatial scales with reductions in variation in structure and composition occurring at the stand level and an increase in variation in vegetation types taking place at the landscape level. Similar to several studies, we found that spruce beetles generally preferred medium and large diameter white spruce ($\text{dbh} > 15 \text{ cm}$) (Hard et al., 1983; van Hees and Holsten, 1994; Matsuoka et al., 2001; Doak, 2004), while black spruce and small white spruce ($\text{dbh} < 15 \text{ cm}$) were infrequently attacked and killed. This selective attack of the larger spruce reduced the structural complexity of stands and returned infested forests to structurally earlier stages of succession (Veblen et al. 1991, Holsten et al. 1995). Under high levels of infestation, stands dominated by mature white spruce were actually converted to shrub or herbaceous plant communities. Furthermore, mixed forests with white spruce lost their mature white spruce component and became more homogeneous in tree species composition often transitioning to black or deciduous forests.

Unlike these reductions in variability at the stand level, the spruce beetle outbreak increased the variability in general vegetation types at the landscape level. Prior to the

outbreak our study area was dominated by stands of mixed spruce (29% of study area) and white spruce (25%), with lesser areas comprised of other land cover types (< 18%). The outbreaks disproportionately reduced the area and patch size of white and mixed spruce stands causing many to shift to black spruce or shrub communities. The outbreak thereby created a post-infestation landscape with more even areas of shrub and white, black, and mixed spruce communities (17–22% of study area). The number of black spruce patches decreased slightly but the average patch size increased significantly (82%) due to the coalescing black spruce stands with adjacent patches of mixed spruce that lost white spruce during the outbreak. However, changes in forest types from mixed to black spruce may have been slightly overestimated in this study, due to errors in assigning white spruce to stands in our vegetation map that were actually dominated by black spruce. Despite these changes, the outbreak did not decrease the overall size or increase the number of patches when the general vegetation types were combined. Thus the natural disturbance by spruce beetles diversified the mosaic structure of vegetation patch types across landscapes (White and Pickett, 1985, Johnson et al., 1998), but did not lead to an overall increase in fragmentation.

The low densities of white spruce seedlings among beetle infested stands that we observed were similar to findings on the Kenai Peninsula (Holsten et al., 1995), Colorado (Veblen et al., 1991), and other locations in the Copper River Basin (Loso, 1998). However, the reasons for low numbers of spruce seedlings may have resulted from somewhat different processes in infested forests of the Copper River Basin and Kenai Peninsula. On the Kenai Peninsula, bluejoint (*Calamagrostis canadensis*) proliferated following spruce beetle outbreaks and likely decreased spruce seedling germination and

growth by lowering soil temperatures and increasing competition for light and nutrients (Holsten et al., 1995). However, we did not detect an increase of grasses in this study, and bluejoint was detected on only 3 or 126 plot sampled. Instead, the thick organic layer ($\bar{x} = 15$ cm; J. Allen, National Park Service, unpublished data) and high moss cover in the forest understory in the Copper River Basin may have acted similarly to decrease soil temperatures and thereby inhibit spruce seedling germination, growth, and survival. White spruce seedlings regenerate best on exposed mineral soil, generally after fires (Lutz, 1956; Zasada, 1986). Unlike a fire, spruce beetles leave the forest floor intact which may not provide a suitable seed bed for spruce seedling regeneration. Therefore, subsequent disturbances that remove the moss and organic layer may be needed in infested forests in the region to increase density, growth, and survival of spruce seedlings to meet reforestation goals (Zasada, 1986; Holsten et al., 1995; Goodman and Hungate, this issue).

