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Are density reduction treatments effective at managing for resistance or resilience to spruce beetle disturbance in the southern Rocky Mountains?

Christian Temperli [a,*], Sarah J. Hart [a], Thomas T. Veblen [a], Dominik Kulakowski [b], Julia J. Hicks [a], Robert Andrus [a]

[a] Department of Geography, University of Colorado, Campus Box 260, Boulder, CO 80309-260, USA
[b] School of Geography, Clark University, Worcester, MA 01610-1477, USA

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ABSTRACT

While bark beetle disturbance is an inherent component of coniferous forest ecosystems throughout the northern hemisphere, associated tree mortality and ensuing changes in forest composition and structure may conflict with timber, wildlife, water and other resource management objectives. Therefore, host tree density reduction has been suggested as a management option to increase forest stand resistance to beetle infestation, protect remaining trees and maintain forest resources. However, little is known about the effectiveness of such treatments to mitigate spruce beetle (*Dendroctonus rufipennis*) infestation or their influence on the stand structural controls of beetle disturbance in subalpine spruce-fir forests in the Rocky Mountains. We addressed this research gap in a retrospective assessment of the impact of density reduction treatments on stand composition and structure and subsequent (ca. 5–20 years later) spruce beetle infestation in southwestern Colorado. The study area was located at the fringe of an ongoing spruce beetle outbreak and at the time of sampling was affected by endemic to incipient beetle pressure. Stand structural attributes and beetle infestation were measured in treated and untreated control stands at four sites. Classification tree analyses revealed spruce diameter and its interaction with spruce basal area percentage as the most important drivers of tree-level beetle infestation. The number, basal area and proportions of beetle-infested spruce were lower in treated stands at sites where treatments significantly reduced the abundance of large spruce trees and where the abundance of large spruce was relatively high prior to tree removal. However, spruce density reduction did not result in a reduction of infestation rates in the remaining large (>25 cm DBH) spruce during the ongoing beetle outbreak. While confirming previous assessments on the limited effectiveness of density reduction treatments for mitigating stand-level beetle infestation, this study provides further insights on the stand structural controls that mediate forest management effects on beetle disturbance dynamics. We conclude by suggesting that priority should be given to management practices that enhance resilience by increasing spruce advance regeneration in the understory as opposed to treatments aimed at achieving resistance to beetle disturbance.

1. Introduction

Bark beetle (Curculionidae: Scolytinae) disturbances are an inherent component of northern hemisphere conifer forests. Given suitable climatic conditions and susceptible forest states, beetle populations from the genus *Dendroctonus* may erupt to landscape or even regional-scale outbreaks (Bentz et al., 2010; Lundquist and Reich, 2014; Raffa et al., 2008). Tree mortality resulting from beetle outbreaks alters forest composition and structure (Hansen, 2014; Veblen et al., 1991), which may affect water quality and quantity and carbon and nutrient cycling, change wildfire fuels and shift habitat qualities for wildlife (Fayt et al., 2005; Hansen, 2014; Hicke et al., 2012; Jenkins et al., 2014a,b; Kurz et al., 2008; Price et al., 2010; Pugh and Gordon, 2013; Saab et al., 2014). Widespread beetle-induced tree mortality may create significant

* Corresponding author. Address: Pflanzschulstrasse 73, 8004 Zurich, Switzerland. Tel.: +41 79 703 22 30.

E-mail addresses: christian.temperli@colorado.edu (C. Temperli), sarah.hart@colorado.edu (S.J. Hart), thomas.veblen@colorado.edu (T.T. Veblen), dkulakowski@clarku.edu (D. Kulakowski), julia.hicks@colorado.edu (J.J. Hicks), robert.andrus@colorado.edu (R. Andrus).

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challenges for forest management with respect to public safety at recreation sites and along roads and where timber production, wildlife habitat and water quality and quantity depend on the maintenance of high timber volume, old-growth forest structures, and relatively closed forest canopies.

In southwestern Colorado a spruce beetle (*Dendroctonus rufipennis* Kirby) outbreak started in the early 2000s and was first detected by the Aerial Detection Survey (ADS) in 2003 (Colorado State Forest Service, 2003; USDA Forest Service, 2013a). In 2013, 87400 new hectares (ha) of subalpine spruce-fir (*Picea Engelmannii* Parry, *Abies lasiocarpa* [Hooker] Nuttall) forest were affected by spruce beetles compared to 74,100 ha in 2012, indicating that this outbreak is still progressing (Colorado State Forest Service, 2014). While warmer temperatures in the past two decades have contributed to increased spruce beetle developmental rates and lower over-winter mortality (Bentz et al., 2010; Hansen et al., 2001), a number of forest stand attributes are known to contribute to the susceptibility of spruce-fir forests in the Rocky Mountains. Spruce beetles preferentially select large diameter trees (>25 cm diameter at breast height; DBH) for attack, because thicker bark protects beetle larvae from cold winter temperatures, provides more nutritional phloem and thus increases the survival rates of the beetle larvae (Dymerski et al., 2001; Hart et al., 2014b; McCambridge and Knight, 1972). Stress-induced slow growth is likely to further predispose spruce trees to attack (Hard, 1985). Dry sites, long-term drought and dense stand conditions that lead to resource competition among trees may reduce tree vigor and result in slow tree growth (Berg et al., 2006; DeRose and Long, 2012; Hart et al., 2014a). At the stand-level the US Forest Service assesses susceptibility using Schmid and Frye's (1976) beetle hazard rating system, which was developed based on research on the large 1940s spruce beetle outbreak in Colorado (e.g. McMahon and Smith, 2002). Besides site quality, this system rates stands according to average DBH of spruce >25.4 cm DBH, stand basal area and percent spruce in the canopy. Stands exceeding 41 cm mean DBH, 34 m^2/ha basal area, and 65% canopy dominant spruce are rated as highly susceptible. However, recent research (Hart et al., 2014a,b) indicates that under current warmer and dry conditions in Colorado, even stands with low hazard ratings are being attacked. These findings call for a reevaluation of stand structural conditions that may be conducive to beetle infestation under current climate, in order to update recommendations for forest management planning.

In general, there are two basic approaches to managing bark beetle disturbances (Fettig et al., 2014). The first, often termed direct control, aims at suppressing the ongoing outbreak of a localized beetle population, slowing beetle spread or protecting individual trees or stands. Such direct control measures may involve sanitation felling and the subsequent burning or debarking of infested trees, the use of pheromone-baits and trap trees and insecticides. These direct control measures are resource intensive, protect only a few trees and the effect is short-lived at best (Carroll et al., 2006; DeRose and Long, in press; Fettig et al., 2014). The second approach, often termed indirect control aims to enhance the resistance and/or the resilience of a stand to bark beetle infestation (DeRose and Long, in press). DeRose and Long (in press) define stand resistance as the effect of stand composition and structure on the severity of spruce mortality due to bark beetles. In contrast, they define a stand's resilience to spruce beetle as the effects of spruce beetle infestation on the post-infestation stand composition and structure. These definitions imply that managing for more resistant (or less susceptible) stands aims at mitigating spruce beetle infestation, whereas managing for resilience manages for specific post-infestation stand composition and structure goals. These goals may include the retention of large spruce or maintaining the potential for future spruce-dominance by favoring abundant advanced reproduction of spruce (DeRose and Long, in press).

