

THESIS

FOREST REGENERATION TRAJECTORIES IN MOUNTAIN PINE BEETLE-
DISTURBED FORESTS OF ROCKY MOUNTAIN NATIONAL PARK

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY MATTHEW DISKIN ENTITLED FOREST REGENERATION TRAJECTORIES IN MOUNTAIN PINE BEETLE-DISTURBED FORESTS OF ROCKY MOUNTAIN NATIONAL PARK BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

FOREST REGENERATION TRAJECTORIES IN MOUNTAIN PINE BEETLE- DISTURBED FORESTS OF ROCKY MOUNTAIN NATIONAL PARK

A severe mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemic in western North America has caused widespread mortality of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) and drastically altered subalpine forest structure and composition over large areas. My research describes possible future forest regeneration trajectories by documenting tree survivorship in Rocky Mountain National Park, CO, and then projecting future forest conditions using an established forest growth model, the Forest Vegetation Simulator. In 2008, I measured stand structure and tree species composition in lodgepole pine-dominated forests in the western portion of the Park. I defined five lodgepole pine forest types that varied with respect to the abundance of seedlings and non-lodgepole pine species. These forest types formed the foundation for further analyses to describe variability in post-epidemic forest regeneration trajectories.

Chapter One documents surviving forest stand structure and composition in the Park, and shows that surviving trees, including larger canopy trees, saplings, and seedlings, were plentiful in most of the post-epidemic forests. Lodgepole pine remained the dominant species in most areas, but modest increases in the relative abundance of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex

Engelm.), and aspen (*Populus tremuloides* Michx.) had occurred. Forest structure and composition varied considerably among the five forest types after the epidemic, setting the stage for variable future forest regeneration trajectories that were explored in Chapter Two.

Future forest conditions were projected over a 100 year time period and are presented in Chapter Two. The projections show that the beetle-disturbed forests remain forested in the future, and emphasize that the most important mechanism for forest renewal is the release of surviving trees, rather than post-epidemic tree seedling establishment. Projected future forest conditions varied depending on the forest type, but indicate that basal area and quadratic mean diameter recovery occurs within 40-100 years in most areas. Spruce, fir, and aspen become dominant in the projected future forests on approximately 60% of the landscape, while lodgepole pine remains dominant in the forests where it formed pure stands prior to the epidemic.

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Chapter 1. Forest regeneration trajectories in mountain pine beetle-disturbed forests of Rocky Mountain National Park

Abstract

A mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemic has caused widespread mortality of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) trees across several Rocky Mountain states, severely impacting subalpine forests across the region. I characterized the initial effects of beetle-induced mortality on forest structure and composition in Rocky Mountain National Park, CO. In 2008, I surveyed stand structure and tree species composition across lodgepole pine-dominated forests in the western portion of the Park. I defined five lodgepole pine forest types using a cluster analysis to describe variability in pre-epidemic forest conditions. My results indicate that surviving trees, including both canopy trees and saplings, were plentiful in most of the post-epidemic forests, even after accounting for anticipated future mortality. Subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and aspen (*Populus tremuloides* Michx.) had modestly higher relative abundances after the epidemic. Lodgepole pine remained the dominant species on approximately 85 percent of the landscape. Forest structure and composition varied considerably among the five forest types after the epidemic. My results suggest

that active efforts to “restore” lodgepole pine forests will not be necessary and that post-epidemic forest regeneration trajectories will vary across the landscape.

Introduction

Subalpine forests in much of western North America have been impacted by a severe mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemic. The beetle outbreak has killed lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) trees on approximately half a million hectares in Colorado since 1996 (Colorado State Forest Service 2009). This massive mortality event has killed most large lodgepole pines in affected areas (Nelson 2009), yet the consequences of this epidemic for the future forest landscape remain unknown. In this study, I describe the initial effects of mountain pine beetle-induced mortality on lodgepole pine forest structure and composition in Rocky Mountain National Park in northern Colorado. This study is a critical first step in characterizing possible future outcomes for beetle-disturbed forests in Colorado and elsewhere in the Rocky Mountain West.

The mountain pine beetle is a native insect that infests many western conifer species, but lodgepole pine is the preferred host (Safranyik and Carroll 2006). Mountain pine beetle populations typically exist at low levels, killing only weakened trees. Periodically, however, populations increase to epidemic levels, and kill a majority of large-diameter trees over large areas. These beetle epidemics can last for a decade or more and typically subside due to either unseasonably cold temperatures or a depletion of large-diameter host trees (Safranyik and Carroll 2006). The widespread mortality associated with the

current epidemic is unprecedented in recorded history (Kaufmann et al. 2008), leading to a concern that patterns of survivorship and forest renewal might differ from what has been observed in the past.

