

Article

If Long-Term Resistance to a Spruce Beetle Epidemic is Futile, Can Silvicultural Treatments Increase Resilience in Spruce-Fir Forests in the Central Rocky Mountains?

Marcella A. Windmuller-Campione * and James N. Long

Ecology Center & Department of Wildland Resources, Utah State University, Logan, UT 84322, USA; E-Mail: james.long@usu.edu

* Author to whom correspondence should be addressed;
E-Mail: marcella.campione@aggiemail.usu.edu; Tel.: +1-435-797-3219; Fax: +1-435-797-3796.

Academic Editors: Phillip G. Comeau and Bill Mason

Received: 11 December 2014 / Accepted: 8 April 2015 / Published: 15 April 2015

Abstract: Within the Central Rocky Mountains, spruce beetle populations have the potential to rapidly transition from endemic to epidemic levels in the spruce-fir (Engelmann spruce and subalpine fir) forest type. Conventional management has focused on creating resistance to spruce beetle outbreaks by manipulating the overstory density and composition. Three silvicultural treatments, single tree selection, group selection, and shelterwood with reserves, were established in a spruce-fir forest in northern Utah with the goals of increasing both resistance and resilience to outbreaks. Resistance and resilience metrics were explicitly defined. Pre-harvest and two post-harvest measurements were used to assess how the different silvicultural treatments influenced the metrics. The shelterwood with reserves was the only treatment to meet both the resistance and resilience criteria. This treatment, while not traditionally used, created a stand structure and composition that will be most resilient to climate induced increases in spruce beetle caused tree mortality. However, there will be a trade-off in composition and structure, especially Engelmann spruce, after a spruce beetle epidemic because the created structure is more uniform with fewer groups and gaps than commonly observed in spruce-fir forests. With changing climatic conditions, proactive forest management, such as the shelterwood with reserves in the spruce-fir forest type, is the best method for increasing short-term resistance and long-term resilience to spruce beetle outbreaks.

Keywords: alternative silviculture; spruce beetle; single tree selection; group selection; shelterwood with reserves; resistance; resilience

1. Introduction

Increasing global temperatures, expected changes in the hydrological system, increasing probability of extreme events, and changing land use patterns will influence the management of forest systems [1–4]. The genus *Picea* is an important component of managed forest systems and is widely distributed throughout the northern hemisphere [5]. Recent destructive insect outbreaks have occurred across Europe (spruce bark beetle (*Ips typographus*) in Norway spruce (*Picea abies* (L.) Karsten.) [6] and western North America (spruce beetle (*Dendroctonus rufipennis*) in Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)) [7–9]. In western North America, the time for a spruce beetle to complete its life cycle is expected to decrease with warming temperatures, having potentially devastating effects on western spruce forests [10].

The spruce beetle is a native insect endemic to spruce forests across North America [7]. The spruce beetle can have a 1 to 3 year life cycle with adult spruce beetles boring into the main stem of the tree, feeding, and breeding in the live phloem; tree death occurs from girdling [11]. Under endemic population levels, spruce beetles live and breed in recently windthrown trees. Destructive storms can greatly increase the amount of recently windthrown trees. Alexander [12] recommended the removal of any large diameter Engelmann spruce trees that have fallen due to their increased susceptibility to a spruce beetle attack. Windthrow events in Europe also influence spruce bark beetle dynamics in Norway spruce forests [13]. Effective removal of down trees can lessen future beetle impacts in many different spruce forest types [12–14].

As population levels increase, spruce beetles will attack standing live trees, potentially transitioning to epidemic levels [7]. Historical spruce beetle epidemics have been reported throughout the Central Rocky Mountains including the White River Mountains in Colorado [15] and the Aquarius Plateau in Utah [16]. Within the last 20 years, epidemic spruce beetle populations have been extremely destructive across the Central Rocky Mountains [17] and outbreaks are expected to continue [18]. Of the 3.8 million hectares in Colorado, Utah, and Wyoming in the spruce and fir forest types, FIA (Forest Inventory and Analysis) data suggest nearly half of the area has experienced some level of mortality due to insects [19]. Recent spruce beetle epidemics have probably been driven by a combination of factors including susceptible stand structure and composition coupled with widespread drought [20]. Spruce beetles favor large diameter (>25 cm diameter at breast height (dbh)) Engelmann spruce for both protection and nutrition [21,22]. Recent dry conditions in high-density stands increase stresses on individual trees, decrease growth rates, and decrease defenses against the beetle, allowing spruce beetle populations to rapidly increase [8,18]. Changing climatic factors, especially increased summer temperatures are associated with an increased shift from semivoltine to univoltine life-cycles [10,23].

Management for the spruce beetle has focused on increasing resistance [24–26]. Resistance (risk *sensu* [27]), in this situation, is the decreased susceptibility to a spruce beetle outbreak through changes in structure and composition [2,28]. DeRose and Long [28] define this change in structure and

composition at both the stand and the landscape level. A spruce beetle resistant stand has attributes, which decrease spruce beetle population growth and spruce beetle caused mortality within the stand. Landscape resistance is defined as the overall spatial heterogeneity and structure, which decreases the likelihood of a spruce beetle epidemic [28]. When spruce beetles are at endemic levels, localized direct suppression techniques such as pheromone traps and trap trees can be used to reduce beetle populations [29,30]. Schmidt and Frye [25] developed a spruce beetle risk rating system that focuses on manipulating the stand structure and composition (*i.e.*, reduction of overstory density and the amount of large diameter spruce) to reduce the risk of spruce beetle outbreaks and increase resistance [25]. Manipulation of overstory structural characteristics has been shown to offer some short-term resistance to endemic spruce beetle populations [18,26,31]. However, once spruce beetle populations transition from endemic to epidemic levels, all mature spruce-fir stands, even ones managed for density reduction are not resistant. For example, on the Markagunt Plateau in southern Utah, spruce beetle populations transitioned from endemic to epidemic levels, killing over 90% of the Engelmann spruce trees greater than 5 cm in dbh over an area of at least 250 km² [18]. At the beginning of the epidemic, the spruce beetle attacked dense stands with large diameter Engelmann spruce [29], as predicted by the Schmid and Frye [25] risk rating system. Under this system, stands with low densities and small diameter spruce trees would be classified as potentially resistant; however, as the epidemic progressed the spruce beetle moved into these initially resistant stands [32]. As a result of this extensive epidemic, forest composition has shifted towards subalpine fir (Abies lasiocarpa (Hook.) Nutt.) and aspen (Populus tremuloides Michx.) due to the limited number of mature live Engelmann spruce to serve as a seed source and the limited amount of spruce advance regeneration [18,32]. Realistically, modification of stand composition and structure might only provide short-term resistance in the face of a spruce beetle epidemic [28,32].

Managing for resistance is only a part of a comprehensive spruce beetle strategy, which should also include a provision for increasing resilience. Resilience at the stand level is associated with desired (or at least acceptable) structure and composition after a spruce beetle epidemic. At the landscape level, resilience reflects desired levels of heterogeneity in composition, structure, and age diversity [28].We define resilience at the stand level as the adequate stocking of Engelmann spruce in the regeneration layer post spruce beetle epidemic. Successful Engelmann spruce regeneration can be a rare event with good cone crops occurring every two to five years [12,33]. This sporadic cone production coupled with climatic variability creates long regeneration windows of 10 to 20 years [33,34]. Since Engelmann spruce regeneration is not guaranteed, it is the most limiting factor in ensuring a resilient forest with a future spruce beetle epidemic occurs, Engelmann spruce would not be lost from the stand. This would reduce the likelihood of the forest type shift that was observed in southern Utah [18,32]. Timely proactive forest management in spruce-fir stands can ensure a minimum level of stocking of Engelmann spruce, creating spruce beetle resilient stands.