Stand manipulations that enhance the resistance and/or the resilience to beetles include density reduction treatments with varying prescriptions and goals (Eaton, 1941; Six et al., 2014). Individual-tree and group-selection harvests aim at regenerating a particular species and thinning from above and shelterwood preparatory cutting are intermediate treatments with the goal of enhancing the growth of commercially valued species such as Engelmann spruce by reducing resource competition (Smith et al., 1997). Direct beetle management through sanitation cutting aims at suppressing beetle population growth by removing infested and susceptible trees and may have the indirect effect of enhancing resistance and resilience to subsequent beetle disturbance through spruce density reduction, and salvage cutting that aims at recovering the potential value of beetle-killed trees can have a similar indirect effect on subsequent beetle disturbance (Alexander, 1986; Bentz and Munson, 2000; Fettig et al., 2014, 2007). In practice these sanitation and salvage cuttings are often conducted in conjunction as a consequence of detecting beetle infestations too late (USDA Forest Service, 2013b; Table 1). Whether intended or unintended, density reduction treatments reduce the density of large susceptible spruce, while increasing the proportion of non-host trees. These structural changes deprive the beetles of their breeding habitat, alter the stand's micro-climate by increasing solar radiation and within-stand wind speeds, which may decrease brood survival (Amman et al., 1988) and foster dilution of semiochemical cues used by the beetles in host location, selection and colonization (Thistle et al., 2004). Hence such treatments may enhance a stand's resistance to beetles by lowering its attractiveness for beetle colonization and by decreasing the chance for the development of an irruptive beetle population

Table 1
Elevation (meters above sea level), aspect and management activity at sampling sites as listed in the Rocky Mountain Management activity database (RMACT).

Site	Treatment	Elevation	Aspect	Management activity
Dunton	Treated	3150	NW	Shelterwood Preparatory Cut, 1989–1990 Sanitation (salvage), 1998
Dunton	Control	3200	N	–
Stoner Mesa	Treated	3150	N	Shelterwood Preparatory Cut, 1989 Salvage Cut (intermediate treatment, not regeneration), 1995
Stoner Mesa	Control	3100	N	–
Hermosa	Treated	3000	N	Sanitation (salvage), 1992–1995 Group Selection Cut, 1992–1995
Hermosa	Control	3000	N	–
Tuckerville	Treated	3350	NW	Improvement Cut, 1991 Sanitation (salvage), 1992
Tuckerville	Control	3400–3500	NW	–

from within the stand until the remaining host trees grow back to susceptible sizes and densities. However, density reduction may also negatively affect stand-level resistance to spruce beetle infestation. Thinning from below (i.e. removal of smaller diameters) intended to increase fire resistance by removing surface and ladder fuels may result in stands dominated by large susceptible host trees (Agee and Skinner, 2005; DeRose and Long, in press). Trees damaged by logging activities along with logging residues offer ideal breeding habitat for beetles for ca. 2 years following treatment and may thus decrease stand resistance to beetles (Fettig et al., 2013; Schmid, 1981).

Depending on management goals, density reduction may enhance stand resilience in several ways. The retention of large spruce following beetle infestation may be achieved through a reduction of spruce dominance prior to beetle outbreak because spruce survival has been found to be higher in stands with a higher proportion of non-host canopy trees (DeRose and Long, 2007). Density reduction may secure the potential for a future dominance of spruce by opening the canopy of mature forests and initiating and favoring spruce regeneration such as in shelterwood cuts (DeRose and Long, in press; Hansen et al., 2010).

The effectiveness of density reduction to increase stand resistance has been examined for mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in many experimental and observational studies in various types of western pine forest (Fettig et al., 2014, 2007). Generally, it has been found that density reduction can be effective in reducing beetle infestation in lodgepole pine (*Pinus contorta* Douglas), ponderosa pine (*Pinus ponderosa* Douglas) and whitebark pine (*Pinus albicaulis* Engelm.) if conducted rigorously over broad spatial extents (Fettig et al., 2014) and when beetle populations are in endemic outbreak stages (Coops et al., 2008). However, the effectiveness of management options to mitigate the infestation of spruce-fir forests by the spruce beetle has received less attention (Fettig et al., 2007). In a retrospective study Hansen et al. (2010) assessed spruce beetle infestation rates in unspecific density reduction treatments and nearby control stands. They found slightly but significantly less beetle-induced mortality in treated stands both numerically and proportionally, but post-outbreak densities of large (>28 cm) spruce were still higher in untreated stands, indicating no effect of density reduction on the retention of large spruce. Hence Hansen et al. (2010) recommended enhancing resilience to beetle disturbance through treatments that favor spruce regeneration and thus the potential for future spruce dominance. Johnson et al. (2014) examined tree mortality attributed to spruce beetle, mountain pine beetle and western balsam fir beetle (*Dryocoetes confusus* Swaine) in two adjacent watersheds, one that was treated with patch cuts and one that served as control. Patch-cutting improved the survival probability of large spruce and lodgepole pine trees within 15 m of treated patches. To our knowledge these are the only two examples that quantified the effects of tree removal on stand resistance and resilience to spruce beetle infestation. In order to improve the scientific basis of spruce beetle management, we require a better understanding of the stand structural controls, by which the effects of density reduction on stand resistance and resilience are mediated.

The aim of this study is (1) to quantify the influence of density reduction on stand (e.g. <3 ha) structural attributes and how changes in these attributes may influence spruce beetle infestation and thus stand resistance. (2) We aim at quantifying the combined effect of spruce beetle infestation and density reduction on stand structure to derive implications for stand resilience to subsequent spruce beetle disturbance. We assess these relationships during an endemic to incipient beetle outbreak, since in this stage beetle population density and thus competition among beetles is low. Under these circumstances beetles have been shown to be selective in their search for host trees (Wallin and Raffa, 2004), which is when differences in stand structure due to density reduction treatments are most influential in determining whether beetles are attracted to a particular stand (Black et al., 2013; Hansen et al., 2010).

We test two main hypotheses. (1) Given a decrease in stand resistance with increasing spruce size, spruce basal area percentage and tree density (Dymerski et al., 2001; McCambridge and Knight, 1972; Schmid and Frye, 1976), we hypothesize that density reduction will reduce these predisposing stand structural traits and result in lower numbers and proportions of beetle infested spruce. (2) If density reduction is intended to enhance the stand resilience to spruce beetle, we hypothesize that the abundance of large (>25 cm DBH) uninfested spruce at this endemic to incipient stage of the outbreak will be larger in treated stands. That is, the combined mortality due to tree removal and beetles in treated stands should be smaller than the beetle-induced mortality in untreated stands. To address these hypotheses we sampled stand structure and beetle infestation in recently (1992–1998) treated and untreated stands at the western fringe of the current spruce beetle outbreak in southwestern Colorado.