The overarching goal for this study is to describe future forest regeneration trajectories in beetle-disturbed forests of Rocky Mountain National Park. To meet this goal, I sought answers to the following questions:

- 1) How abundant are surviving trees in each of the canopy, sapling, and seedling layers?
- 2) To what extent does lodgepole pine mortality increase the relative abundance of other tree species?

I approached these questions by emphasizing how variability in pre-epidemic forest structure and composition influences post-epidemic forest conditions.

The abundance of surviving trees – and how they are distributed among the canopy, sapling, and seedling layers – is an important indicator of future regeneration trajectories. The reduction in competition that results from beetle-induced mortality increases resources for surviving trees. The resulting growth increase is thought to be more important for forest regeneration than the establishment of new trees in many stands (Veblen et al. 1991, Hawkes et al. 2004, Astrup et al. 2008). Indeed, a recent study of mountain pine beetle-disturbed lodgepole pine forests in British Columbia found that almost half of the stands remained fully stocked with surviving trees (Coates et al. 2006). A quarter of the stands were poorly stocked, however, indicating that the establishment of

new seedlings will be important in some cases. Despite the high profile of the bark beetle epidemic and the associated impacts across Colorado, little quantitative information is available to characterize surviving trees. In particular, we do not know what proportion of the Rocky Mountain National Park landscape retains adequate densities of surviving trees to regenerate beetle-disturbed stands, and what proportion of stands will require abundant new seedling establishment for regeneration.

The broad ecological amplitude of lodgepole pine further inhibits our ability to predict post-epidemic forest regeneration patterns. Because lodgepole pine trees grow with many other tree species (Peet 1981), I expected that beetle-induced mortality would cause a shift to forests dominated by the non-host species in our study area (subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), aspen (*Populus tremuloides* Michx.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and limber pine (*Pinus flexilis* James)). Past research from the Southern and Central Rocky Mountains supports this hypothesis, but also demonstrates that lodgepole pine remains dominant in areas that are unsuitable for other species or where seed sources for other species are not present (Moir 1969, Amman 1977, Sibold et al. 2007). The outbreaks studied in the past, however, were less extensive than the current epidemic, and it remains uncertain to what degree these patterns hold for the current large-scale, high severity epidemic in Colorado.

Methods

Study area

Rocky Mountain National Park (Figure 1-1) covers 108,000 ha along the spine of the Rocky Mountains in north-central Colorado's Front Range. The Park spans elevations from 2240-4350 m and the continental divide runs approximately north-south, bisecting the Park. Weather records for the neighboring town of Grand Lake approximate the climate in the study area. The average minimum January temperature is -16.5 °C and the average July maximum temperature is 24.6 °C. Precipitation averages 480 mm/yr, with no pronounced dry season. Measurable snow frequently falls in September and snow typically remains on the ground until May (Western Regional Climate Center 2010).

Stand-replacing fires occurred regularly in the western portion of the Park, and many of today's lodgepole pine forests regenerated following extensive fires in the mid and late 1800's (Sibold et al. 2006). Lodgepole pine forests dominate the lower elevations of the western portion of the Park at elevations ranging from approximately 2500-3500 m (Rocky Mountain National Park 2007). The fire-free interval at higher elevations appears to be longer, and these areas are dominated by Engelmann spruce-subalpine fir forests (Sibold et al. 2006).

I restricted the study to the Park's lodgepole pine-dominated forests west of the divide, where the epidemic was most severe as of 2008. At the time field measurements were taken in 2008, the epidemic was subsiding in much of the study area.

Data collection

I used a spatially balanced random sampling design (Theobald et al. 2007) and the Park's vegetation map (Rocky Mountain National Park 2007) to sample a population of 11,200 hectares of lodgepole pine forests west of the continental divide. The spatially balanced design helped to ensure that samples were well-distributed across the extent of the lodgepole pine forest type, while maintaining randomness (Theobald 2007). Data were collected in the summer of 2008 at 38 sites (Figure 1-1). At each site, crews established two 20 m x 20 m square plots spaced 90 m apart in a random direction. Negligible alterations to this protocol occurred at a few sites to ensure that all plots met site selection criteria. In total, 75 plots were measured at the 38 sites. Because plots within a cluster frequently exhibited drastically different characteristics, I treated each plot as an independent sample for a total sample size of 75.