In the Central Rocky Mountains, spruce beetle populations appear to be increasingly likely to transition from endemic to epidemic levels, and in some locations this has already occurred (e.g., southern Utah, [32]). In northern Utah, an experimental silvicultural trial was established to compare three silvicultural treatments: single tree selection, group selection, and shelterwood with reserves. In this paper, we present results showing the short-term effect of these treatments on metrics of stand level resistance and resilience.

2. Methods

2.1. Study Species

Across the Central Rocky Mountains, the subalpine forest zone (2400–3200 m above sea level (asl)) is often typified by Engelmann spruce and subalpine fir coexisting in late successional communities [12]. This broad forest type can occur as low 1830 meters and as high as 3650 meters in elevation [35]. The FIA database from 2003 to 2012, estimates 3.8 million hectares of forested land in the fir and spruce forest types in Colorado, Wyoming, and Utah [19].

Engelmann spruce and subalpine fir have complementary life history strategies which allow for coexistence ([12,33,35–40], and references therein). Across the Rocky Mountains, the individual life histories of spruce and fir influence the structure. Engelmann spruce can be long-lived, (300+ years) but has inconsistent regeneration. Subalpine fir has more consistent and prolific regeneration but a shorter lifespan, e.g., 150 years [41]. Engelmann spruce is commonly dominant in number and basal area of large diameter trees with subalpine fir dominating in number and basal area of the small diameter trees and regenerating individuals [35,42].

The structure and composition of spruce-fir forests are influenced by disturbance history. Standreplacing disturbances are infrequent (+300 years) and typically reset succession with early dominance by lodgepole pine (*Pinus contorta* Dougl.) and/or aspen and the eventual succession to Engelmann spruce and subalpine fir [43]. In northern Utah, fires in spruce-fir forests increased in frequency during the Settlement Period (1856–1909) due to increased human activity but then sharply decreased after 1910 due to fire suppression [44]. Intermediate disturbances, creating small or medium sized gaps, are common and create the characteristic variable structure and composition in spruce-fir forests of this region [45]. A number of interacting disturbance agents influences the creation of these small and medium gaps: windthrow, bark beetles, and rot root [45]. These disturbances collectively create both stand and landscape heterogeneity.

Spruce-fir forests in the Central Rocky Mountains have been managed using a variety of silvicultural systems [12,33,46]. A common management objective is to maintain stand heterogeneity and vertical structure by utilizing uneven-aged silvicultural methods [9,12,35,45,47]. Much of the focus is on the successful regeneration of Engelmann spruce [45–47]. Group selection historically has been the most commonly used treatment since windthrow, endemic spruce beetles, and root rot create stands dominated by groups and openings [45,46]. Group openings are generally less than twice the height of mature trees, resulting in favorable microsites for Engelmann spruce regeneration [45]. Single tree selection is generally not used in this forest type because openings are presumed to be too small for successful spruce regeneration [45].

2.2. Site Description

Utah State University's T.W. Daniel Experimental Forest (TWDEF) (41.86° N, 111.50° W) is located in the Bear River Range of northeastern Utah at an elevation of 2600 m (Figure 1). The TWDEF contains approximately 405 hectares in the spruce-fir type with an additional 6880 hectares in the surrounding Logan Ranger District of the Uinta-Wasatch-Cache National Forest. The TWDEF experiences a semi-arid climate, characteristic of the Intermountain West with 1044 mm of precipitation [48]. On average 80% of the precipitation falls as snow, melting between mid-May and mid-June. There is a pronounced summer drought with warm temperatures; highest average monthly temperatures occur in July (14.5 °C) [49]. Winter months are cold with January having the lowest average monthly temperature (–10 °C) [49]. Winter storms with high wind speeds occur frequently on the TWDEF. Due to these storms and extensive areas of root rot, there is the potential for high rates of windthrow especially adjacent to gaps. The soils on the TWDEF are generally classified within two soil orders, Mollisols or Alfisols [50,51]. These soils are considered to be carbonate-free and well drained with the majority of soil organic carbon observed in the O horizon [50]. Spodosols rarely occur on the TWDEF due to limited soil moisture [50]. Additional information on climatic variables, past, and current research can be found at the T.W. Daniel Experimental Forest website (http://danielforest.usu.edu/).

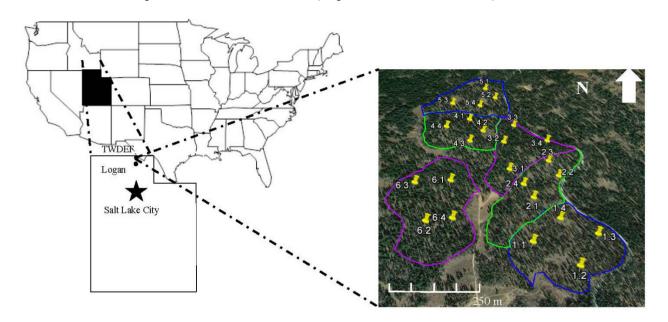


Figure 1. Location and study design layout for the spruce-fir silvicultural treatments at the Utah State University's T.W. Daniel Experimental Forest (TWDEF). Each treatment is outlined in a different color: shelterwood with reserves (blue); group selection (green); single tree selection (purple). Plot locations are highlighted in yellow. A stratified random sampling design was used within each treatment. Additional information on data collected at each sampling point can be found in following paragraphs and Figure 2. The map with the plot locations was made in Google Earth.

2.3. Silvicultural Treatments

In 1996, increasing spruce beetle populations were observed on the TWDEF, which led to successful suppression efforts [29]. A timeline of specific events is presented in Table 1.

In collaboration with the Logan Ranger District in 1999, three silvicultural treatments were established with the goals of increasing resistance and resilience to the spruce beetle. The three treatments were single tree selection, group selection, and shelterwood with reserves. An uncut control was established to explore future spruce beetle spread; those data are not presented here. Individual harvest units are about 8 hectares; silvicultural treatments were assigned randomly to the harvest units and replicated twice.

Т.У	V. Daniel Experimental Forest Spruce Beetle Management Timeline
Year	Event
	- Increasing populations of spruce beetle
1996	- Survey to identify infested host trees
	- Removal of infested trees, trap trees established, and brush pile burning
1007	- Ground Surveys
1997	- Additional trap trees and pheromone baited traps
1000	- Ground Surveys
1998	- Additional trap trees and pheromone baited traps
	- Establishment of the study to explore resistance and resilience to the
1000	spruce beetle
1999	- 18 variable radius plots were sampled to collect pre-treatment
	stand conditions
2000 2005	- Litigation
2000–2005	- Collection of Engelmann spruce seeds
	- Harvesting of the single tree selection, group selection, and shelterwood
2006	with reserves
	- Seedlings grown in USDA Forest Service Lucky Peak Nursery
	- Planting of Engelmann spruce seedlings in the openings of the group
2008	selection and throughout the shelterwood with reserves
	- Establishment of 8 permanent plots per treatment
2013	Remeasurement of permanent plots

Table 1. T.W. Daniel Experimental Forest in northern Utah spruce beetle management timeline. Additional information on suppression efforts and results can be found in [29].