2. Methods

2.1. Study area

Sampling occurred in summer 2013 in the western half of the San Juan National Forest in southwestern Colorado, west of the epicenter of the current spruce beetle outbreak, where the ADS recorded scattered spruce beetle activity that we considered in endemic or incipient stage (Fig. 1, Safranyik and Carroll, 2006; USDA Forest Service, 2013a). While patch and small clear cuts were common in the 1950–1970s, forest management in the subalpine spruce-fir zone (ca. 2850–3500 m above sea level, m a.s.l., Peet, 1981) was thereafter dominated by density reduction treatments such as commercial thinning from above and sanitation and salvage cuts (USDA Forest Service, 2013b). Southwestern Colorado's climate is characterized by a bi-seasonal precipitation regime with 30% falling as snow from December to March and 35% as rain from July through September (Toney and Anderson, 2006). The climate normal (1971–2000) of the station in Rico (2676 m a.s.l.) in the center of our study area lists an average annual precipitation of 68 cm and average January and July temperatures of −6 °C and 14 °C, respectively (http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?corico, last accessed June 5, 2014).

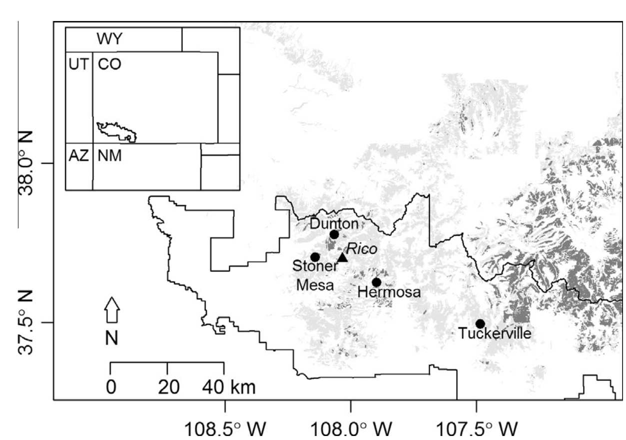

Fig. 1. Location of sampling sites (dots) within the San Juan National Forest (SJNF, black line) and the climate station in Rico (triangle). Light-grey shaded areas depict the distribution of spruce-fir forest (R2Veg) and dark grey areas depict aerially detected spruce beetle infestation between 2003 and 2012 (ADS). The inset at the top-left shows the location of SJNF in Colorado (CO).

Potential sampling sites were located by intersecting the spruce-fir forest type layer of the Rocky Mountain region vegetation database (R2Veg) with the ADS-spruce beetle layers of years 2003–2012 and the polygons of the US Forest Service's Rocky Mountain Region Management Activities database (RMACT, USDA Forest Service, 2013b) that indicated at least one recent but pre-outbreak (years 1990–1998) density reduction entry (e.g. salvage and sanitation cuts, commercial thinnings, shelterwood preparatory cuts and shelterwood cuts). Freely available orthoimagery (USDA National Agriculture Imagery Program: NAIP, and Google Earth) was used to visually confirm mapped beetle infestation (ADS) and density reduction treatments (RMACT). Potential sites were visited in the field and included for sampling if all of the following conditions were met: (1) ca. >5% of spruce trees showed signs of spruce beetle infestation (frass, pitch tubes, galleries and needle death or discoloration), (2) if previous tree removal could be identified by the presence of stumps, (3) if treated and untreated (control) but topographically similar stands could be clearly distinguished, and (4) if treatment and control stands were large enough to randomly place five plots at 200 m intervals, such that the spatial dependence of plots in terms of stand structure is minimized (e.g., Johnson et al., 2014). We considered four sites as suitable (Table 1). Sites at the localities of Dunton and Stoner Mesa were in the western and the sites at Hermosa and Tuckerville in the central San Juan Mountains. At each of these sites we randomly located five plots in the treated and the adjacent control stand resulting in a total of 40 plots.

2.2. Field methods

Rectangular plots were installed parallel to the slope with a fixed 20 m side length upslope and a >20 m side length parallel to the slope. Plot size (>400 m^2) was varied to include at least 20 spruce trees. In each plot we tallied all living and dead trees, snags and stumps by species. We measured all trees >4 cm DBH and recorded diameter at breast height (1.37 m) and relative canopy position (suppressed, co-dominant and dominant). Diameters of stumps <1.37 m in height were measured at the top-most full stem intersection. We assessed tree status and time since spruce beetle infestation following Hansen et al. (2010) based on the occurrence of a range of visual cues (Table 2). Spruce beetle attack was additionally confirmed by identifying spruce beetle galleries (Furniss and Johnson, 2002).

2.3. Analyses

We binned spruce status and time-since-infestation classes (Table 2) as "infested" (green attack through branch stage) and "uninfested" (live) as we considered the effect of density reduction treatments on stand and tree susceptibility to beetles as being relatively long-lasting. That is, beetles that attacked trees a few years after the last treatments in 1992–1998 (i.e. trees that are in branch stage today, Table 1) encountered very similar stand structures as beetles that attacked trees only recently (i.e. those that are currently in green attack through needle drop stage).

To test if density reduction affected resistance to infestation, we compared beetle infestation in treated and control plots by the absolute number and basal area of beetle infested spruce and the percentages thereof to the total (uninfested and infested spruce). Using Mann–Whitney U (MWU) tests we tested for differences in beetle infestation between treated and control stands for each site. We measured the intensity of density reduction treatments by the total and percent spruce basal area removed during treatments and related these measures to beetle infestation. The removed spruce basal area was derived from measurements of stump diameters and heights using species-specific stem taper functions (Ung et al., 2013). Spearman's rank correlation (SRC) tests were used to test these relationships at each site.

To relate stand structural attributes to beetle infestation we used stand structural variables that have previously been found to be predictive of spruce beetle infestation (DeRose and Long, 2012; Hansen et al., 2010; Hart et al., 2014b). As a plot-level measure of spruce size we used the quadratic mean diameter of spruce (QMD). Spruce basal area and density of spruce >25 cm DBH were used to measure the abundance of large spruce trees. The spruce percentage of total basal area was used to measure the proportion of spruce. To capture competition- (for light and other resources) related stress that may be conducive to beetle infestation (Eaton, 1941), we used a stand density index (SDI). SDI describes the utilization of the plot area of n individual trees taking tree size (DBH) into account. Considering all species, SDI was calculated as follows (Hart et al., 2014b; Negrón and Popp, 2004):

$$SDI = \sum_{m=i}^{n} \left(\frac{DBH_i}{25} \right)^{1.6} \quad (1)$$

For each site we tested for site-specific differences in stand structural attributes between treated and control stands using MWU tests and for correlations between stand structural variables and beetle infestation we used SRC tests.