In each plot, I measured the densities of canopy trees, saplings, and seedlings by species. Diameter at breast height (dbh) was recorded for each tree taller than 1.4 m. Canopy trees, saplings, and seedlings were distinguished by the following criteria: trees ≥ 10 cm dbh were defined as canopy trees; saplings were < 10 cm dbh and taller than 1.4 m; and trees shorter than 1.4 m and at least one year old were considered seedlings. Canopy trees and saplings were measured in the 20 m x 20 m plot and seedlings were counted in a

2 m x 20 m transect that ran through the center of the plot. Living and beetle-killed lodgepole pines were tallied separately, allowing descriptions of pre-epidemic conditions.

Data analysis

I used a hierarchical agglomerative cluster analysis to define groups of plots with similar pre-epidemic species compositions and structures (McCune and Grace 2002).

Subsequent analyses were conducted separately for each group of plots (hereafter *forest types*). Two species (Douglas-fir and limber pine) occurred in only two plots and these species were not considered in the cluster analysis. Densities for each of the remaining four species (lodgepole pine, subalpine fir, Engelmann spruce, and aspen) were tallied separately for the canopy, sapling, and seedling layers. Canopy trees, saplings, and seedlings were thus treated as separate taxa in the cluster analysis, allowing us to distinguish between forest types with different structural attributes. The data were relativized by taxon totals to give equal weight to canopy trees, saplings, and seedlings in the analysis. Compositional dissimilarity between groups was defined using Sorenson distance, and the cluster analysis proceeded using the flexible beta linkage method with beta equal to -0.25. The PC-ORD software package was used for this and subsequent multivariate analyses (McCune and Mefford 2006).

Multi-response permutation procedures (MRPP, Mielke and Berry 2001) based on Sorenson distance tested for statistical differences between the groups identified by the cluster analysis. Nonmetric multidimensional scaling (NMS) using Sorenson distance was used to visualize patterns of tree species composition among plots and to confirm the

distinctiveness of the groups found in the cluster analysis (Kruskal 1964, Mather 1976). Two gradients of species composition were extracted, and correlations were calculated between these axes and taxon abundance.

Although the epidemic appeared to be subsiding in most of the study area, I observed mortality in the year following field sampling and expect additional mortality. For this reason, I present results based both on documented mortality through 2008 and from a “hypothetical extreme scenario,” in which I considered all lodgepole pine trees greater than 10 cm dbh to be dead. The 10 cm cutoff is based on the fact that, as of 2008, nearly all (99%) lodgepole pine trees less than 10 cm dbh were still living. While the hypothetical extreme scenario probably overstates the ultimate severity of the epidemic, it provides an extreme bookend against which 2008 conditions can be compared.

I calculated standard forest descriptors to describe the abundance and species composition of surviving trees for each forest type defined in the cluster analysis. Absolute and relative stem densities and basal areas were calculated for the pre-epidemic forests, with observed 2008 mortality, and with hypothetical extreme scenario mortality. I also evaluated changes in species dominance by categorizing plots (before and after mortality) according to the species present with the highest basal area. Engelmann spruce and subalpine fir were grouped together as one taxon in this analysis of species dominance because they frequently occur together, distinguishing a unique forest type (Peet 1981).

Results

Pre-epidemic patterns of lodgepole pine forest structure and composition

Five forest types defined from the cluster analysis effectively described pre-epidemic patterns of lodgepole pine forest structure and composition. The five types differed (p-value < 0.0001) with high homogeneity within types (chance-corrected within-group agreement, $A = 0.291$; McCune and Grace 2002). I used these forest types to describe variability in the abundance and species composition of surviving trees.

The five forest types varied with respect to their pre-epidemic species composition and structure (Table 1-1). Lodgepole pine dominated the canopy and sapling layers of all of the forest types, as would be expected because sampling was restricted to sites with a major lodgepole pine component in the overstory. Non-lodgepole pine species dominated the seedling layer in three of the five forest types. A description of the five forest types follows:

Lodgepole-sparse understory: this type was nearly pure lodgepole pine and had extremely sparse sapling and seedling layers. It was found primarily on drier sites at lower elevations (average 2860 m). Total vegetation cover on the forest floor was very low.

Lodgepole-lodgepole seedlings: this type was also nearly pure lodgepole pine, but had a high density of lodgepole pine seedlings. It too was found primarily at

lower elevations (average 2780 m) but on flatter terrain than the lodgepole-sparse understory type.

Lodgepole-fir seedlings: a moderate amount of fir seedlings characterized this type. Engelmann spruce and subalpine fir were present in low densities in the canopy and sapling layers. It was found on relatively dry sites at higher elevations (average 3000 m) and had low vegetation cover on the forest floor.