Ground disturbance may also be needed to trigger the increases in cover and number of herbaceous plant species that typically follow bark beetle outbreaks in temperate forests (Kovacic et al., 1985; Stone and Wolfe, 1996) but were absent in this study. This was also quite different from the Kenai Peninsula, where bluejoint and fireweed (*Chamerion angustifolium*) proliferated after spruce beetle outbreaks in white and Lutz spruce (Holsten et al., 1995). In general, the low cover of grasses found in the study area should lower the potential for fast spreading fires (Anderson, 1982). This may be particularly true in infested forests with high densities of alders (*Alnus* spp.) (Matsuoka et al., 2001) or willows (*Salix* spp.) in the region, which generally do not carry fire well (Rowe and Scott, 1973; Anderson, 1982). At the time of our study most of the

dead spruce were still standing, and increases in woody debris were not yet evident (Wesser and Allen, 1999). As beetle-killed spruce begin to fall we expect to see increased fuel loads (Schulz, 1995), which could increase fire intensity (Anderson, 1982).

5. Conclusions

Spatially explicit models of landcover are increasingly used in decision making for resource planning, modeling wildlife habitat use, and predicting fire spread. For example, fire growth models, such as FARSITE (Finney, 1998), could be used in conjunction with our landcover maps of vegetation and beetle outbreaks to assess differences in fire potential between pre- and post-infestation landscapes and identify important areas for focusing on reducing hazardous fuels. Such models may be particularly useful as current rates of warming (ACIA, 2004) and related landscape drying in the Copper River Basin (Riordan, 2005) may increase the likelihood of large fires occurring in the area.

In this study we examined changes in vegetation at the stand and landscape level relatively soon after a massive infestation of spruce beetles (1–5 years post infestation). The vegetation structure of infested forests in the Copper River will continue to change as seedlings and residual understory trees grow in size and become a dominant vegetation form. Forest stands with low to moderate levels of infestation will probably see a release in the growth of the residual spruce and, over time, will look similar to how they were prior to infestation (Veblen et al., 1991). Thus diversity in the size and species of trees within these stands will likely increase with time. However, stands with the high spruce

mortality (>60% mortality) had the lowest spruce seedling densities, which could result in a longer regeneration time and low white spruce stem densities in the future. Large contiguous patches of tall willows (*Salix* spp.) dominated parts of our study area that were previously reported to have had spruce beetle infestations or wildfires in the early 1900's (Moffit, 1922; Lutz, 1956; Holsten, 1990; J. Allen, National Park Service, unpublished data). This suggests that shrubs may continue to dominate sites nearly 100 years following a large natural forest disturbance in the region and raises questions as to whether forests heavily infested by spruce beetle in the 1990s will return to spruce forests.

Stands that were infested by spruce beetles were generally late successional white spruce stands with a dense feather moss cover and thick organic layers on the forest floor. We suspect that relatively few changes will occur to the herbaceous species in terms of cover or diversity unless a significant ground disturbance occurs. Shrub cover may increase with greater incidence of light, but this may not occur until dead trees lose their branches or fall further opening the canopy 10–15 years after the infestation (Schultz, 1995). In addition, we do not expect a change in shrub types due to spruce beetle infestation, but only an increase in cover of shade-intolerant shrub species already present prior to the infestation.

The diversity of community types we grouped together under various infestation levels and the relatively short period of time post infestation (65% of our plots were infested < 5 years prior to our field measurements) may have reduced our ability to detect changes in the understory composition. We recommend that future assessments of the effects of spruce beetles on forest vegetation resample plots through time rather than take

the point-in-time sampling used in this study. Resampling through time will help control for spatial variation in plant communities that results from variation in soils, topography, and other disturbances; will be more sensitive in detecting successional changes in plant communities; and will help provide greater insight into the longer-term effects of the outbreak.

Acknowledgments

This project was funded through the National Park Service's Natural Resources Preservation Program and initiated by R. Galipeau, P. Happe, and K. Jenkins, former staff at Wrangell-St. Elias National Park and Preserve. D. Sharp, M.B. Cook, and C. Mitchell of Wrangell-St. Elias National Park and Preserve provided valuable oversight and input from a natural resource management perspective. We thank K. Oakley, E. Holsten, S. Matsuoka, C. Handel, B. Schulz, K. Boggs and D. McGuire for helpful suggestions on sample design, data analysis, and improving earlier versions of this manuscript. The vegetation and infestation map was completed by the U.S. Forest Service, Forestry Sciences Laboratory in Anchorage, Alaska with help from R. Koleser, T. Kelley, W. Burgess, and P. Smith. The GIS analysis and accuracy assessment was initiated by M. Murray, and completed by USGS EROS Alaska Field Office, through the work of M. Fleming, K. Brunt and E. Binnian. Field data collection and a myriad of other tasks were completed by V. Ables, J. Balcomb, T. Burke, S. DiGiacomo, C. Fletcher-Gilbert, I. Herfindahl, A. Martin, M. Moody, R. Murray, G. Royce, D. Swaim,

475 M. Swaim, and J. Wilder. We also thank Ahtna Native Corporation for kind permission
476 to access their forested lands.