To assess the effectiveness of density reduction treatments in preserving the growing stock of uninfested spruce we compared the plot means of the above stand structural variables that measure spruce abundance (percent and absolute spruce basal area, spruce density > 25 cm DBH and spruce QMD) between control and treated stands and between conditions before and during the current outbreak. Values of stand structural variables that refer to conditions during the current outbreak were calculated based on the remaining uninfested trees at the time of sampling, whereas to represent the pre-infestation conditions all standing trees were included. We tabulated plot mean and standard errors of each measure of spruce abundance by treatment and site.

At the level of individual spruce trees we tested for more frequent than expected infestation in large (>30 cm DBH) spruce trees using contingency table analysis and a Chi-squared test. Additionally, we assessed the importance of tree-level DBH and height class (suppressed, co-dominant, dominant), the plot-level stand

Table 2
Visual criteria used to classify tree status and time since beetle infestation.

Status	Time since beetle infestation	Visual criteria
Live	–	No signs of spruce beetle attack
Green attack	0–1 year	Frass below beetle entry holes and at stem base, green needles (indicative of current year attack)
Yellow attack	1 year	Yellow needles, frass, pitch tubes
Needle drop	<5 years	>50% of needles dropped
Twig stage	6–10 years	>50% of <1 cm twigs and <50% needles on tree, >90% bark retention
Branch stage	11–15 years	<50% of 1 cm twigs, <10% of needles, variable bark retention
Snag	–	No branches, >1.37 m
Stump	–	<1.37 m, cut by chainsaw

structural variables described above, the factor site (one level for each of the 4 sites), and treatment (control and partially cut) in determining tree-level beetle infestation (presence vs. absence). To this end we built a classification tree model using the Random Forest machine learning technique in R (Breiman, 2001; R Core Team, 2013). Variable importance was determined by the mean decrease in accuracy statistic, and the generalization error of the model was assessed by the out-of-bag error rate (OOB). Random forest is not dependent on any assumed distribution of the variables, and thus has proven to be an efficient statistical tool to assess variable importance in complex ecological data sets (Cutler et al., 2007).

To detect and illustrate interactions among variables predictive of tree-level beetle infestation we constructed a classification tree based on recursive partitioning. The selection of tree- and plot-level variables was based on the variable importance ranking of the random forest model and excluded variables with redundant information content. We used the rpart package in R to construct the classification tree (Therneau et al., 2014). We pruned the full classification tree based on cost-complexity, which retained the full tree.

3. Results

In total we recorded 1570 stems and 123 were stumps; 656 were standing spruce trees, of which 61 were infested by spruce beetles. Based on the means for all sites combined, we did not find a statistically significant trend of larger numbers of infested spruce, higher infested spruce basal area, higher percent infested spruce stems and higher percent infested spruce basal area in control stands than in treated stands (Table 3). However, at Dunton beetle infestation was significantly ($p < 0.05$) higher in the control stand as it was at Tuckerville (except for percent infested spruce stems). At Stoner Mesa beetle infestation did not differ between the control and the treated stand, while at Hermosa beetle infestation tended to be higher ($p < 0.1$) in the treated stand.

Plot-level treatment intensity (absolute and percentage spruce basal area removed) in treated stands did not correlate with any measure of beetle infestation at all sites (Spearman's correlation coefficients were not significantly different from 0: p-values > 0.05, Fig. 2, Supplementary Figs. S1–S3).

Analysis of stand structure revealed how tree removal has affected site-specific differences in beetle infestation (Fig. 3). At a site level there are some differences in stand structural variables between control and treated stands and relationships between stand structural variables and beetle infestation. In Dunton and Tuckerville spruce basal area correlated significantly with percentages and absolute numbers of beetle infested spruce basal area and stem numbers (p-value < 0.05, except for spruce basal area and percent spruce stems in Tuckerville: p-value = 0.08) and was higher in control than in treated stands (p-value < 0.05, Figs. 3 and S4–S6). At these two sites percent spruce basal area, spruce density > 25 cm DBH and spruce QMD were not or marginally (p-value < 0.1, i.e. spruce QMD and percent spruce basal area in Tuckerville and spruce QMD in Dunton) higher in control stands. In Tuckerville where we measured the highest number and percentage of infested spruce trees and basal area (Table 3), also percent spruce basal area, spruce density > 25 cm DBH and spruce QMD, correlated with beetle infestation (p-value < 0.05). In Dunton percent spruce basal area and spruce density > 25 cm DBH were both positively related to beetle infested spruce basal area and number of infested spruce stems (p-value < 0.05, Figs. S4 and S6). At Stoner Mesa and Hermosa we did not find any significant

Table 3
Plot means of number of infested spruce, infested spruce basal area, percent (%) infested spruce trees and percent infested spruce basal area by site and treatment (control and treated). The bottom row shows mean values over all sites. All values were scaled to one hectare (ha). "*", "(·)," and "ns" indicate significant ($p < 0.05$), marginally significant ($0.05 < p < 0.10$) and no significant differences in the distribution of beetle infestation between treatments based on MWU tests.

Site	No. infested spruce stems			Infested spruce basal area			% infested spruce stems			% infested spruce basal area		
	Control	Treated	MWU test	Control	Treated	MWU test	Control	Treated	MWU test	Control	Treated	MWU test
Dunton	75.0	10.0	*	13.2	1.2	*	12.6	2.5	*	25.6	4.1	*
Stoner Mesa	20.0	55.0	ns	3.2	4.4	ns	3.2	17.0	ns	5.8	19.3	ns
Hermosa	0.0	25.0	(·)	0.0	4.0	(·)	0.0	10.9	(·)	0.0	17.0	(·)
Tuckerville	93.3	15.0	*	23.3	2.0	*	20.9	5.6	ns	42.9	8.9	*
All sites	47.1	26.3	ns	9.9	2.9	ns	9.4	8.5	ns	20.7	11.8	ns

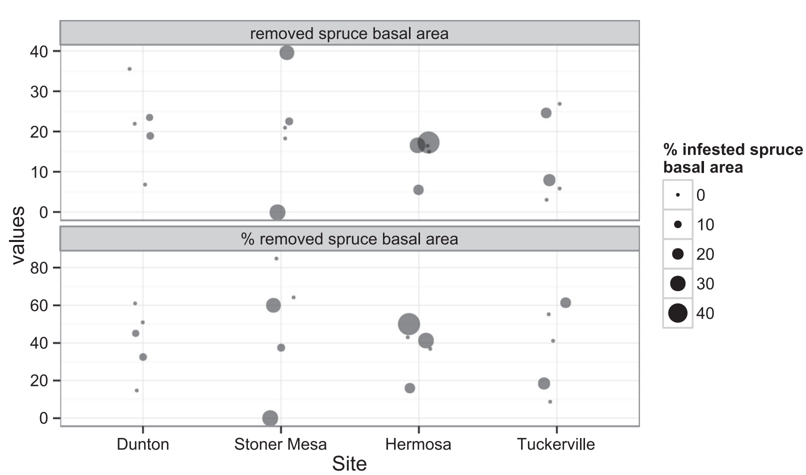

Fig. 2. Plot-level removed spruce basal area (top, m²/ha) and the percentage of removed spruce basal area (bottom) by site is indicated by dot positions along the y-axis. The size of dots indicates percent infested spruce basal area with the legend showing lower bounds of binned values.