Stand density index (SDI; ([52–54]) was used to determine the residual density for each treatment. SDI was calculated based on the trees per hectare and the quadratic mean diameter (QMD) [54]. The maximum SDI will vary by individual species but at 35% of maximum SDI, trees will fully occupy the stand [55]. As SDI increases, competition can increase individual tree stress and limit growth. The maximum SDI for Engelmann spruce is 1500 [56]. The maximum SDI for Engelmann spruce was used since all treatments favored the removal of subalpine fir. The single tree selection treatment left a residual SDI of 520 (37% of maximum SDI) favoring the removal of subalpine fir and the retention of aspen. Within the group selection treatment, 0.1 hectare patches were created, collectively treating 1/6th of the harvest units; the forest matrix was thinned to a residual SDI of 520 (37% of the maximum SDI) favoring the removal of subalpine fir and the retention of aspen. The uniform shelterwood with reserves treatment involved thinning from below to a residual SDI of 415 (28% of the maximum SDI), favoring the retention of Engelmann spruce.

In 1999, using a stratified random design, six variable radius plots with a basal area factor of $4.6 \text{ m}^2 \cdot \text{ha}^{-1}$ were placed within each of the treatments for a total of 18 plots across the 50 ha study area. On each plot, species, diameter at breast height (1.37 m), total height, and height to the base of the live crown were measured for each tree. In 2008, using a stratified random design, eight permanent plots were established within each treatment for a total of 24 plots across the study area (Figure 2). The radius of the nested subplots increased in size from the center point: (A) 0.01 hectare plot measuring trees between 4.1 and 10 cm dbh; (B) 0.05 hectare plot measuring trees between 10.1 and 25 cm dbh;

(C) 0.10 hectare plot measuring trees greater than 25 cm dbh [57]. All standing trees within the designated size class were tagged. Species, diameter at breast height, and total height were measured for all live and dead trees; height to live crown was recorded for live trees. Four permanent subplots were established in the cardinal directions to measure tree regeneration. All regenerating trees with heights greater than 20 cm and diameters less than 4 cm dbh within the 0.001 hectare subplots were tallied. Plots were remeasured following the same methods during the fall of 2013; ingrowth was tagged and measured.

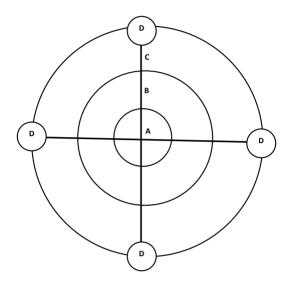


Figure 2. Permanent plot design established in 2008 and remeasured in 2013. The radius of the nested subplots increased in size from the center point; (A) 0.01 hectare plot measuring trees between 4.1 and 10 cm dbh; (B) 0.05 hectare plot measuring trees between 10.1 and 25 cm dbh; (C) 0.10 hectare plot measuring trees greater than 25 cm dbh. Regeneration plots were established at the four cardinal directions; (D) 0.001 hectare measuring tree regeneration with heights greater than 20 cm and diameters less than 4 cm dbh.

Prior to harvesting, Engelmann spruce seeds were collected from the site. Subsequently, one-year-old seedlings were grown at the USDA Forest Service Lucky Peak Nursery in Idaho. In 2008, Engelmann spruce seedlings were planted at an effective density of 60 trees per hectare in the openings of the group selection and throughout the shelterwood with reserves units.

2.4. Defining Resistance and Resilience Metrics

2.4.1. Resistance

Resistance was defined as a function of overstory density, composition, and site index [25]. The Schmid and Frye [25] spruce beetle risk rating uses four different metrics: physiographic location, QMD of spruce tree greater than 25.4 cm in dbh, stand basal area $(m^2 \cdot ha^{-1})$, and proportion of the stand basal area $(m^2 \cdot ha^{-1})$ that is spruce [40] (Table 2). Values for each metric are rated as high (3), medium (2), or low (1) and the sum of the values is the stand risk rating. A stand risk overall score of 11–12 is defined as high, 10 as medium/high, 7–9 as medium, 6 as medium/low, and 4–5 as low (Table 2). Each metric was calculated by year and by treatment to assess overall risk to a spruce beetle outbreak.

	Physiographic Location/ Site Index	QMD of Spruce >25.4 cm dbh	Stand Basal Area (m ² ·ha ⁻¹)	Proportion of Stand That Is Spruce (%)	
High (3)	Spruce on well-drained sites in creek bottoms	>40.6 cm	>34. 44	>65	
Medium (2)	Spruce on sites with site index of 24.4 to 36.6 m	30.5–40.6 cm	22.96-34.44	50–65	
Low (1)	Spruce on sites with site index of 12.2 to 24.4 m	<30.5 cm	<22.96	<50	

Table 2. Risk rating system developed by Schmid and Frye [25].

Proportion of spruce in a stand was defined as the percent of basal area in spruce versus total overstory basal area.

2.4.2. Resilience

Resilience was defined at the stand level as being the minimum amount of Engelmann spruce regeneration necessary to maintain a spruce component post spruce beetle epidemic. Regenerating Engelmann spruce was defined as trees less than 4 cm in dbh but greater than 20 cm in height because the spruce beetle generally attacks trees greater than 5 cm in dbh [18]. If the primary management objective is spruce timber production, Alexander and Edminster [58] recommend approximately 1975 trees per hectare when using natural regeneration. However, their suggestion "is more than required for adequate stocking, but necessary to achieve uniform spacing, allow for possible future mortality, and provide options in selecting crop trees in subsequent thinnings" [59]. Since our primary goal is not spruce timber production and artificial regeneration was used to supplement natural regeneration, we used a minimum of 245 trees per hectare of regenerating Engelmann spruce.

2.5. Analysis

Stand data for 1999, 2008, and 2013 were expanded to trees per hectare, basal area per hectare, and SDI using the summation method [52,53]. Welch's one sided *t*-tests were used to compare differences between pre- and post-treatment total trees per hectare and total basal area per hectare. A *t*-test was performed on the pre-treatment data *versus* each of the post treatments (pre *vs.* single tree selection, pre *vs.* shelterwood). Since sampling techniques varied from pre-harvest (variable radius) and post-harvest (fixed area), all trees less than 4 cm in dbh were excluded from this analysis, since trees less than 4 cm in dbh in 2008 and 2013 were classified as regeneration. Ducey [60] and Curtis [61] detail how inconsistent truncation can influence SDI. Repeated measures ANOVA was used to test differences between years and treatments for density measures in the overstory. To assess resistance, the pre-harvest stand and the structures following the three treatments were rated using the spruce beetle risk rating system [25]. To assess resilience, one-way ANOVA was used to test differences between generation spruce regeneration in 2013.

3. Results

3.1. Overstory Composition, Structure, and Density

The three silvicultural treatments influenced the stand structure and composition on the TWDEF. The pre-treatment diameter distribution was characteristic of spruce-fir forests with large diameter live Engelmann spruce and smaller diameter subalpine fir (Figure 3A). Dead Engelmann spruce and subalpine fir occurred across the range of diameter classes. All treatments shifted the diameter distributions to being more left skewed and decreased the amount of basal area in small diameter subalpine fir (Figure 3B–D). The shelterwood with reserves was thinned from below leaving primarily large diameter Engelmann spruce (Figure 3B). However, there was a wider range of diameters of Engelmann spruce among the single tree selection and the group selection (Figure 3C,D). The single tree selection had the highest residual basal area across all the size classes, including the smallest size class (4–9.9 cm). These small diameter trees do not greatly influence the overall basal area per hectare but do greatly influence the number of trees per hectare.