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571 Dyrness, C.T. (Eds.), Forest ecosystems in the Alaskan taiga. Springer-Verlag,
572 New York, pp. 45-73.

573 Table 1. Classification of attributes used to map vegetation and infestation levels for the
 574 Copper River Basin, Alaska. A final map class would appear as W230 or W-BS210.

Map Attribute	Code	Definition
Dominant species	W	White spruce
	BS	Black spruce
	DU	Deciduous forest, species undifferentiated
	Shrub	Shrub species undifferentiated
Canopy closure	1	Woodland canopy (10–24%)
	2	Open canopy (25–59%)
	3	Closed canopy (>60%)
Diameter size class	1	Small (<15 cm dbh)
	2	Medium (15–22.9 cm dbh)
	3	Large (>23 cm dbh)
Infestation	0	Trace ($\leq$ 10% of spruce killed by spruce beetles)
	1	Low (11–30% spruce mortality)
	2	Moderate (31–60% spruce mortality)
	3	High (>60% spruce mortality)

575 Table 2. Forest types sampled ($\underline{n}$ = number of plots) for structure and composition,
 576 1997–1999, Copper River Basin, Alaska. Twenty-two additional plots were sampled, but
 577 were classified as other vegetation types not originally within the stratification.

Vegetation type	Class description	$\underline{n}$
BS21 or BS22	Black spruce, open canopy, small or medium trees	14
W-DU	Mixed white spruce & deciduous. Deciduous species, canopy, and size were not designated.	10
W-BS22	White-black spruce, open canopy, medium-sized trees	2
W-BS21	White-black spruce, open canopy, small trees	1
W12	White spruce, woodland canopy, medium-sized trees	1
W13	White spruce, woodland canopy, large trees	12
W21	White spruce, open canopy, small trees	6
W22	White spruce, open canopy, medium-sized trees	13
W23	White spruce, open canopy, large trees	37
W32	White spruce, closed canopy, medium-sized trees	6
W33	White spruce, closed canopy, large trees	12

Table 3. Average percent cover ($\pm$ SE) of common understory plant species among forest stands with different levels of spruce beetle infestations in the Copper River Basin, Alaska, 1997–1998. Infestation levels included Trace (0-10% spruce killed by spruce beetles, $\bar{n}$ = 39 plots), Low (11-30%, $\bar{n}$ = 34), Moderate (31-60%, $\bar{n}$ = 16), and High (>60%, $\bar{n}$ = 12). Chi-square statistics (χ^2) and related P -values are from Kruskal-Wallis tests for the effects of infestation level on cover.

