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Disturbance, structure, and composition: Spruce beetle and Engelmann spruce forests on the Markagunt Plateau, Utah

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Abstract

In the 1990s a spruce beetle (*Dendroctonus rufipennis*) outbreak killed nearly all canopy Engelmann spruce (*Picea engelmannii*) across the Markagunt Plateau, southern Utah, USA. We quantified attributes of the forest before and after the spruce beetle outbreak, including tree ages, structure and composition on three sites. Greater than 99% of the Engelmann spruce measured in this study were dead and 93% of those died as a result of the beetle outbreak. Age structure analysis revealed each site had originally regenerated from a different antecedent disturbance, and not from a single, landscape-wide event comparable to the recent spruce beetle outbreak. Profound structural and compositional changes from spruce dominance to subalpine fir (*Abies lasiocarpa*), aspen (*Populus tremuloides*), or limber pine (*Pinus flexilis*) were found. No site was resistant to the spruce beetle and post-outbreak forest composition suggested that the response to the disturbance is at least partially due to species diversity. We suggest short-term (decades) system response will tend toward structures similar to pre-outbreak conditions however, composition will differ. Sparse Engelmann spruce regeneration (6% of understory trees <5 cm diameter at breast height) compared with subalpine fir (62%) and aspen (32%) will likely preclude spruce from dominance for many decades. Long-term (centuries) forest reorganization will tend toward structures similar to the pre-outbreak system (i.e. forest); however, dominance by Engelmann spruce will likely take longer.

Keywords: Disturbance ecology; ‘Spruce-fir’ forest; Species diversity; Spruce beetle; Resilience

1. Introduction

Fire is often cited as the most important stand-replacing disturbance in Rocky Mountain, Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) -dominated ecosystems (Peet, 2000). However, spruce beetle (SB, *Dendroctonus rufipennis* Kirby) outbreaks may be equally important (Baker and Veblen, 1990). Behavior of both disturbance types is affected by forest structure and composition and resultant communities are shaped by the nature of disturbance. While these interactions are fairly well understood for stand-replacing fire in spruce, much less is known about interactions of SB outbreaks with community composition and structure. SB epidemics in southern Utah have been observed to kill every mature Engelmann spruce with a diameter at breast height (DBH, 1.3 m) >10 cm (Mielke, 1950). The result of this host-specific mortality is a shift in post-disturbance community composition to non-host species such as subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), accelerating succession (Veblen et al., 1991) or to early successional species such as aspen (*Populus tremuloides* Michx.). Although these species dominate the community in the short-term, spruce regeneration, if present, may eventually come to dominate the canopy (Veblen, 1986) given a window of roughly 40–60 years before another SB outbreak (Veblen et al., 1994). Indeed, the pre-disturbance diversity of tree species should effect how the community reacts to a SB outbreak, with the pre-disturbance age- and size-structure in large part dictating what percentage of the host species succumbs to attack (Mielke, 1950).

SB and Engelmann spruce have a long evolutionary history. Coadaptations as a result of herbivore—host interactions are evident in physiological traits of both the beetle and their hosts (Raffa and Berryman, 1987). Endemic populations of SBs are common in mature Engelmann spruce communities, annually killing only a few individuals over the landscape. As a population builds it becomes incipient; if continued increases occur, an epidemic (outbreak) is likely. The ability of a tree toward off SBs at endemic population levels is closely related to

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its vigor (Paine et al., 1997). The transition from endemic to epidemic beetle populations may be catalyzed when mature host trees are left prostrate after landslide, logging, or windthrow (Schmid and Frye, 1977) all of which may be mediated by root disease (Lewis and Lindgren, 2002). Drought has also been implicated in creating outbreak conditions for some bark beetle populations (mountain pine beetle (*Dendroctonus ponderosae* Hopk.) (Logan and Powell, 2001)). However, it is not known whether this is true for Engelmann spruce. If incipient SB populations have access to nearby, suitable mature hosts an endemic-to-epidemic threshold may be crossed (Christiansen et al., 1987) after which host vigor likely does little to dissuade attacking beetles in light of the huge population numbers.