Prior to harvest, total overstory basal area and live basal area was 36.3 m²·ha⁻¹ and 33.0 m²·ha⁻¹, respectively. Total trees per hectare (tph) and live trees per hectare were 264 and 232, respectively. There was a significant decrease in total basal area per hectare and trees per hectare in the shelterwood with reserves (p = 0.002; p = 0.01) by 2008. The group selection treatment also had a significant decrease in basal area per hectare by 2008. There was little change in the basal area between pre- and post-treatment in the single tree selection units. However, there was an increase in the number of trees per hectare pre- and post-treatment, which was probably due to the large number of small diameter subalpine fir trees (Figure 3).

Live SDI and live basal area did significantly differ between treatments but not years (Figure 4). The single tree selection treatment had significantly greater live basal area per hectare and live SDI than either the shelterwood with reserves or the group selection treatments (Figure 4). Prior to harvest, the stand had an SDI of 516 or 34% of the maximum. By 2013, the group selection and the shelterwood with reserves both had SDIs of approximately 20% of the maximum. Single tree selection had a SDI of 34% of the maximum SDI in 2013.

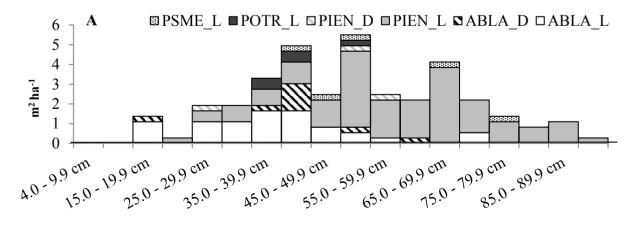


Figure 3. Cont.

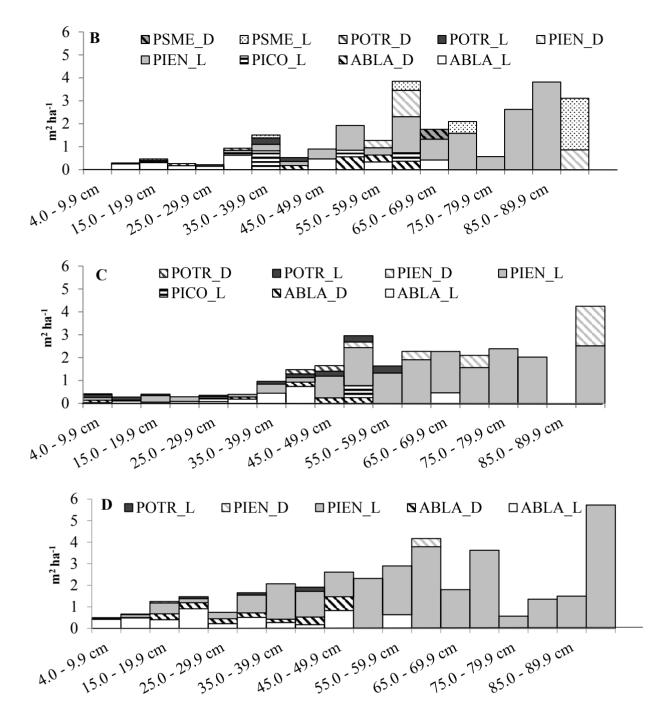


Figure 3. Diameter distribution (**A**) pre-treatment; (**B**) shelterwood with reserves 2013; (**C**) group selection 2013; (**D**) single tree selection 2013. Species codes are: PSME = *Pseudotsuga menziesii*; POTR = *Populus tremuloides*; PIEN = *Picea engelmannii*; PICO = *Pinus contorta*; ABLA = *Abies lasiocarpa*. The suffix L represents 'live' trees, while D is for "dead" trees.

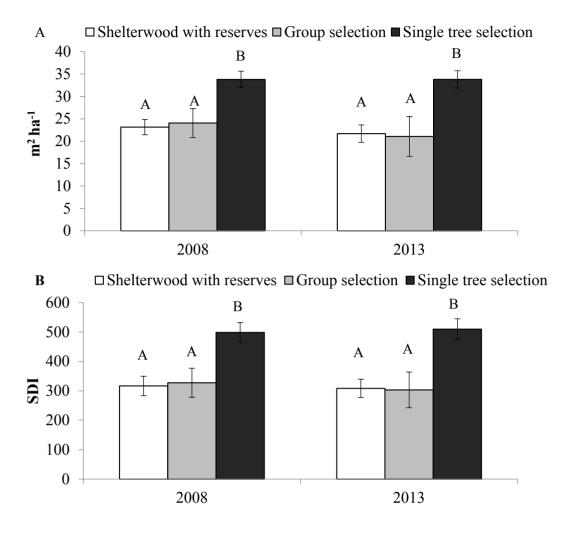


Figure 4. Repeated measures ANOVA for (**A**) live basal area per hectare and (**B**) live stand density index (SDI). The error bars represent the standard errors. Letters represent significant differences between treatments. No significant differences were observed between years.

3.2. Spruce Beetle Risk Rating System

The scores of the different treatments using the spruce beetle risk rating system [25] showed little change after they were implemented on the TWDEF (Table 3). The pre-harvest stand was rated as having a medium risk, with a total score of 8. This rating was due to the large diameter spruce, high stand basal area, and the high proportion of spruce. The shelterwood with reserves did lower the risk slightly to a 7.

Exploring how the individual components influenced the overall risk rating, the site index (base age 50 years) for Engelmann spruce was rated as a low risk for all years since it is slightly less than 24.4 m [61]. The QMD of Engelmann spruce greater than 25.4 cm in diameter metric was rated as high across all years and all treatments (Table 3). The stand basal area metric was rated as having a medium risk to the spruce beetle pre-harvest. Post-harvest, by 2008 there were significant decreases in the basal area in the group selection and shelterwood with reserves, but there were only modest changes in the risk rating (Table 3). Small amounts of mortality between 2008 and 2013 caused a further small decrease in basal area ($<3.0 \text{ m}^2 \cdot \text{ha}^{-1}$) which resulted in a lowered risk rating for the stand basal area metric for the group selection and the shelterwood with reserves treatments (Table 3). There were no significant decreases in density in the single tree selection or changes in the risk rating. The proportion of the stand

Table 3. T.W. Daniel Experimental Forest Spruce Beetle Risk Rating by treatment adapted from Schmidt and Frye [25]—see Table 2. Numbers in parenthesis represent the rating from the spruce beetle risk rating system. The risk rating ranges between 1 and 3 with the lowest total score possible of 4 and highest total score possible of 12. Site index equations were from Clendenen [62]. Stand basal area is live standing trees greater than 4 cm in diameter. The proportion of stand that is spruce was calculated based on the proportion of live Engelmann spruce to total live basal area [40].