Lodgepole-spruce-fir: Engelmann spruce and subalpine fir attained their highest relative abundance in this type. This type also had the highest absolute density of seedlings. It was found on relatively moist sites at higher elevations (average 3000 m) and had high vegetation cover on the forest floor.

Lodgepole-aspen: this type was characterized by aspen suckers in the seedling layer. Aspen attained its highest relative abundance in this type as well. It was found on a variety of site types.

The five forest types were found on roughly equal proportions of the landscape (12-28%, Table 1-1), with the *lodgepole-fir seedlings* type slightly more common, and the *lodgepole-aspen* type slightly less common.

The NMS ordination confirms the distinctiveness of the five forest types defined in the cluster analysis (Figure 1-2). The segregation of the five forest types in the two-

dimensional NMS ordination space suggests that the forest types follow a gradient along Axis 1 from *lodgepole-sparse understory*, *lodgepole-lodgepole seedlings*, *lodgepole-fir seedlings*, to *lodgepole-spruce-fir*. This pattern reflects increases along Axis 1 in Engelmann spruce ($r = 0.71, 0.61, \text{ and } 0.28$ for canopy trees, saplings, and seedlings), and subalpine fir ($r = 0.70, 0.70, \text{ and } 0.55$). The *lodgepole-sparse understory* type is separated from the *lodgepole-lodgepole seedlings* type along Axis 2. This separation is associated with a negative correlation between Axis 2 and lodgepole pine saplings ($r = -0.23$) and seedlings ($r = -0.24$), which would be expected given the sparse sapling and seedling layers of the *lodgepole-sparse understory* type (Table 1-1). The *lodgepole-aspen* type has negative Axis 2 values, which is associated with aspen ($r = -0.59, -0.46, \text{ and } -0.67$ for canopy trees, saplings, and seedlings).

Abundance of surviving canopy trees, saplings, and seedlings

Post-epidemic stands in 2008 had high densities of surviving trees and a moderate residual basal area on average (Table 1-2 and Figure 1-3). Although the average canopy tree density had been reduced to 495 trees/ha (from an average of 973 canopy trees/ha prior to the epidemic), the presence of hundreds of saplings/ha and thousands of seedlings/ha raised the average total stem density to nearly 4000 stems/ha. The average post-epidemic stand had a basal area of $12 \text{ m}^2/\text{ha}$ in 2008, down from over $33 \text{ m}^2/\text{ha}$ prior to the epidemic. Only 81 canopy trees/ha and a total basal area of $3.9 \text{ m}^2/\text{ha}$ would survive, on average, in the hypothetical extreme scenario. Even with hypothetical extreme scenario mortality, however, an average of over 3500 stems/ha would survive in the canopy, sapling, and seedling layers.

The forest types showed relatively minor differences in the abundance of surviving trees, with two notable exceptions. The *lodgepole-sparse understory* type had by far the smallest number of saplings and seedlings in 2008, and also had the smallest total residual density (Table 1-2). If mortality after 2008 removed all of the largest surviving lodgepole pine trees, this type would average about 550 surviving stems/ha. Conversely, the *lodgepole-spruce-fir* type had by far the highest post-disturbance density and basal area, with averages of >8,000 stems/ha and >10 m²/ha even under the hypothetical extreme mortality scenario (Table 1-2 and Figure 1-3).

Species composition of the post-epidemic forests

Lodgepole pine was still the dominant species in terms of both relative density and relative basal area in the average stand in the Park's western lodgepole pine forests in 2008 (Figure 1-4). Even with hypothetical extreme scenario mortality, lodgepole pine would still have the highest average relative density (in the combined canopy, sapling, and seedling layers) and basal area (in the combined canopy and sapling layers) across the landscape. Engelmann spruce, subalpine fir, and aspen had a higher relative abundance in 2008 compared to the pre-epidemic forests, but the degree of change varied among the forest types. Decreases in the relative abundance of lodgepole pine were extremely small in the *lodgepole-sparse understory* and *lodgepole-lodgepole seedlings* forest types. Moderate decreases in the relative abundance of lodgepole pine had occurred in the *lodgepole-fir seedlings*, *lodgepole-spruce-fir*, and *lodgepole-aspen* types, with larger changes possible in the hypothetical extreme scenario. The low-moderate

relative density and high relative basal area of lodgepole pine in these three forest types reflects high numbers of non-lodgepole species in the understory of stands dominated by lodgepole pine in the overstory. One plot in 2008 (or 8 plots in the hypothetical extreme scenario) had no surviving lodgepole pine trees.