The short- and long-term dynamics of SB outbreaks and their role in shaping post-disturbance Engelmann spruce forests can be assessed using the concepts of resistance and resilience to disturbance. Resistance is the ability of a system to resist change when perturbed (Walker et al., 2004). Resilience, one of the most important aspects of disturbance ecology, is the ability of an ecological system to return to similar pre-disturbance structures, functions, and feedbacks post-disturbance (Walker et al., 2004). Quantification of stand age structures, understory stocking and comparisons of species composition pre- to post-outbreak, can reveal whether communities have been permanently changed or have only been temporarily altered and are reorganizing after a disturbance (Drever et al., 2006).

Recent widespread mortality of mature Engelmann spruce forests in southern Utah was caused by the SB (Fig. 1). The largest (Dymerski et al., 2001) outbreak recorded in the state likely began in the late 1980s in Sydney Valley on the Markagunt Plateau, southern Utah, approximately 30 km northeast of Cedar City (Steve Munson, personal communication). The SB then appeared northward affecting large tracts of spruce on the Fish Lake and Manti La Sal National Forests of the Wasatch Plateau (Dymerski et al., 2001). Spruce beetle activity is still occurring in the northern parts of the state where some successful abatement has been conducted (Bentz and Munson, 2000). The temporal and spatial magnitude of the SB outbreak and its influence on Engelmann spruce forests represent diverse research opportunities (Bentz and Munson, 2000) as it is not known what factors instigated the outbreak.

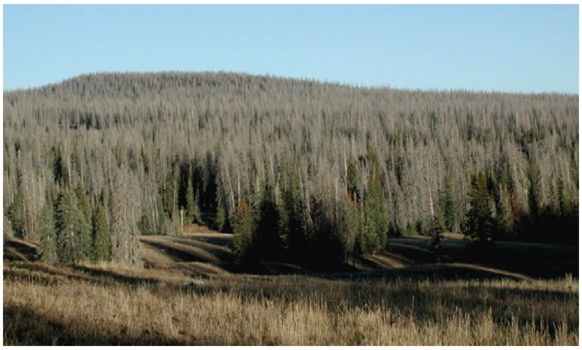

Fig. 1. Extensive Engelmann spruce mortality near Cedar Breaks National Monument caused by the 1990s spruce beetle outbreak on the Markagunt Plateau, Utah. Live trees are subalpine fir. Photograph: James N. Long.

The mortality on the Markagunt Plateau is substantial (Fig. 1); and leaves the impression the forest has been ‘destroyed’. However, SB outbreaks of this scale may, in fact, be part of the normal dynamics of this ecological system (Schmid and Hinds, 1974). The apparent simultaneous maturation of Engelmann spruce across the Plateau, which made it susceptible to the beetle outbreak, suggests similar, landscape-level, antecedent disturbance(s) resulted in relatively homogenous age structures and species compositions across the landscape. In this paper we describe the relationship of the recent SB outbreak to antecedent disturbances. We address the following questions: (1) what was the magnitude of SB-caused mortality? (2) Was the pre-outbreak forest the result of a single, landscape-level antecedent disturbance? (3) How has structure and composition changed from pre- to post-outbreak? (4) What will be the short- and long-term system responses to the recent SB outbreak?

2. Methods

2.1. Study area

The Markagunt Plateau (meaning ‘highland of trees’ derived from indigenous Piute) is the western-most flank of the greater Colorado Plateau and covers ~2000 km^2. Most of the Markagunt Plateau is public land managed by the USDA Forest Service. The area of interest for this study is the high elevation (3000–3300 m asl) forest south of Cedar Breaks National Monument where spruce was the dominant species and subalpine fir rarely reached the upper canopy. Aspen is also abundant particularly on southerly aspects. Understory plant diversity is low; species include *Juniperus communis* L., *Ribes montigenum* McClatchie, and *Mertensia arizonica* Greene. The reddish, silty, soil was derived from Tertiary deposits of the Claron Lake formation. Basalt flows dating from the late Holocene (1000–5000 BP) cover an extensive area of the Claron formation on the Plateau. These conspicuous lava flows are underlain by silicic, Tertiary volcanic rock (Chronic, 1990). Annual precipitation is bimodal with a majority occurring during winter in the form of snow with a late summer peak due to monsoonal influence (Anderson et al., 1999). Pacific air brings most of the winter snowpack, whereas summer monsoons originate from the south (Mock, 1996). Mean annual precipitation recorded from the SNOTEL site ~3 km from Stand LF (http://www.nrcs.usda.gov/) for the period 1982–2005 was 909 mm (range 368–1709 mm among years). Mean annual temperature for the period 1982–2005 was 1.7 °C (range −0.9–3.1 °C among years). Palynological studies suggest the presence of Engelmann spruce on the Plateau since ~13,000 years BP (Anderson et al., 1999), i.e. since the late Wisconsin deglaciation.