	Physiogr Location Inde	/Site	Spr	D of ruce cm dbh	Aı	Basal rea ha ⁻¹)	Proportion of Stand That is Spruce (%)		Total Risk Rating	
Pre	<24.4 m	(1)	55.1	(3)	33.0	(2)	65	(2)	8	
2008										
Shelterwood with reserves	<24.4 m	(1)	67.0	(3)	23.2	(2)	64	(2)	8	
Group selection	<24.4 m	(1)	64.4	(3)	24.1	(2)	76	(3)	9	
Single tree selection	<24.4 m	(1)	62.1	(3)	33.8	(2)	84	(3)	9	
2013										
Shelterwood with reserves	<24.4 m	(1)	69.6	(3)	21.7	(1)	65	(2)	7	
Group selection	<24.4 m	(1)	66.3	(3)	21.1	(1)	81	(3)	8	
Single tree selection	<24.4 m	(1)	62.9	(3)	33.8	(2)	84	(3)	9	

3.3. Regeneration

Total regeneration was greater than 1500 tph for all treatments in 2013 (Table 4 and Figure 5). There was no significant difference between treatments for total regeneration in 2013. However, there was significantly more Engelmann spruce regeneration in the shelterwood with reserves compared to the single tree selection treatment by 2013 (Figure 5). The group selection was not significantly different from the other two treatments. The shelterwood with reserves and the group selection received supplemental planting of Engelmann spruce seedlings in 2008. This planting design created high variability in stocking within the group selection. The shelterwood with reserves was the only treatment that met the minimum stocking requirement of at least 245 tph of well distributed Engelmann spruce (Figure 5).

Treatment	Subalp	oine Fir	Lodge	pole Pine	0	Engelmann Spruce		Asp		spen	Grand Total	
2008												
Shelterwood with reserves	812.5	(187.5)	0.0	(0)	0.0	(0)	750.0	(566.9)	1562.5	(640.4)		
Group selection	437.5	(147.5)	0.0	(0)	0.0	(0)	250.0	(182.9)	687.5	(181.5)		
Single tree selection	812.5	(244.4)	0.0	(0)	125.0	(47.5)	281.3	(185.6)	1218.8	(264.9)		
2013												
Shelterwood with reserves	812.5	(220.3)	218.8	(218.8)	406.3	(124.4)	750.0	(592.0)	2187.5	(711.4)		
Group selection	1031.3	(524.9)	0.0	(0)	125.0	(66.8)	937.5	(633.4)	2093.8	(710.2)		
Single tree selection	781.3	(269.1)	0.0	(0)	62.5	(62.5)	750.0	(491.0)	1593.8	(528.1)		

Table 4. Regeneration density (trees per hectare) by treatment for 2008 and 2013 for the T.W. Daniel Experimental Forest. The associated standard errors are in parenthesis.

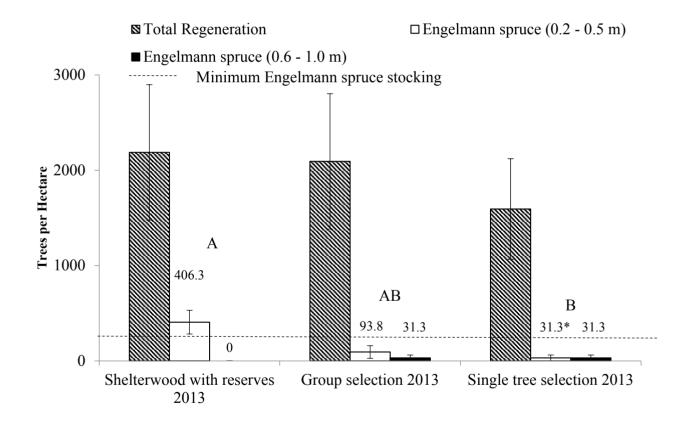


Figure 5. One-factor ANOVA for total tree regeneration and Engelmann spruce regeneration. The bars represent the standard errors. There were no significant differences between treatments for total density. Letters represent significant differences between treatments for total density of all size classes of Engelmann spruce trees per hectare (see Table 4 for total). * Engelmann spruce height was not recorded in 2013. Prior height measurement in 2008 was less than 0.5 m.

4. Discussion

This study was initiated in 1998 to explore silvicultural treatments that could increase short-term resistance and long-term resilience to spruce beetle caused mortality at the stand level. Since the development of this study, there has been increased research, mostly retrospectively, on spruce beetle dynamics [18,32,40,63]. However, our study is unique for two reasons: (1) it tests a pro-active management strategy and (2) utilizes explicitly defined metrics of resistance and resilience to spruce beetle outbreaks. Management focused on stand density reduction techniques intended to create "resistant" (*sensu* [25]) stands is likely to be unsuccessful [26].

On the TWDEF, there was little change between the pre-treatment risk rating and any of the post-treatment risk ratings. The prescriptions for the three treatments favored the retention of Engelmann spruce. Furthermore, across, all three treatments, the majority of Engelmann spruce basal area was in trees greater than 25 cm dbh which is characteristic of spruce-fir forests of the Central Rocky Mountains [35]. Increasing resistance would require drastic changes in the structure and composition of these forests. Large diameter Engelmann spruce would need to be removed in order to decrease the QMD and proportion of live spruce [36]. It is important to note, however, that during an epidemic, even in low risk stands, Engelmann spruce greater than 4 cm in dbh can be attacked by spruce beetles [18,20]. Once at epidemic levels, it is no longer just the high-risk stands that are impacted but the entire landscape.

The shelterwood with reserves and group selection treatments implemented at the TWDEF resulted in substantial decreases in overstory basal area by 2008 from pre-harvest conditions. However, even with these significant decreases in basal area there were only modest changes in the risk rating. Between 2008 and 2013, there was a slight decrease in basal area due to mortality and this small decrease changed that specific metric from a two to a one. Within the spruce beetle risk rating system, small changes can influence the risk rating. While, the spruce beetle risk rating system can be sensitive to small changes, it does give managers a starting point when implementing forest management practices. Our study is one of the first to demonstrate that these three different silvicultural treatments resulted in relatively similar spruce beetle risk ratings. However, these results are in line with retrospective studies that found limited "resistance" to stands treated for density reduction [26].

We propose that management of spruce-fir forests in the Central Rocky Mountains should focus on creating short-term resistance and long-term resilience. Short-term resistance is crucial to allow for the establishment of Engelmann spruce regeneration and is key to maintaining long-term resilience. Our study was conducted at the stand level, and we explicitly characterized a resilient stand as one with a minimum of 245 tph of Engelmann spruce regeneration. This metric was chosen because it will likely produce characteristic spruce-fir stand composition. As these trees mature and reach a QMD of 25 cm, the SDI of just Engelmann spruce will be 245 or approximately 16% of the maximum SDI. If we assume a stand basal area of 20 m²·ha⁻¹ which is slightly lower than the stand basal area measurements for the group selection and shelterwood with reserves in 2013, Engelmann spruce basal area will be 12 m²·ha⁻¹ or represent 60% of the total stand basal area. This stand composition would also produce a low (5) overall spruce beetle risk rating. The group selection had the second highest amount of Engelmann spruce regeneration with an average of 125 tph in 2013. Without any subsequent regeneration, Engelmann spruce would only compose about 30% of the basal area and 8% of the maximum SDI. As the study continues to be monitored in the future, this metric can be adjusted based on future recruitment

and mortality of the regenerating Engelmann spruce. This is one of the first studies to put a lower limit on Engelmann spruce regeneration when timber management is not the primary goal.