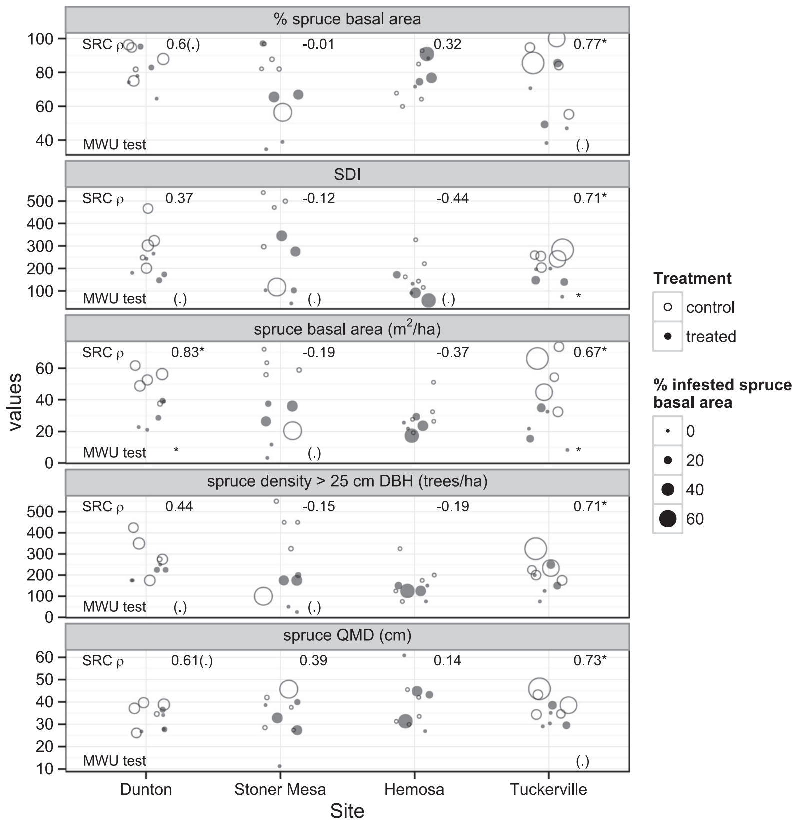

Fig. 3. Stand structural variables (panels) by site and treatment. Position of dots along the *y*-axis show plot-level values of stand structural variables and dot size indicates the plot-level percentage of infested spruce basal area (legend shows lower bin bounds). "*" and "(·)" at panel bottoms indicate significant (*p*-value <0.05) and marginally significant (0.05 <*p*-value <0.10) differences, respectively, in mean ranks between control and treated plots for each site and stand structural variables based on Mann–Whitney U (MWU) tests. Coefficients of Spearman's rank correlations (SRC ρ) between stand structural variables and percent infested spruce basal area are displayed at panel tops whereby "*" and "(·)" indicate that ρ is significantly and marginally significantly different, respectively, from zero.

correlation between stand structural variables and beetle infestation and stand structure did not differ between control and treated plots. At Stoner Mesa the abundance of large spruce was relatively high in four of the control plots but at this site we recorded beetle infestation mostly in treated plots and in one control plot that was dominated by five large spruce trees (25–66 cm DBH), two of which were infested. At Hermosa where we recorded the lowest beetle infestation the abundance of large spruce was comparatively low. SDI correlated with all measures of beetle infestation at Tuckerville (*p*-value < 0.05, except for percent infested spruce stems) and was at this site also lower in the treated stand (*p*-value < 0.05). At other sites this measure of competition was not related to beetle infestation and was only marginally lower in treated stands (*p*-value < 0.1). In sum, density reduction treatments effectively reduced beetle infestation in situations where the treatment significantly reduced the abundance of large spruce trees (Dunton and Tuckerville) and was ineffective where the abundance of large spruce trees was low irrespective of treatment (Hermosa) or where the treatment did not significantly reduce the abundance of large spruce trees (Stoner Mesa).

The abundance of uninfested large spruce trees in control stands approximated those in treated stands following beetle infestation at Dunton and Tuckerville (Table 4). At these sites the differences between control and treated stands in terms of the abundance of uninfested spruce (spruce basal area, percent spruce basal area, density of spruce >25 cm DBH, spruce QMD) were smaller during the outbreak than before the outbreak. This confirms the above finding of lower beetle infestation at Dunton and Tuckerville in the treated stands. However, at both of these sites in the treated stand the remaining spruce basal area and percent spruce basal area were lower and the spruce density >25 cm DBH and spruce QMD were very similar. This suggests that density reduction could not mitigate beetle infestation to the extent where the overall spruce loss (due to tree removal and beetles) in the treated stand would be smaller than spruce loss due to beetles only in the control stand. At Stoner Mesa and Hermosa beetle infestation further reduced the abundance of uninfested spruce in the treated stand as compared to the control stand both in terms of spruce basal area and density of spruce >25 cm DBH, which suggests no mitigating effect of density reduction on beetle infestation at all.

At the level of individual trees we found that 84% of infested spruce trees were >30 cm while only 44% of all (uninfested and infested) spruce were >30 cm, indicating the beetle's preference for larger spruce trees (Pearson's Chi-squared test: Chi-squared = 40.9, *p*-value < 0.001; Fig. 4). However, the largest trees in a plot were not always infested by beetles. The smallest and largest infested spruce trees were 9 and 82 cm DBH, respectively. Additionally, we found that infestation rates in treated and control stands differed among tree size classes (Fig. 4, Fig. S7). The infestation percentage in spruce trees between 20 and 30 cm DBH was higher in treated (12%) than in control stands (4%), whereas in spruce between 50 and 60 cm DBH the infestation percentage was with 11% and 33%, respectively, higher in the control stands. While the relatively small number of sampled trees for this analysis and the variation among sites need to be acknowledged, this broad pattern suggests that density reduction (1) increased the resistance of the remaining large spruce trees but also (2) resulted in a shift towards decreased resistance in smaller size classes. In

Table 4
Stand structural variables in control and treated stands before and during beetle infestation. Shown are plot means (M) and standard errors of means (SEM). Note that stand structural variables during infestation only account for remaining uninfested trees.