2.2. Sampling

To characterize a range of recently killed spruce communities, sites were chosen if they (a) were relatively homogeneous in stand condition, with no signs of ecotone conditions and (b) had no obvious signs of human influence (logging, recreation). Three stands with varying structural and compositional characteristics were measured for this study. All stands were clearly dominated by Engelmann spruce in terms of basal area and composition prior to the SB outbreak. The Lava Flow (LF, latitude: +37.608, longitude: −112.818) stand was a closed canopy forest located near recent (∼1000 BP, see above) lava flows and, as a result, was part of a larger heterogeneous landscape of open areas and closed forest. The second stand, Midway Face (MF, latitude: +37.566, longitude: −112.798), was located on a northerly aspect and appeared to have had an even-aged overstory of Engelmann spruce. The third stand, South Face (SF, latitude: +37.572, longitude: −112.810), was located on a southerly aspect and had more tree species diversity. All three stands serve as case studies in the face of the larger SB outbreak mosaic which did not noticeably discriminate between spruce stands regardless of species dominance, species composition or position on the landscape.

Three intensive measurement plots were located randomly within each stand and were at least 100 m apart. In each intensive measurement plot variable radius prism plots were used to sample trees greater than 5 cm DBH. Variable radius plots provide an unbiased estimate of basal area on a per hectare basis and when adjusted for tree DBH also provide an unbiased estimate of the number stems ha^{-1} represented by each sampled tree (Husch et al., 1993). Sampled trees were measured for DBH along with species, status (dead or alive) and mortality agent if recognizable. For example SB-killed trees as a result of the recent outbreak (<10 years) were very conspicuous as their bark was full of emergence holes and often sloughing off the bole. To capture within-site variation at each stand satellite plots in three compass azimuths (120°, 240°, 360°), 40 m from the intensive sampling plot, were also measured for a total of 12 plots per stand. At these points variable radius plots identified trees to be tallied for species, DBH, status, and mortality agent. Three regeneration plots (3 m^2), one nested in the center of each intensive measurement plot, were assessed for all seedlings >10 cm in height (HT) but <1 m in HT, and saplings >1 m in HT but <5 cm in DBH. Seedling and sapling HTs and species were recorded and then cross sections taken at ground level. For age structure analysis an increment core was removed from each tree on the intensive plot at <30 cm above the ground. Coarse woody debris (CWD) >10 cm in diameter was assessed along a 20 m transect radiating in a random direction from the sampling plot center.

2.3. Analysis

Terms describing the magnitude of change and time needed to return to pre-disturbance dynamics are common in the literature but rarely evaluated (Grimm and Wissel, 1997). In this study we follow the terminology of Drever et al. (2006) when assessing whether the post-SB outbreak forest will return to spruce dominance. The Engelmann spruce forests on the Markagunt Plateau were not capable of resisting the SB outbreak (Fig. 1) but we can assess their response to the disturbance. Quantification of stand age structures by species, through our use of increment cores, provides insight into stand origin. Similarly, species size structures (basal area) will suggest the magnitude of change as a result of the SB outbreak. Assessing understory stocking and comparisons of species composition changes pre- to post-outbreak, can reveal whether communities have been permanently altered or have only been temporarily shifted and are reorganizing after a disturbance (*sensu* Drever et al., 2006).

In the lab increment cores were prepared with progressively finer sandpaper, and annual rings were counted under a dissecting scope. Fourteen percent of the trees were too rotten to core, and 6% provided only conservative age estimates due to failure to bore through to the pith. For age structure analysis a total of 28 cores were used for Stand LF, 21 for Stand NF, and 29 for Stand SF. Core samples from each stand were distributed across a range of DBHs. Actual dates of spruce mortality (outer ring) are known within 4 years (1998–2001, Phil Eisenhauer, personal communication), falling well within our decadal age structure analysis. Stand average basal areas (Fig. 2) were determined by summing tree count from variable radius prism plots. The stems ha^{-1} represented by each sampled tree were then determined by dividing basal area per tree into the prism factor for age structure analysis. Species diversity was measured as tree species richness. Stand CWD biomass was estimated using the Fire Fuels Calculator 1.0 (Hammond, 2004) which utilizes standard fuels equations to estimate biomass per unit area from linear field measurements. Dead overstory (snags) volume was estimated using predictive equations developed by the Forest Service and compiled in the USDA