The long regeneration windows of Engelmann spruce are a major barrier in building resilient spruce-fir forests in the Central Rocky Mountains [12,64]. Resilience pre-harvest was very low due to the limited natural regeneration of Engelmann spruce. Natural regeneration of Engelmann spruce can be limited by irregular cone production, drought and extreme high and low temperatures, as well as, unfavorable microsite conditions [39,64]. Planting of Engelmann spruce is the only way to ensure adequate stocking in the short-term. Because seeds in our study were collected from numerous overstory spruces at the TWDEF, these seedlings are presumed to be locally adapted and to represent a range of genetic variability. An additional benefit of supplemental planting of Engelmann spruce is that these small diameter trees (<4 cm dbh) are generally not attacked by spruce beetles, decreasing the likelihood of a potential vegetation shift to aspen and/or subalpine fir. The lack of resistance and the resulting vegetation shift to aspen and subalpine fir on the Markagunt Plateau, highlights how important resilience (adequate Engelmann spruce regeneration) is in maintaining the composition of spruce-fir forests in the Central Rocky Mountains. Resilience on the Markagunt Plateau will be low in the future due to the elimination of mature Engelmann spruce and limited spruce advanced regeneration [18,28]. Proactive density reduction methods that increase short-term resistance coupled with supplemental spruce planting to increase long-term resilience can reduce the likelihood of a complete vegetation type shift after a spruce beetle epidemic.

Management for spruce beetle outbreaks currently and in the future at both the stand and landscape levels will need to be assessed in light of trade-offs between traditional management by group selection and silvicultural alternatives such as shelterwood with reserves (Table 5). This study was conducted at the stand level. At the TWDEF, the shelterwood with reserves coupled with supplemental planting met many of the objectives. However, by thinning from below, the structure shifted from a wide diameter distribution, containing small to large diameter trees in various gaps and densities, to more uniformly spaced large diameter spruce trees. Although, these large diameter spruces are attractive to the spruce beetle [18,40] they will produce large amounts of seeds and potentially supplement planted seedlings [28].

Forest management activities in the Central Rocky Mountains can be delayed by appeals and ligation (5 years for our study). This potential delay must be taken into consideration when planning forest management activities. The shelterwood with reserves, once implemented could be used to treat the entire stand, potentially influencing landscape level resistance and resilience. By contrast, the small area treated at each entry is a limitation of the group selection. A larger group opening could be used but is not recommended due to limitation in natural regeneration and increased mortality due to extreme temperatures and sunscald [12]. An additional issue with the group selection is time. Even with supplemental planting, the group selection treatment did not meet the minimum metric of resilience. In the absence of a spruce beetle epidemic, in future harvests, overstory density will be reduced and planting of Engelmann spruce will continue; entries every 20 years will create age class and structural diversity, characteristic of spruce-fir stands [12]. Under this treatment, it will take another two cutting cycles to treat just half the stand. The cutting cycle could be reduced but due to the low productivity of the site would not be recommended because a 20-year cutting cycle is likely a minimum to ensure an economically viable harvest.

	Shelterwood with Reserves	Group Selection	Single Tree Selection	
Stand Level				
Reduced Basal Area	Х	Х		
Retention of Groups & Gaps		Х	Х	
Diversity of Overstory Species	Х	Х		
Minimum Levels of Spruce Regeneration	Х			
Landscape Level				
Ability to Treat Large Areas	Х			

Table 5. Trade-offs between the different treatments assessed at the stand and landscape level.

An X represents a treatment meeting the desired objective.

The traditional structure of spruce-fir forests would be retained in the group selection treatment. However, composition may shift with a spruce beetle outbreak because resilience (*i.e.*, adequate regeneration) would be limited in the short term. Given the increasing likelihood of stressed spruce trees due to increasing summer drought, the group selection method would not treat a large enough area of the stand quickly enough to provide adequate short-term resistance and long-term resilience at either the stand or landscape scale [20,30,65].

An additional concern, in any treatment, but especially the shelterwood with reserves and the group selection is the potential for windthrow [66]. Between 2008 and 2013, there were only minor differences in live basal area measurements and no discernible differences in incidence of windthrow between treatments (data not shown). While catastrophic windthrow did not happen in any of the silvicultural treatments on the TWDEF, any reduction in density has the potential for significant windthrow [12,66]. Collection of pre-harvest data, including crown ratio, may aid in selecting and removing less vigorous trees which may be more vulnerable to windthrow.

5. Conclusions

Forest managers across the world are confronted with uncertainty about how changing climatic conditions and subsequent interactions with disturbances will influence forest composition and structure [67,68]. Changing conditions in spruce-fir forests throughout the Rocky Mountains and the boreal forest are greatly influencing disturbance regimes [69,70]. Managers will have to weigh trade-offs between traditional and novel management approaches [71]. Long-term studies on experimental forests allow researchers and scientists to explore how different management approaches can influence both short and long-term forest dynamics.

Future climate change is expected to greatly influence spruce beetle dynamics across western North America and changing disturbance dynamics will greatly influence how spruce-fir forests are managed [13,65,68,72,73]. Our study on the TWDEF is one of the first studies to test how different silvicultural treatments influence explicitly defined and quantified metrics of resistance and resilience to the spruce beetle. By using a long-term study design with permanent plots, both short (results presented here) and long-term forest dynamics can be explored. Additionally, when spruce beetle activity increases again on the TWDEF, our study will provide insight into potential differences in how spruce beetle

populations build and spread in each of the different treatments. By using this long-term study design, these metrics of resistance and resilience can be tested and potentially adapted.

Managers will have to make difficult decisions as they plan for spruce beetle outbreaks. Traditional group selection harvests will maintain openings and groups, but potentially result in a loss of Engelmann spruce. Alternatively, the shelterwood with reserves will maintain a spruce component but with a novel structure. The shelterwood with reserves with supplemental planting was the only treatment to meet the resilience criteria on the TWDEF. If desired, increased structural variability could be built into this treatment by varying the type of reserve trees in the shelterwood (*i.e.*, strip, uniform or clumped). To increase size diversity and decrease overall average diameter of Engelmann spruce, stands could be thinned from below to remove smaller diameter subalpine fir and thinned from above to remove some of the larger Engelmann spruce. However, as the planted Engelmann spruce mature, they will become susceptible to the spruce beetle with any of the treatments. The shelterwood with reserves and supplemental planting allows for the retention of Engelmann spruce in the future forest and time to plan future management activities which may include group selection. Our results suggest that in spruce-fir stands in northern Utah, shelterwood with reserves best meets the goals of short-term resistance and long-term resilience to the spruce beetle.

Acknowledgments

This research was supported by the Utah Agricultural Experiment Station, Utah State University, and approved as journal paper number 8760. The authors are grateful for the outstanding efforts of Dwayne Bell, Chuck Frank, Jim Gibson, Kent O'Dell and Evelyn Sibbersen in the establishment of this trial. Critical reviews by Barbara Bentz, R. Justin DeRose, by two anonymous reviewers, and by the editors of the special issue improved the article. Funding for this project was provided through the T.W. Daniel Fellowship, USDA National Needs Graduate Fellowship Competitive Grant (No. 2011-38420-20087), and McIntire-Stennis Cooperative Forestry Research Program.

Author Contributions

James Long designed the study. Marcella Windmuller-Campione analyzed the data. Both authors equally contributed to the writing of this manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

References

- 1. Spittlehouse, D.; Stewart, R. Adaptation to climate change in forest management. J. Ecosyst. Manag. 2003, 4, 1–11.
- 2. Millar, C.I.; Stephenson, N.L.; Stephens, S.L. Climate change and forests of the future: Managing in the face of uncertainty. *Ecol. Appl.* **2007**, *17*, 2145–2151.