	Dunton				Stoner Mesa				Hermosa				Tuckerville			
Variable	Control		Treated		Control		Treated		Control		Treated		Control		Treated	
Before infestation	M	SEM	M	SEM	M	SEM	M	SEM	M	SEM	M	SEM	M	SEM	M	SEM
Spruce basal area (m^2/ha)	51.4	4.0	30.2	3.9	54.2	8.8	23.0	6.8	31.4	5.4	23.6	2.0	54.3	7.3	22.6	5.1
% Spruce basal area	87.1	4.0	78.9	5.1	81.0	6.7	60.6	11.3	73.9	6.4	80.5	3.8	83.9	7.7	58.1	8.7
Spruce density >25 cm (#/ha)	300.0	41.8	210.0	15.0	375.0	77.5	125.0	36.2	180.0	42.1	125.0	13.7	231.7	25.5	160.0	30.2
Spruce QMD (cm)	35.3	2.4	30.6	2.0	36.2	3.6	30.0	5.2	36.5	3.1	41.4	5.9	39.4	2.3	32.5	1.8
During infestation																
Spruce basal area (m^2/ha)	38.2	2.0	28.9	3.5	51.0	11.2	18.6	5.3	31.4	5.4	19.6	3.0	31.0	7.7	20.6	4.5
% Spruce basal area	83.9	4.9	78.6	4.9	76.2	11.1	57.3	11.0	73.9	6.4	77.0	3.8	75.3	10.3	56.5	8.5
Spruce density >25 cm (#/ha)	225.0	34.5	200.0	13.7	360.0	87.2	90.0	23.2	180.0	42.1	100.0	15.8	138.3	13.3	145.0	24.2
Spruce QMD (cm)	33.1	2.5	30.4	1.9	34.5	2.9	30.2	5.6	36.5	3.1	40.4	6.5	32.9	1.7	32.1	1.8

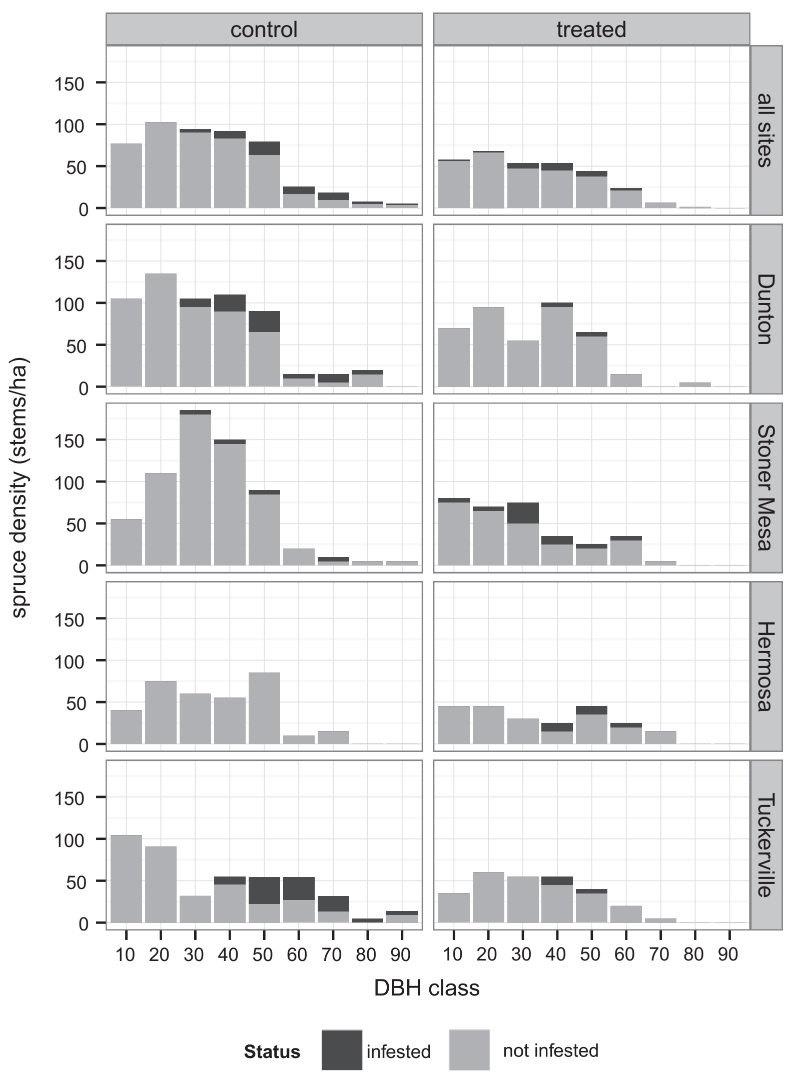

Fig. 4. Number of infested and uninfested spruce trees by DBH class, site and treatment (control and treated). "all sites" refers to spruce densities averaged over all sites.

other words, large spruce are more susceptible in untreated control stands, but beetles appear to exploit smaller spruce as breeding habitat in treated stands that lack a high density of large spruce.

The importance of tree size for beetle infestation was confirmed by the random forest model (Fig. 5). Tree-level DBH was by far the most important variable followed by plot-level spruce QMD, tree height class, percent spruce basal area, absolute spruce basal area, SDI and spruce density >25 cm DBH. Removed spruce basal area, site, percent removed spruce basal area and treatment (control vs. density reduction treatment) were of comparatively low importance. While the random forest OOB error was 9.9% indicating that >90% of spruce trees were correctly classified, 9 of 61 infested

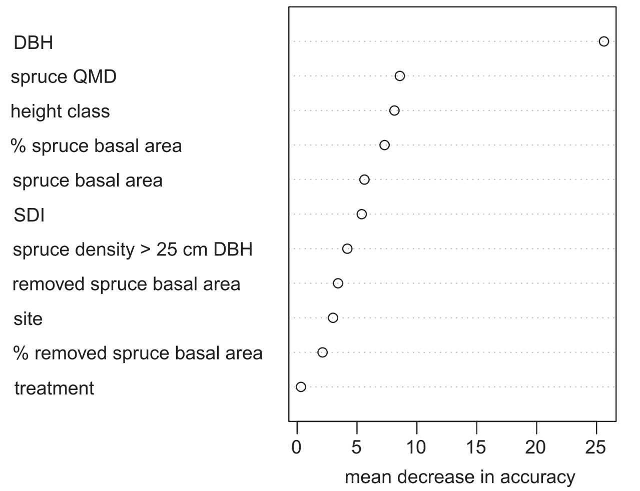

Fig. 5. Importance of tree-level (DBH, height class), plot-level (spruce quadratic mean diameter [QMD], percent spruce basal area, tree density, spruce basal area, spruce density >25 cm DBH, removed spruce basal area and percent removed spruce basal area) variables and site and treatment (control and treated) in random forest model classifying spruce trees as infested and uninfested.

spruce trees were correctly classified as infested and 13 of 595 uninfested spruce trees were mis-classified as infested.

As the most important (based on the random forest variable importance ranking) and non-redundant variables for inclusion in the classification tree model we selected tree-level DBH as a measure of spruce size, percent spruce basal area for the proportion of spruce, spruce basal area for the abundance of large spruce trees and SDI for potential competition-induced stress. The most parsimonious classification tree then retained DBH and percent spruce basal area as predictor variables (Fig. 6). Absolute spruce basal area and SDI did not improve the classification model and were dropped. The first split of the classification tree is based on DBH confirming the importance of tree size for infestation. The subsequent splits are based on percent spruce basal area revealing the interaction between these two tree- and plot-level variables.