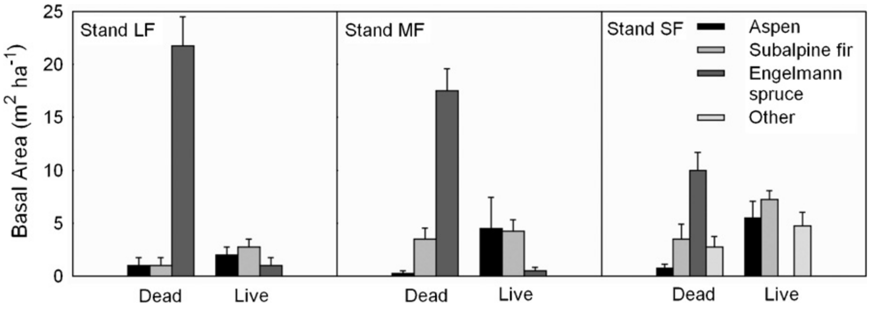

Fig. 2. Basal area (m^2 ha^{-1}) by species and status (dead or live) in 2005. Error bars indicate one standard error. Note: 93% of dead Engelmann spruce trees were a result of the spruce beetle outbreak. The category, other, includes limber pine (*Pinus flexilis*), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) in order of abundance.

Forest Service National Volume Estimator Library (http://www.fs.fed.us/fmsc/measure/volume/nvel/index.php/) and converted to biomass with equations used for the Utah Fire and Fuels Extension (Reinhardt and Crookston, 2003).

3. Results

The extensive mortality, obvious when viewing the landscape (Fig. 1), was reflected in the data (Fig. 2). Ninety-three percent of the dead, overstory spruce were killed in the recent outbreak and <1% of the sampled spruce >10 cm DBH were alive. In Stands LF and MF Engelmann spruce is now extremely rare in the live component of the overstory and is missing completely from Stand SF. This result reflects the situation across the entire Markagunt Plateau.

Although pre-outbreak stands were relatively similar in species composition and structure (Fig. 2) it appears the antecedent disturbances creating these stands differed (Fig. 3). The lack of congruence between age class distributions (Fig. 3) of the three, relatively close proximity stands makes it unlikely that stands over the entire study area regenerated following a single, landscape-level disturbance such as the recent SB outbreak or a large, stand-replacing fire. It is more likely that a different kind of disturbance created each stand. Therefore, the answer to our second question is that the pre-outbreak forest did not originate from the same antecedent disturbance.