Species	Infestation level				χ^2	P
	Trace	Low	Moderate	High		
Shrubs						
<i>Alnus</i> spp.	5.8 ± 1.8	3.2 ± 1.7	10.9 ± 4.7	3.4 ± 2.1	2.27	0.52
<i>Arctostapholos rubra</i>	4.1 ± 1.3	7.4 ± 1.8	4.3 ± 2.1	1.3 ± 0.6	6.57	0.09
<i>Empetrum nigrum</i>	13.8 ± 3.2	16.5 ± 3.4	15.7 ± 4.9	12.4 ± 4.8	2.023	0.57
<i>Ledum palustre</i>	11.5 ± 2.4	9.4 ± 2.1	11.5 ± 3.5	7.0 ± 3.16	0.38	0.94
<i>Linnaea borealis</i>	14.4 ± 2.4	9.0 ± 1.7	16.5 ± 3.6	16.0 ± 3.8	5.18	0.16
<i>Rosa acicularis</i>	5.0 ± 0.8	4.5 ± 0.7	7.1 ± 1.6	5.3 ± 1.2	1.59	0.66
<i>Salix</i> spp.	17.5 ± 3.1	9.1 ± 1.4	12.9 ± 3.7	8.9 ± 3.2	4.78	0.19
<i>Shepherdia canadensis</i>	2.5 ± 0.8	2.2 ± 0.8	3.4 ± 1.9	0.3 ± 0.2	3.43	0.33
<i>Vaccinium uliginosum</i>	5.8 ± 1.9	3.1 ± 1.0	3.8 ± 2.0	3.8 ± 2.6	0.23	0.97
<i>Vaccinium vitis-idaea</i>	20.0 ± 2.8	17.5 ± 2.7	26.0 ± 5.3	16.1 ± 4.8	2.10	0.55
Forbs and graminoids						
<i>Cornus canadensis</i>	8.2 ± 2.4	3.6 ± 1.3	4.6 ± 2.0	4.4 ± 1.8	2.78	0.43
<i>Chamerion angustifolium</i>	2.2 ± 0.6	0.6 ± 0.3	0.7 ± 0.4	0.7 ± 0.5	6.76	0.09
<i>Geocaulon lividum</i>	6.0 ± 1.1	3.3 ± 0.8	9.4 ± 3.9	4.8 ± 2.0	1.92	0.59
<i>Lupinus arcticus</i>	2.5 ± 0.6	1.2 ± 0.4	1.3 ± 1.0	1.5 ± 0.6	5.75	0.13

Species	Infestation level				χ^2	<u>P</u>
	Trace	Low	Moderate	High		
<u>Equisetum</u> spp.	8.0 ± 2.4	14.6 ± 3.9	15.9 ± 5.0	11.0 ± 5.8	2.57	0.46
Grasses ¹	4.8 ± 1.5	5.7 ± 1.6	7.4 ± 2.3	4.7 ± 1.6	3.06	0.38
Bryophytes and lichens						
<u>Hylocomium splendens</u>	42.5 ± 4.1	48.5 ± 3.9	54.0 ± 6.6	53.3 ± 8.4	3.11	0.37
<u>Peltigera aphthosa</u>	10.2 ± 1.7	9.8 ± 1.9	7.2 ± 2.8	3.5 ± 1.1	5.90	0.12

584

585

¹ Grasses include species of the genus Calamagrostis, Poa, and Festuca.

586 Table 4. Average density of tree seedlings (<2.5 cm dbh, stems per ha) by species and
 587 level of infestation by spruce beetles, 1997–1998, Copper River Basin, Alaska.
 588 Infestation levels included trace (0-10% spruce killed by spruce beetles, $\underline{n}$ = 39 plots),
 589 low (11-30%, $\underline{n}$ = 34), moderate (31-60%, $\underline{n}$ = 16), and high (>60%, $\underline{n}$ = 12).

Tree species	Infestation level				χ^2	$\underline{P}$
	Trace	Low	Moderate	High		
<u><i>Picea glauca</i></u>	3203	4399	936	410	9.62	0.02
<u><i>Picea mariana</i></u>	1674	504	290	104	7.51	0.06
<u><i>Populus tremuloides</i></u>	303	106	0	188	3.10	0.37
<u><i>Populus balsamifera</i></u>	84	140	360	125	2.04	0.56
<u><i>Betula papyrifera</i></u>	197	8	203	0	4.28	0.23

Table 5. Transition matrix of pre- and post-infestation vegetation types following different levels of infestation by spruce beetles, 1997–1998, Copper River Basin, Alaska. Sample size (n) indicates the number of plots from which we used measurements of stand structure to model changes from pre- to post-infestation vegetation.