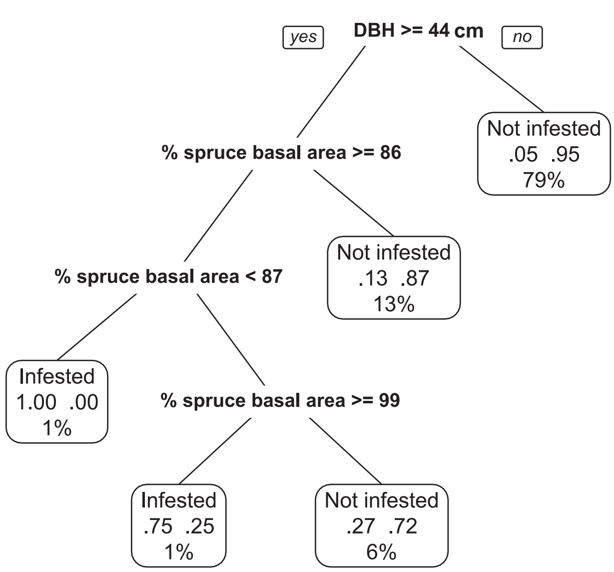

Fig. 6. Classification tree based on recursive partitioning. If condition is met proceed to the left branch. Tree nodes describe the predicted condition (infested/not infested), the probability of infestation (left) and no-infestation (right) and the percentage of the observation ($n = 656$).

Once a tree is ⩾44 cm DBH, according to this model, it must also be located in a plot with high (⩾86%) spruce basal area percentage to experience an increased probability of spruce beetle infestation. This model correctly classified 13 of the 61 infested spruce trees and 2 of the 595 uninfested spruce trees were misclassified as infested.

4. Discussion

This study showed that density reduction treatments reduced beetle infestation only at sites where spruce basal area was significantly reduced. At sites where spruce basal area was not significantly lower in treated than in untreated control stands, beetle infestation did not differ between treated and control stands. The combined loss of spruce trees due to density reduction and beetle infestation resulted in a lower or very similar (Tuckerville) abundance of large uninfested spruce trees in treated than in control stands; thus, density reduction was ineffective in preserving high densities of large spruce. These results confirm previous assessments on the limited effectiveness of indirect beetle management strategies. Density reduction may be effective in reducing subsequent beetle infestation depending on how treatment affected stand composition and structure and thus stand resistance to beetles (DeRose and Long, in press; Fettig et al., 2014,2007; Hansen et al., 2010; Johnson et al., 2014). However, the generally lower density of large spruce in treated stands at the time of sampling confirms the ineffectiveness of thinning to enhance stand resilience to beetles if the retention of large spruce during an ongoing endemic to incipient outbreak is a management goal (DeRose and Long, in press; Hansen et al., 2010).

Differences in beetle pressure, climatic and other environmental drivers and stand structure may have acted together to result in site-specific differences in beetle infestation. With beetle populations in our study area being in an endemic or at the transition to an incipient outbreak stage, beetle pressure was relatively low. Hence, the relative importance of stand structure in driving site-specific differences in beetle infestation is likely to have been large relative to later stages in the development of an outbreak (Hart et al., 2014b; Raffa et al., 2008; Reynolds and Holsten, 1994). Schmid and Frye (1976) account for environmental drivers by using site index in their spruce beetle hazard rating system. However, the low relative importance of the site variable in the random forest model indicates that site-specific differences in environmental conditions, which could have led to differences in site index, were unimportant in determining beetle infestation. Therefore, and because the short distance (1 km) between treated and control stands subjected them to similar beetle pressure, we consider variations in stand structure as most important in controlling differences in beetle infestation between treated and control stands.

Consistent with previous research on stand- and tree-level factors of susceptibility to spruce beetles we found the highest infestation rates in stands with the highest abundance of large spruce trees (Hart et al., 2014b; Jenkins et al., 2014a,b; Schmid and Frye, 1977). This commonly observed pattern reflects the spruce beetles' preference for large diameter trees with thicker bark that provides more phloem for larval feeding and increases winter survival (Schmid and Frye, 1977). At the tree-level we found an increased infestation probability for large spruce trees. Interestingly, the classification tree analysis revealed a spruce size threshold for increased infestation probability of 44 cm DBH. While this threshold needs to be interpreted cautiously (the model classified only 13 of 61 infested spruce trees correctly), it is considerably higher than the 20–30 cm that previous studies found for the early 2000s in Colorado and 1980s in Alaska (Hard, 1985; Hart et al., 2014a) and the 25.4 cm threshold that Schmid and Frye (1976) use in their stand rating system as a threshold for spruce that contribute to increased beetle hazard. We explain this discrepancy with the endemic or incipient outbreak stage and thus considerably lower beetle pressure at the time of sampling. In the studies cited above beetle-induced mortality rates were well over 50%, whereas at our sites beetle infestation rates (% infested spruce trees, Table 1) were maximally 21%. At low population densities, beetles preferentially attack the largest trees first and only proceed to trees of smaller diameters as the outbreak progresses and the largest highest-quality trees are depleted (DeRose and Long, 2012; Hart et al., 2014b).

Susceptibility to beetle infestation was further increased when larger trees were located within a plot with a high spruce basal area proportion (Fig. 6). This interaction may be explained by the requirement that large spruce trees must be in high densities. At high spruce densities kairomone plumes (host tree volatiles that attract female beetles that then attract the males with pheromones) are large and dense enough to attract endemic beetles that search-fly at relatively low densities (Wallin and Raffa, 2004). The differences in size class-specific infestation percentages between treated and control stands (Fig. 4) reflect these mechanisms. In treated stands, where the density of large spruce and thus the percentage of spruce basal area were reduced, large (>45 cm DBH) trees were less likely to be infested. Conversely, the low abundance of large spruce in treated stands may have forced beetles that developed within the stand or immigrated from neighboring stands to be less selective, which resulted in our observation of increased infestation probability in smaller (<45 cm DBH) spruce in treated stands.

SDI showed an intermediate importance ranking in the tree-level analysis and at the plot-level it was correlated with beetle infestation only at Tuckerville, which was the only site were we also found significantly lower SDI values in the treated stand. With SDI increasing with both the number and size of trees on a plot (Eq. (1)), these results reflect the strong association between the abundance of large spruce and beetle infestation in Tuckerville, which at this site was also significantly reduced in the treated stand (over all plots, SDI correlated with spruce basal area with Spearman's $\rho = 0.78$ and a p-value < 0.001). While SDI may capture differences in tree resistance due to resource competition-induced stress to some extent (Hard, 1985), it also integrates the abundance of large susceptible spruce, i.e. the abundance of suitable breeding habitat for the beetles. More detailed tree physiological observations or experiments would be necessary to disentangle these two drivers of stand resistance to beetles (Baier et al., 2002).