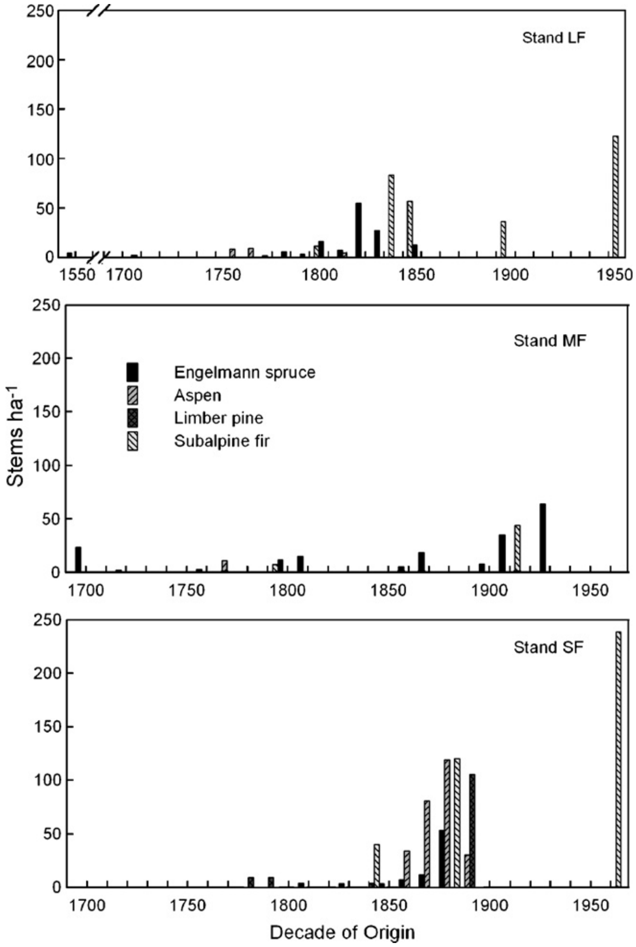

Fig. 3. Age structure of all (live and dead) trees >5 cm DBH for the three stands. Note: similar *y*-axis scale and similar *x*-axis scale with the exception of one sample tree in Stand LF.

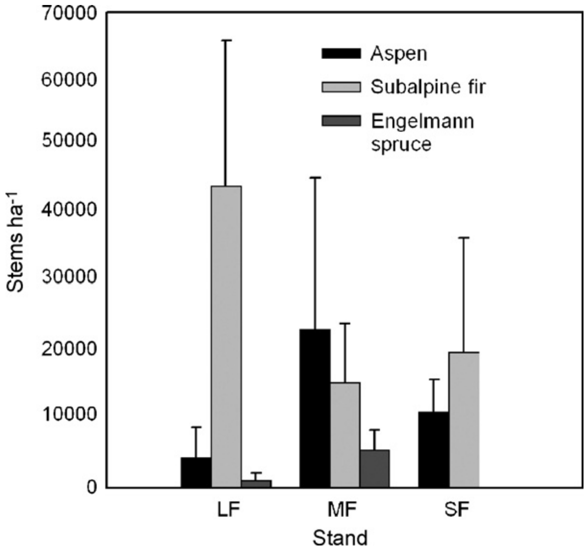

Fig. 4. Understory density (stems ha^{-1}) by species for all seedlings >10 cm in HT but <1 m in HT and saplings >1 m in HT but <5 cm DBH for three fixed area plots in each stand. Error bars indicate one standard error.

The pre-outbreak Engelmann spruce forests appeared homogeneous in structure based on field observation and basal area (Fig. 2) despite having substantial differences in stand age structures. Indeed all three stands were dominated to various degrees by spruce in terms of basal area (Fig. 2). In Stands LF and MF Engelmann spruce accounted for nearly all the stocking. Stand SF, while richer in diversity of tree species, was also dominated by spruce before the outbreak. Species composition has clearly shifted pre- to post-outbreak from spruce to aspen (Stand LF and MF, Fig. 2), subalpine fir (Stand LF, Fig. 2), or limber pine (*Pinus flexilis* James) (Stand SF, Fig. 2). Stand SF has fewer dead stems ha^{-1} and a more closed canopy relative to the other two stands.

Subalpine fir represented 62% of the understory stocking (Fig. 4), aspen 32%, and spruce 6%. The ages of the understory trees (DBH <5.0 cm) ranged from 5 to 148 years (mean 45) for subalpine fir, 10–53 years (mean 37) for spruce and <3 years for aspen. The large range of ages for the conifer species suggests relatively continual understory recruitment.

There was an abrupt shift in live to dead standing biomass (Fig. 5) as a result of the SB outbreak. This change in the fuel profile may influence future fire behavior.

4. Discussion

Extensive Engelmann spruce mortality like that observed in this study has been reported for other spruce-fir systems. Dymerski et al. (2001) reported 90% spruce mortality of trees >5 cm DBH in central Utah. Schmid and Hinds (1974) noted 99% of the overstory was killed during a 1940s SB outbreak in the White River Mountains of Colorado. Werner et al. (2006) reported 1.19 million ha^{-1} of spruce forest in Alaska were