- Allen, C.D.; Macalady, A.K.; Chenchouni, H.; Bachelet, D.; Mcdowell, N.; Vennetier, M.; Kitzberger, T.; Rigling, A.; Breshears, D.D.; Hogg, E.H.; *et al.* A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manag.* 2010, *259*, 660–684.
- 4. IPCC. *Climate Change 2014: IPCC Fifth Assessment Synthesis Report*; Cambridge University Press: Cambridge, UK; New York, NY, USA, 2014; pp. 1–115.
- 5. Grossnickle, S.C. *Ecophysiology of Northern Spruce Species: The Performance of Planted Seedlings*; National Research Council of Canada: Ottawa, Canada, 2000; pp. 1–10.
- 6. Faccoli, M.; Bernardinelli, I. Composition and elevation of spruce forests affect susceptibility of bark beetle attacks: Implications for forest management. *Forests* **2014**, *5*, 88–102.
- Holsten, E.H.; Munson, R.W.; Munson, A.S.; Gibson, K.E. *The Spruce Beetle, USDA Forest Service, Forest Insect and Disease Leaflet 127*; USDA Forest Service: Washington, DC, USA, 1999; pp. 1–11.
- Berg, E.E.; Henry, J.D.; Fastie, C.L.; DeVolder, A.D.; Matsuoka, S.M. Spruce beetle outbreaks on the Kenai Peninusula, Alaska and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperature and regional differences in disturbance regimes. *For. Ecol. Manag.* 2006, 227, 219–232.
- Fettig, C.J.; Klepzig, K.D.; Billings, R.F.; Munson, A.S.; Nebeker, T.E.; Negron, J.F.; Nowak, J.T. The effectiveness of vegetation management practices for prevention and control of bark beetle outbreaks in coniferous forests of the western and southern United States. *For. Ecol. Manag.* 2007, 238, 24–53.
- Bentz, B.J.; Régnière, J.; Fettig, C.J.; Hansen, E.M.; Hayes, J.L.; Hicke, J.A.; Kelsey, R.G.; Negrón, J.F.; Seybold, S.J. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. *BioScience* 2010, *60*, 602–613.
- 11. Juday, G.P. Spruce beetles, budworms, and climate warming. Available online: http://www.cgc.uaf.edu/Newsletter/gg6_1/beetles.html (accessed on 3 February 2015).
- Alexander, R.R. Ecology, Silviculture and Management of the Engelmann Spruce—Subalpine fir Type in the Central and Southern Rocky Mountains; Research Paper RM-121; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1987; p. 121.
- Kärvemo, S.; Rogell, B.; Schroeder, M. Dynamics of spruce bark beetle infestation spots: Importance of local population size and landscape characteristics after a storm disturbance. *For. Ecol. Manag.* 2014, 334, 232–240.
- Alexander, R.R. Silviculture of Subalpine Forests in the Central and Southern Rocky Mountains: The Status of our Knowledge; Research Paper RM-121; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1973; p. 88.
- Schmid, J.M.; Hinds, T.E. Development of Spruce-Fir Stand Following Spruce Beetle Outbreaks; Research Note RM-131; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1974; p. 16
- 16. Mielke, J.L. Rate of deterioration of beetle-killed Engelmann spruce. J. For. 1950, 48, 882-888.

- Raffa, K.F.; Aukema, B.H.; Bentz, B.J.; Carroll, A.L.; Hicke, J.A.; Turner, M.G.; Romme, W.H. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *BioScience* 2008, *58*, 501–517.
- DeRose, R.J.; Long, J.N. Factors influencing the spatial and temporal dynamics of Engelmann spruce mortality during a spruce beetle outbreak on the Markagunt Plateau, Utah. *For. Sci.* 2012, 58, 1–14.
- 19. Forest Inventory and Analysis National Program. Available online: http://apps.fs.fed.us/ fia/fido/index.html (accessed on 17 November 2014).
- 20. Hart, S.J.; Veblen, T.T.; Eisenhart, K.S.; Jarvis, D.; Kulakowski, D. Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology* **2014**, *95*, 930–939.
- 21. McCambridge, W.F.; Knight, F.B. Factors affecting spruce beetles during a small outbreak. *Ecology* **1972**, *53*, 830–839.
- Dymerski, A.D.; Anhold, J.A.; Munson, A.S. Spruce beetle (*Dendroctonus rufipennis*) outbreaks in Engelmann spruce (*Picea engelmannii*) in central Utah, 1986–1998. West. N. Am. Nat. 2001, 61, 19–24.
- 23. Hansen, E.M.; Bents, B.J.; Turner, D.L. Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae). *Can. Entomol.* **2001**, *133*, 827–841.
- 24. Eaton, C.B. Influence of the mountain pine beetle on the composition of mixed pole stands of ponderosa pine and white fir. *J. For.* **1941**, *39*, 710–713.
- Schmid, J.M.; Frye, R.H. *Stand Ratings for Spruce Beetles*. Research Note RM-309; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1976; p. 4.
- 26. Temperli, C.; Hart, S.J.; Veblen, T.T.; Kulakowski, D.; Hicks, J.J.; Andrus, R. Are density reduction treatments effective at managing for resistance or resilience to spruce beetle disturbance in the southern Rocky Mountains? *For. Ecol. Manag.* **2014**, *334*, 53–64.
- 27. Seidl, R. The shape of ecosystem management to come: Anticipating risks and fostering resilience. *Bioscience* **2014**, *16*, 1159–1169.
- 28. DeRose, R.J.; Long, J.N. Resistance and resilience: A conceptual framework for silviculture. *For. Sci.* **2014**, *60*, 1205–1212.
- 29. Bentz, B.J.; Munson, A.S. Spruce beetle population suppression in northern Utah. *West. J. Appl. For.* **2000**, *15*, 122–128.
- Munson, S. Management Guide for Spruce Beetle: Dendroctonus Rufipennis Kirby. In *Forest Health Protection and State Forestry Organizations*; USDA Forest Service: Washington, DC, USA, 2010; p. 16.
- Hansen, E.M.; Negron, J.F.; Munson, A.S.; Anhold, J.A. A retrospective assessment of partial cutting to reduce spruce beetle-caused mortality in southern Rocky Mountains. *West. J. Appl. For.* 2010, 25, 81–87.
- 32. DeRose, R.J.; Long, J.N. Disturbance, structure, and composition: Spruce beetle and Engelmann spruce forests on the Markagunt Plateau. *For. Ecol. Manag.* **2007**, *244*, 16–23.
- Alexander, R.R. Silvicultural Systems and Cutting Methods for Old-Growth Spruce-Fir Forests in the Central and Southern Rocky Mountains; General Technical Report RM-126; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1986.