Pre-infestation type ¹	n	Post-infestation type by infestation level			
		Trace	Low	Moderate	High
W13	12	W13	Shrub	Shrub	Shrub
W21	6	W21	W21	W21	Shrub
W22	13	W22	W22	W12	Shrub
W23	37	W23	W23	W13	Shrub
W32	6	W32	W32	W32	W22
W33	12	W33	W33	W23	W23
W-BS11	3	W-BS11	Shrub	Shrub	Shrub
W-BS21 / W-BS22	3	W-BS21 / W-BS22	BS21	BS11	Shrub
W-DU23	2	W-DU23	DU23	DU12	Shrub
W-DU32	4	W-DU32	DU-W32	DU32	D32
W-DU33	3	W-DU33	DU-W33	DU32	D32

¹ Letters indicate the dominant or co-dominant tree types (BS = black spruce, W = white spruce, DU = deciduous species unspecified). The first number represents canopy closure class (1 = 10–24% cover; 2 = 25–59% cover; 3 = 60–100% cover). The second number represents dominant size class of trees [1 = small (<15 cm dbh); 2 = medium (15–22.9 cm dbh); 3 = large (>23 cm dbh)].

599 Table 6. General landscape metrics of pre- and post-infestation vegetation in the Copper
600 River Basin, Alaska.

Description	Pre-infestation	Post-infestation
Number of patches	2235	2301
Number of patches per km ²	0.87	0.90
Mean patch size (ha)	114.93	111.63
Mean shape index	1.89	1.90
Area weighted mean shape index	4.61	4.31

601 Table 7. Landscape-level changes in pre- to post-infestation vegetation, Copper River Basin, Alaska.

Generalized vegetation class	Area (ha)		Number of patches		Mean patch size (ha)	
	Pre-infestation	Percent change	Pre-infestation	Percent change	Pre-infestation	Percent change
Mixed spruce	75,425	-24.9	262	9.9	287.9	-31.7
Black spruce	25,716	72.7	252	- 5.2	102.1	82.0
White spruce	63,513	-17.5	480	- 5.2	132.3	-12.9
White spruce - deciduous	9,620	- 9.0	172	-12.2	55.9	3.8
Deciduous	6,954	12.3	158	15.8	44.0	- 3.1
Shrubland	43,524	25.7	322	23.0	135.2	2.2

FIGURES

Fig. 1. Study area and locations of 136 forest vegetation plots (●) in the Copper River Basin, Alaska, 1997–1998. Dark grey areas show the extent of spruce beetle outbreaks from 1989–2002 (U.S. Forest Service, 2004).

Fig. 2. The relationship between the reduction of spruce basal area (m^2/ha , $\underline{y}$) and percent of spruce attacked by spruce beetles ($\underline{x}$) in the Copper River Basin, Alaska was:

$$\underline{y} = 0.58 + 0.42 \cdot \underline{x}; \underline{r}^2 = 0.83.$$

Fig. 3. The relationship between the percent of canopy reduced ($\underline{y}$) and percent of spruce attacked by spruce beetles ($\underline{x}$) in the Copper River Basin, Alaska was $\underline{y} = -0.29 + 0.53 \cdot \underline{x}; \underline{r}^2 = 0.83$.

Fig. 4. The relationship between basal area reduction (m^2/ha ; $\underline{y}$) and the percent of spruce attacked by spruce beetles ($\underline{x}$) in the Copper River Basin, Alaska was significant for white spruce (▲; $y = 0.49 + 0.42 \cdot \underline{x}; \underline{r}^2 = 0.83$) but not for black spruce (○).

Fig. 5. The reduction in basal area ($\underline{y}$) that resulted from increasing percentages of spruce infested by spruce beetles ($\underline{x}$) were greater for large white spruce (■; $\underline{y} = 0.37 + 0.33 \cdot \underline{x}; \underline{r}^2 = 0.70$) than for either medium spruce (▲; $y = 0.10 + 0.08 \cdot \underline{x}; \underline{r}^2 = 0.42$) or small spruce (○; $\underline{y} = 0.12 + 0.01 \cdot \underline{x}; \underline{r}^2 = 0.12$), Copper River Basin, Alaska.

624 Fig. 6. Maps of the pre-infestation and post-infestation vegetation generalized in to seven
625 classes, Copper River Basin, Alaska. Notice the increase in pure black spruce and patchy
626 increase of shrublands post-infestation.