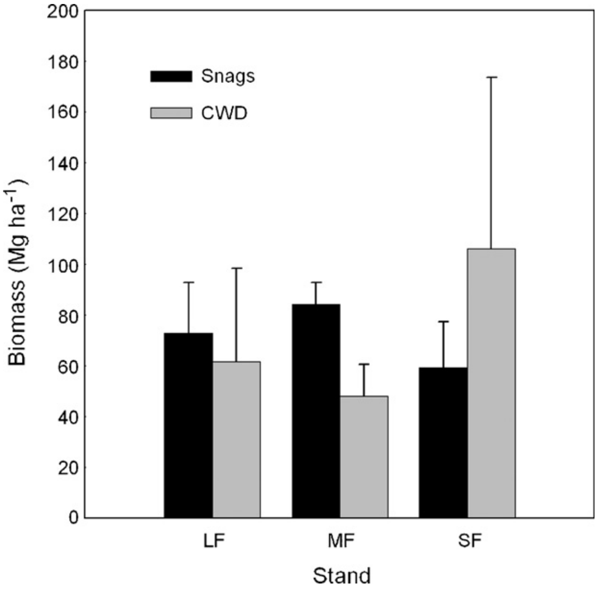

Fig. 5. Dead biomass (Mg ha^{-1}) grouped by snags (dead overstory) and coarse woody debris (CWD, logs) components for three transects in each site. Error bars indicate one standard error.

affected by the SB from 1990 to 2000. We observed 98% mortality of Engelmann spruce stems >5 cm DBH due to the SB outbreak. Mielke (1950) noted that all mature spruce (DBH >10 cm) on the Aquarius Plateau, directly east of our study area, were killed by a SB outbreak that started in 1916. Although not quantified, Mielke (1950) found abundant regenerating spruce 25 years after the outbreak and attributed it to smaller spruce which were not attacked by the beetle, likely due to the uneven-aged structure of the pre-outbreak forest on the Aquarius Plateau (Hanley et al., 1975).

4.1. Antecedent disturbances

Differences in age-structures between the three stands (Fig. 3) make it unlikely spruce over the entire Plateau was regenerated from a single, landscape-level antecedent disturbance such as a SB outbreak or stand-replacing fire. Both fire and SB have been proposed as primary disturbance agents in spruce-fir forests (Baker and Veblen, 1990). Madsen et al. (2002) have reconstructed fire return intervals (charcoal layers as a proxy for fire events) ranging from 330 to 410 years from a bog located on the Markagunt Plateau. Although we found charcoal in the soil on all sites it may represent many fire events. Similar evidence for historical recurrence of SB outbreaks is lacking. Although we expected to find that a common age structure on the Plateau set-up the forest for the recent SB outbreak, differences between stands perhaps suggest a more interesting story.

Establishment of trees in Stand LF occurred in the late 1700s and increased until about 1860. However, this site showed residual spruce established as far back as 1550, surviving many centuries. The unimodal age class distribution centered on ~1830 is consistent with fire that left residual trees (1550 and 1710 age classes). Episodes of subalpine fir recruitment appeared later reflecting succession as the overstory trees aged. A large pulse of subalpine fir (~125 stems ha^{-1}) occurs in the 1960s after nearly 50 years with no recruitment.

Stand MF has had pulses of establishment from the beginning of the 18th century when spruce entered the stand. This may indicate a late 1600s stand-replacing fire. It is likely that intense competition ensued and eventually in the late 1700s and early 1800s representatives of all species, but primarily spruce, established. Another gap in establishment lasted until the late 1800s when another cohort of spruce was recruited, consistent with observations of ‘spruce reinitiation’ (Aplet et al., 1989). After the early 1900s subalpine fir and spruce continued to regenerate, likely in gaps in the now 250-year-old spruce canopy.

Stand SF was the youngest stand where the oldest individuals (limber pine) regenerated in the late 1700s. The most prominent regeneration event began in the late 1800s, with all species represented. This pulse in regeneration may have resulted from fall burning by local sheep herders as they were leaving the summer foraging grounds (Sampson, 1923). Upslope, undated fire scars on the most fire-resistant species, limber pine, is consistent with this scenario. We would expect the 1840 group of subalpine fir to have been killed in a large fire, but it is possible they could have escaped a heterogeneous burn. Newly established subalpine fir, aspen and limber pine appear around 1890, near the end of the putative post-fire cohort (Fig. 3). Similar to Stand LF, subalpine fir appears in large numbers in the 1960s. This pulse, apparent in two stands may indicate an area wide change in weather or decreased grazing pressure.