- Fiedler, C.E.; McCaughey, W.W.; Schmidt, W.C. Natural Regeneration in Intermountain Spruce-Fir Forests—A Gradual Process; USDA Forest Service Research Paper INT-343; USDA Forest Service, Intermountain Forest and Range Experiment Station: Odgen, UT, USA, 1985; p. 16.
- 35. Peet, R.K. Forests and meadows of the Rocky Mountains. In *North American Terrestrial Vegetation*, 2nd ed.; Barbour, M.G., Billings, W.D., Eds.; Cambridge University Press: New York, NY, USA, 2000; p. 75–121.
- Schmid, J.M.; Frye, R.H. Spruce Beetle in the Rockies; General Technical Report GTR RM-49; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1977; p. 38.
- 37. Aplet, G.H.; Laven, R.D.; Smith, F.W. Patterns of community dynamics in Colorado Engelmann spruce-subalpine fir forests. *Ecology* **1988**, *63*, 312–319.
- 38. Veblen, T.T.; Hadley, K.S.; Reid, M.S.; Rebertus, A.J. Blowdown and stand development in a Colorado subalpine forest. *Can. J. of For. Res.* **1989**, *19*, 1218–1225.
- Alexander, R.R.; Sheppard, W.D. *Picea engelmanii* Parry ex Engelm. In *Silvics of North America, Volume 1, Conifers*; Burns, R.M., Honkala, B.H., Eds.; USDA Forest Service, Agricultural Handbook 654, USDA Forest Service: Washington, DC, USA, 1990; pp. 187–203.
- 40. Hart, S.J.; Veblen, T.T.; Kulakowski, D. Do tree and stand-level attributes determine susceptibility of spruce-fir forests to spruce beetle outbreaks in the 21st century? *For. Ecol. Manag.* **2014**, *318*, 44–53.
- Alexander, R.R.; Shearer, R.C.; Shepperd, W.D. *Abies lasiocarpa* (Hook.) Nutt. In *Silvics of North America, Volume 1, Conifers*; Burns, R.M., Honkala, B.H., Eds.; USDA Forest Service, Agricultural Handbook 654, USDA Forest Service: Washington, DC, USA, 1990; pp. 60–70.
- 42. Hobson, E.R.; Foster, J.H. *Engelmann Spruce in the Rocky Mountains*; USDA Forest Service Circular 170: Washington, DC, USA, 1910; p. 23.
- 43. Stahelin, R. Factors influencing the natural restocking of high altitude burns by coniferous trees in the central Rocky Mountains. *Ecology* **1943**, *24*, 19–30.
- 44. Wadleigh, L.; Jenkins, M.J. Fire frequency and the vegetative mosaic of a spruce-fir forest in northern Utah. *Gt. Basin Nat.* **1996**, *56*, 28–37.
- 45. Long, J.N. The Middle and Southern Rocky Mountain. In *Regional Silviculture of the United States*, 3rd ed.; Barrett, J.W., Ed.; John Wiley and Sons: New York, NY, USA, 1994; pp. 335–386.
- Alexander, R.R. *Partial Cutting in Old Growth Spruce-Fir*; Research Paper RM-110; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1973; p. 16.
- 47. Alexander, F.F. Cutting methods in relation to resource use in central Rocky Mountain spruce-fir forests. *J. For.* **1977**, *75*, 395–400.
- 48. Hart, G.E.; Lomas, D.A. Effects of clearcutting on soil water depletion in an Engelmann spruce stand. *Water Resour. Res.* **1979**, *6*, 1598–1602.
- 49. Schimpf, D.J.; Henderson, J.A.; MacMahon, J.A. Some aspects of succession in the spruce-fir forest zone of Northern Utah. *Gt. Basin Nat.* **1980**, *40*, 1–26.
- Van Miegroet, H.J.; Boettinger, J.L.; Baker, M.A.; Nielsen, J.; Evans, D.; Stum, A. Soil carbon distribution and quality in a montane rangeland-forest mosaic in northern Utah. *For. Ecol. Manag.* 2005, *220*, 284–299.

- 51. Olsen, H.R.; van Miegroet, H. Factors affecting CO₂ release from forest and rangeland soils in northern Utah. *Soil Sci. Soc. Am. J.* **2010**, *74*, 282–291.
- 52. Shaw, J.D. Application of stand density index to irregularly structured stands. *West. J. Appl. For.* **2000**, *15*, 40–42.
- 53. Long, J.N.; Daniel, T.W. Assessment of growing stock in uneven-aged stands. *West. J. Appl. For.* **1990**, *5*, 93–96.
- 54. Reineke, L.H. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 1933, 46, 627-638.
- 55. Long, J.N. A practical approach to density management. For. Chron. 1985, 61, 23-27.
- 56. Shaw, J.D. US Forest Service Rocky Mountain Research Station & Utah State University, Logan, UT, USA. Unpublished work, 2014.
- 57. Curtis, R.O.; Marshall, D.D. *Permanent-Plot Procedures for Silvicultural and Yield Research*; General Technical Report PNW-GTR—634; USDA Forest Service, Pacific Northwest Research Station: Portland, OR, USA, 2005; p. 86.
- 58. Alexander, R.R.; Edminster, C.B. *Engelmann Spruce Seed Dispersal in the Central Rocky Mountains*; Research Paper RM—217; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1986; p. 14.
- Alexander, R.R. Engelmann Spruce Seed Production and Dispersal, and Seedling Establishment in the Central Rocky Mountains; General Technical Report RM—134; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1986; p. 9.
- 60. Ducey, M.J. The ratio of additive and traditional stand density indices. *West. J. Appl. For.* **2009**, *24*, 5–10.
- 61. Curtis, R. Effect of diameter limits and stand structure on relative density indices: A case study. *West. J. Appl. For.* **2010**, *25*, 169–175.
- 62. Clendenen, C.W. Base-Age Conversion and Site Index Equations for Engelmann Spruce Stands in the Central and Southern Rocky Mountains; Research Note INT-223. USDA Forest Service, Intermountain Forest and Range Experiment Station: Odgen, UT, USA, 1977; p. 6.
- 63. DeRose, R.J.; Long, J.N. Regeneration response and seedling bank dynamics on a *Dendroctonus rufipennis*-killed *Picea engelmannii* landscape. *J. Veg. Sci.* **2010**, *21*, 377–387.
- 64. Noble, D.L.; Alexander, R.R. Environmental factors affecting natural regeneration of Engelmann spruce in the Central Rocky Mountains. *For. Sci.* **1977**, *23*, 420–429.
- 65. DeRose, R.J.; Bentz, B.J.; Long, J.N.; Shaw, J.D. Effects of increasing temperatures on the distribution of spruce beetle in Engelmann spruce forests of the Interior West, USA. *For. Ecol. Manag.* **2013**, *308*, 198–206.
- 66. Mitchell, S.J. Wind as a natural disturbance agent in forests: A synthesis. *Forestry* **2013**, *86*, 147–157.
- IPCC. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change; Stocker, T.F.; Qin, D., Plattner, G-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M., Eds.; Cambridge University Press: Cambridge, UK; New York, NY, USA, 2013; pp. 867–953.

- 68. Yousefpour, R.; Jacobsen, J.B.; Thorsen, B.J.; Mieilby, H.; Hanewinkel, M.; Oehler, K. A review of decision-making approaches to handle uncertainty and risk in adaptive forest management under climate change. *Ann. For. Sci.* **2012**, *69*, 1–15.
- 69. Volney, W.J.A.; Fleming, R.A. Climate change and impacts of boreal forest insects. *Agric. Ecosyst. Environ.* **2000**, *82*, 283–294.
- 70. Flower, C.E.; Gonzalez-Meler, M.A. Responses of temperate forest productivity to insects and pathogen disturbance. *Ann. Rev. Plant Biol.* **2015**, doi:10.1146/annurev-arplant-043014-115540.
- 71. Seastedt, T.R.; Hobbs, R.J.; Suding, K.N. Management of novel ecosystems: Are novel approaches required? *Front. Ecol. Environ.* **2008**, *6*, 547–553.
- 72. Miller, L.K.; Werner, R.A. Cold-hardiness of adult and larval spruce beetles *Dendroctonus rufipennis* (Kirby) in interior Alaska. *Can. J. Zool.* **1987**, *65*, 2927–2930.
- Rousseau, J.; Bauce, E.; Lavallee, R.; Guertin, C. Winter mortality and supercooling point of the spruce beetle (Coleoptera: Curculionidae) not affected by host tree vigor in Nova Scotia, Canada. *J. Acadian Entomol. Soc.* 2012, *8*, 1–10.

 \bigcirc 2015 by the authors; licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution license (http://creativecommons.org/licenses/by/4.0/).