We expected to find a negative relationship between removed and beetle infested spruce basal area at the plot level, but results do not show any correlation. There may be two reasons for this null result. First, the spatial scale of this analysis (plots of 400–600 m^2) may have been too small to capture thinning-induced changes in stand structure that may influence beetle infestation. An aggregation at the stand level may be more appropriate, but for a meaningful analysis at this scale our sample size of 4 sites would have to be increased. Second, it is the post-treatment stand structure that dictates susceptibility to beetles. However, our measures of density reduction intensity (i.e. the absolute and relative amount of removed spruce basal area) do not reflect the resulting stand structure and thus may have performed poorly in predicting beetle infestation. As the effect of thinning depends on the pre-thinning stand structure, an assessment of the effects of various thinning intensities would have to be conducted in stands of varying pre-treatment strand structures. While we were able to reconstruct pre-treatment stand structure based on stump diameters to calculate percent removed spruce basal area our data set is too small to capture variation in stand structure and thinning intensity independently. A factorial experiment would be necessary to yield further insights on the interacting effect of pre-treated stand structure and treatment intensity, from which stand structure-specific density reduction recommendations can be derived (cf. Whitehead et al., 2004).

The density of large spruce in control and treated stands in our study tends to exceeded density reduction targets that are recommended to mitigate beetle infestation in spruce-fir forests. Total basal area in all treated stands is higher than the 18 m^2/ha and 25.5 m^2/ha that Alexander (1986) and Jenkins et al. (2014a), respectively, recommend (Table 4). This is also reflected by a discrepancy between measured and recommended diameter distributions. In all stands, densities in the largest size classes (>40 cm DBH) were ca. twice as high, while in the smaller size classes densities were mostly lower than recommended (Fig. 4, Jenkins et al., 2014a,b). Furthermore, spruce basal area percentages in treated stands were higher (Dunton and Hermosa) or only slightly lower (Stoner Mesa and Tuckerville) than the recommended 65% (Alexander, 1986). Even though density reduction resulted in lower abundance of large spruce at all sites (Table 4), they were not intense enough to bring spruce abundance substantially below recommended values. This may be part of the explanation for treated stands at Stoner Mesa and Hermosa being attacked, and implies that all of the stands that we surveyed may remain relatively susceptible to beetle infestation.

High-intensity thinning to enhance stand resistance to beetles conflicts with maintaining stand resilience if the management goal is to retain a high density of large and uninfested spruce trees as wildlife habitat and for future commercial timber yield. Comparing the abundance of large spruce between control and treated stands showed that this goal was not achieved at the surveyed sites (Table 4). After beetle infestation, the abundance of large uninfested spruce trees were lower or very similar (Tuckerville) in treated stands. This finding is consistent with Hansen et al. (2010) who also found smaller differences in stand structural variables between treated and control stands following beetle infestation as stands with reduced spruce abundance experienced less infestation. At the same time our results agree with Hansen et al. (2010) in that the density of large spruce after beetle infestation is still lower in treated stands. It is unlikely that under higher beetle pressure, e.g. if the current outbreak in our study area were to proceed to an epidemic stage, spruce survival would have been larger in the treated than in the control stands, because beetles are likely to extend their host preference to also attack smaller, less susceptible spruce trees as beetle population densities increase. This behavior allows beetles to exploit a larger source of host trees and to avoid density dependent competition (Wallin and Raffa, 2004) and may over-compensate the effect of reduced stand susceptibility due to density reduction to the extent that in treated stands both overstory spruce and smaller spruce trees are lost. In sum, under the endemic to incipient conditions that we surveyed more spruce may survive in untreated stands, such that the no-treatment option may be more effective in preserving a high abundance of large spruce trees and maintaining stand resilience.

The effectiveness of density reduction as a management option to enhance stand resistance and resilience to beetles may be affected by several other factors. The resistance of remaining trees in a particular stand is likely to attenuate if during an epidemic there is an influx of beetle populations from adjacent untreated stands (Whitehead and Russo, 2005). Thus, to be effective during an epidemic outbreak, density reduction would need to be conducted over large areas while taking into account the landscape-scale context (Whitehead et al., 2004). Such intensive landscape-scale density reduction may not be financially or legally feasible (DeRose and Long, in press). Furthermore, density reduction requires great care to prevent damage to remaining trees and their root systems in order to prevent infestations of other subcortical insects and root pathogens (Harrington et al., 1985). Stand openings caused by density reduction may increase the risk of blowdown, which subsequently may favor beetle breeding success (Schmid, 1981; Valinger and Fridman, 2011). Finally, beetle management needs to account for climate change. With increasing temperatures and drought, temperature-driven beetle population dynamics and drought-induced reduction of tree defense mechanisms may become more important in driving beetle outbreak dynamics than stand composition and structure, the component influenced by forest management (Bentz et al., 2010; Hart et al., 2014a; Temperli et al., 2013). Hence, density reduction for increased resistance to beetles may become even less effective with continued warming. In the light of these circumstances the most practical approach to manage beetles is to manage for forest resilience and to accept and factor-in beetle-induced spruce mortality. The most achievable management goal may not be the preservation of a high density of large spruce, but the preservation of the potential for a future dominance of spruce (DeRose and Long, in press). We agree with Hansen et al. (2010) that the appropriate use of density reduction would be as a tool to promote the advanced regeneration of spruce, such as a shelterwood overstory removal.

In conclusion, we found support for the effectiveness of density reduction in mitigating beetle infestation in remaining spruce only where the abundance of large spruce was substantially reduced. However, density reduction did not increase the overall density of remaining large spruce during the endemic to incipient outbreak that we surveyed and is not likely to do so if the current outbreak were to become epidemic. While these results are based on a limited data set comprising four sites in southern Colorado, they suggest that density reduction cannot be seen as a means to maintain high growing stocks of large spruce trees. Hence, management to mitigate beetle disturbance needs to be planned in accordance and balanced with other resource values and management objectives. In areas where large spruce trees are valued primarily as a timber resource, commercial density reduction may have the positive side-effect of preventing the remaining spruce from subsequent beetle infestation, but may conflict with other management goals such as the retention of large spruce and maintenance of old-growth structure for wildlife habitat or for regulation of water quality and quantity. Beetle management needs to be planned in a landscape context to diminish the likelihood of the influx of beetles from adjacent stands but this is unlikely to be achievable during a broad-scale beetle outbreak. In the face of a warming climate, accelerated beetle brood development and weakening tree resistance due to drought-stress, the more achievable management objective appears to be to manage spruce-fir forests for resilience rather than resistance to future outbreaks. Managing for resilience implies assessment of current spruce regeneration potential and consideration of any need for vegetation treatments that would promote advanced spruce regeneration to support recovery to spruce dominance following inevitable spruce beetle outbreaks.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.08.028.

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