4.2. Temporal patterns of recruitment

Hanley et al. (1975) performed the only previous age structure analysis on the Markagunt Plateau. They found a relatively continuous distribution of overstory Engelmann spruce, not unlike our Stand 2. They also found subalpine fir exhibited a pulse in age structure (their Fig. 6). Studies of Colorado and southern Wyoming spruce-fir forests have revealed various age structures (Kulakowski et al., 2003; Aplet et al., 1989; Whipple and Dix, 1979; Miller, 1970) useful for comparative purposes. More or less continuous recruitment has been hypothesized for Colorado spruce-fir forests (Whipple and Dix, 1979, their Fig. 2), and exhibited by our Stand MF. Stand SF, and to some extent Stand LF, display more episodic age structures, although biological legacies (residuals) from antecedent disturbances and more recent ingrowth of subalpine fir complicate the patterns (Fig. 4). Similarly, spruce-fir studies from British Columbia (Antos and Parish, 2002a,b; Parish et al., 1999; Kneeshaw and Burton, 1997) revealed variations in spruce and fir age structures ranging from pulses to continual recruitment. As an example (Antos and Parish, 2002b), reconstructed age structures in a fire-initiated spruce-fir forest which revealed initial post-fire establishment of lodgepole pine and Engelmann spruce (their Fig. 4). Subalpine fir were present but did not increase in numbers until spruce establishment ceased ~100 years post-disturbance. As subalpine fir numbers peaked and declined a second group of spruce became established. This pattern of balanced life history traits has been described for equilibrium coexistence models of spruce-fir forests in the absence of disturbance (Aplet et al., 1989; Veblen, 1986). Alternatively, non-equilibrium coexistence requires disturbance. As observed by Aplet et al. (1989), and seen in the contradictory example of (Antos and Parish, 2002b), neither model fully explains the dynamics of spruce-fir succession. Likewise neither model explains the dynamics of the Markagunt Plateau Engelmann spruce forests.

Some caution analyzing static age structures (Fig. 3) is warranted as they may not capture large fluxes of regeneration and mortality that may have occurred since stand initiation (Johnson et al., 1994). Given the differing longevity of the species in our system, it is likely some early members of these communities (i.e. subalpine fir and aspen) died, and subsequently decayed, hiding them from our age structure analysis. Regardless, the closed canopy condition of the pre-outbreak, Engelmann spruce forest suggests the growing space was fully occupied and the past turnover of individuals due to competition-related mortality will not substantially change age structure interpretation. Interpretive complication may also result from the observation that following a stand-replacing disturbance some species (e.g. subalpine fir) can take up to 75 years to regenerate (Little et al., 1994; Agee and Smith, 1984). While this may be true for subalpine fir-dominated stands, post-disturbance recruitment of Engelmann spruce and aspen occurred in our age structures (Fig. 3). Given the >98% overstory mortality and the virtual elimination of a seed source, Engelmann spruce recruitment post-SB outbreak is questionable.

4.3. Disturbance interactions

The possibility that disturbances are not independent but rather are linked make historical interpretation tenuous. For example, we suggest that stand-scale fire originated Stand MF; however, it is possible that a pre-fire SB outbreak actually created fuel loads for a catastrophic wildfire. In other words, a beetle outbreak might catalyze subsequent fire. In our SB-killed Engelmann spruce forest there has been a relatively abrupt shift in live- to dead-standing biomass (Fig. 5). Over time CWD will increase as snags fall which may influence future fire behavior. Indeed, the evidence for large-scale wildfires in SB-killed forests is mixed, with some corroboration (Bigler et al., 2005), some evidence of interaction with other disturbances (Kulakowski et al., 2003; Kulakowski and Veblen, 2002), and some refutation of increased fire potential after beetle outbreaks (Bebi et al., 2003; Veblen et al., 1994). The ubiquity of charcoal at all study sites suggests fire has played a role in disturbance dynamics but does not indicate how fire may have interacted with SB outbreaks. The quantity of standing dead is visually obvious (Fig. 1); however, whether the forests on the Markagunt Plateau are actually more susceptible to large-scale fire is debatable and should be an area of future research. Knowing the type of the antecedent disturbance would be helpful in predicting the fuel loading in place for future disturbances. Similarly, quantifying the entire fuels profile (*sensu* Agee and Huff, 1987), i.e. 1-, 10-, 100-, 1000-h fuels, duff, litter, and overstory fuels would facilitate fire behavior prediction.

4.4. Short- and long-term system response

The abundance of subalpine fir and virtual absence of Engelmann spruce in the understory will strongly influence short-term forest reorganization (*sensu* Drever et al., 2006). Taken in combination with post-disturbance overstory composition (Fig. 2), the understory data suggest short-term forest dominance by subalpine fir and aspen (Stands LF and MF) or subalpine fir and limber pine (Stand SF). The stand with the greatest species diversity (Stand SF, Fig. 2) appears to have been affected the least by the host-specific SB. Stands maintaining a large percentage of living, non-host trees post-outbreak will more easily reorganize (*sensu* Drever et al., 2006) post-collapse (beetle outbreak) in both the short- and long-term. The long-term outlook is likely to include some Engelmann spruce in Stands LF and MF. Sampling and field observations detected no spruce regeneration in Stand SF (Fig. 4); if it is ever to be dominated by spruce, regeneration must come from an off-site seed-source.

Our observation that many ages of subalpine fir exist in the understory is consistent with Antos et al. (2000) who noted continual understory seedling bank recruitment in spruce-fir forests of British Columbia. However, seed and seedling bank spruce are limited in our study sites (Fig. 4) which might be due to unsuitable micro-site conditions such as lack of mineral soil or decaying CWD (Knapp and Smith, 1982). In contrast Schmid and Hinds (1974) observed 590 spruce stems ha^{-1} and 67 subalpine fir stems ha^{-1} on average in uneven-aged spruce forests on the Aquarius Plateau of southern Utah 50 years post-beetle outbreak. Subalpine fir accounted for the majority of the understory stocking in our study (Fig. 4) perhaps reflecting its ability to establish on thick litter common in mature forests (Knapp and Smith, 1982), and its greater shade tolerance (Kobe and Coates, 1997). Subalpine fir is likely to become the primary overstory species after near-complete spruce mortality. Although aspen accounted for nearly a third of the total understory trees (Fig. 4) strong browsing pressure of large populations of deer, elk, and sheep (personal observation) will likely continue to maintain young understory ages (<3 years) as aspen ramets respond to intense sprout herbivory.

The data presented here are not sufficiently comprehensive or extensive to conclude whether the recent SB outbreak was a novel disturbance event. However, it appears the pre-outbreak forest had the structure and composition to recover from the outbreak without shifting system states (e.g. from forested to subalpine meadow). The difference in pre- to post-outbreak structure and composition (Fig. 2) suggests that the stands will not maintain the pre-outbreak spruce forests condition. A diverse species composition appears to maintain the most similar pre- to post- disturbance forest structure. Therefore, although none of the stands were resistant to the SB outbreak, it appears Stand SF is the most resilient, owing to its species mixture. In contrast both Stands LF and MF have lost most of the forest canopy and will exhibit differing stand structure and composition for many decades (Fig. 2). The relatively open canopy of resultant communities has left abundant growing space for shrubs or herbaceous species and created conditions for subalpine fir, and possibly aspen (in the absence of herbivory), to regenerate and move into the canopy. Although short-term (decades) canopy dominance may be achieved by subalpine fir, a long-term outlook (centuries) may again include spruce, at least in Stands LF and MF (Fig. 4). The understory stocking appears more than adequate (Fig. 4) for maintenance of forested conditions; however, clearly none of the stands will retain similar composition.

5. Summary

- It is clear the level of overstory spruce mortality in combination with its rare regeneration will long delay the return of Engelmann spruce-dominated forests. The magnitude of overstory spruce mortality is consistent with other SB studies; however, the paucity of spruce <5 cm DBH (Fig. 3) suggests understory density is not adequate to maintain spruce as other than a minor component of the future landscape.
- Our initial idea that a single, landscape-level, antecedent disturbance set-up the current (pre-outbreak) forest for the SB-outbreak was rejected. Instead different disturbances initiated each stand. It is interesting that the three apparently different disturbance histories reconstructed here (Fig. 2) all created conditions suitable for epidemic levels of the SB across the study area and the Markagunt Plateau landscape.
- The short-term response to the outbreak suggests sites will continue to be dominated by forests but they will be compositionally and structurally different. No stand was resistant to the SB outbreak and the level of resilience to the disturbance was heavily influenced by species diversity.
- In the very long-term (i.e. centuries) it is likely forest structure will be similar to pre-outbreak conditions. However, a return to species composition dominated by Engelmann spruce is unlikely as a seed source is necessary for spruce establishment.

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