Stands in which lodgepole pine was the dominant species were still by far the most abundant type on the landscape in the beetle-disturbed forests in 2008 (Table 1-3). Non-lodgepole pine dominated stands were more abundant in 2008 than in the pre-epidemic forests, but even in the hypothetical extreme scenario, stands dominated by lodgepole pine would cover 55 percent of the landscape. Engelmann spruce-subalpine fir dominated stands covered approximately 15 percent of the landscape in 2008, with further increases possible in the hypothetical extreme scenario. In the hypothetical extreme scenario, aspen would be dominant on five percent of the landscape, but was not dominant in any plots in 2008.

Discussion

Forests on the western side of Rocky Mountain National Park remained fully stocked with surviving trees, despite widespread mountain pine beetle-induced mortality in the canopy. The large decreases in basal area reflect substantial changes in forest structure associated with this epidemic. However, nearly all of the measured stands (96%) contained sufficient surviving trees to exceed the minimum post-harvest stocking requirement of 370 stems/ha used on adjacent National Forests (United States Forest Service 1997). This formal requirement does not apply in Rocky Mountain National

Park, where the management emphasis is on maintaining natural ecological processes, but it is a useful general indicator of “successful” forest regeneration following disturbance.

The large reduction in basal area that had occurred in most areas indicates that competition among surviving trees for limiting resources will be low in the years following this disturbance. Surviving trees are therefore likely to experience accelerated growth, similar to what has been found in other areas following beetle epidemics (Roe and Amman 1970, Heath and Alfaro 1990, Romme et al. 1986). Due to both their abundance and size advantage over newly established seedlings, it is likely that these surviving trees, legacies of the pre-epidemic forest, will form the core of most future forests in the Park. While post-epidemic tree seedling establishment will likely occur in most areas (Sibold et al. 2007), and be important in a few areas where surviving trees were scarce, it appears that the most important mechanism for forest renewal in the Park following this epidemic will be the release of surviving trees. My focus has been on surviving stems, most of which pre-dated the outbreak, so any new establishment of seedlings will add to the densities of stems reported here. Nineteen percent of seedlings included in my tallies were young enough to have germinated since the onset of the outbreak, but I found no relationship between canopy mortality and density of post-outbreak seedlings (unpublished data). I suspect, therefore, that by 2008 I had not yet observed a pulse of new seedling recruitment brought on by the epidemic, in part because most dead trees still retained many needles and understory light levels had not appreciably changed. The processes of canopy mortality, accelerated growth of surviving

trees, and seedling establishment will promote uneven-aged, multi-layered, forest structure in the Park (Roe and Amman 1970, Romme et al. 1986, Sibold et al. 2007).

Lodgepole pine still dominated the beetle-disturbed forests in the western portion of Rocky Mountain National Park as the epidemic was subsiding in 2008, and would remain dominant even if future mortality resembles the hypothetical extreme scenario. It appears highly unlikely that lodgepole pine will be eliminated from more than a very small percentage of stands in the foreseeable future. Moderate increases in the relative abundance of spruce, fir, and aspen had occurred in many areas, and on a small portion of the landscape these species became dominant due to lodgepole pine mortality. However, about 40 percent of the area remained nearly pure lodgepole pine in 2008; this pattern holds true even in the hypothetical extreme scenario. My results support previous studies showing that either shade tolerant species or lodgepole pine can dominate following mountain pine beetle-induced mortality (Amman 1977, Sibold et al. 2007). However, my results also indicate that increases in the relative abundance of shade tolerant species are not always necessarily large, and that aspen could potentially be favored as well.

Although often regarded as a “simple” forest type, lodgepole pine forests in fact exhibited highly variable structure and composition both prior to and after the beetle epidemic, as described by the five different forest types identified in this study (Table 1-1). These forest types resemble the community types described by Peet (1981) in his study of forest vegetation on the Colorado Front Range. The variability in lodgepole pine forest structure and composition is important because it means that the impacts of lodgepole

pine mortality and subsequent regeneration trajectories will not be uniform. Two of the five forest types are nearly pure lodgepole pine; these two types are distinguished by the density of lodgepole pine in the sapling and seedling layers. While it appears likely that forest renewal in the *lodgepole-lodgepole seedlings* type will largely be characterized by the release of surviving lodgepole pine in the canopy and understory, the nature of post-epidemic seedling establishment will likely be an important determinant of forest development trajectories in the *lodgepole-sparse understory* type, where the lowest densities of surviving trees were found. Moderate to large increases in the relative abundance of Engelmann spruce and subalpine fir will likely occur in the *lodgepole-spruce-fir* and *lodgepole-fir seedlings* forest types, although lodgepole pine was still the dominant species in many of these areas in 2008. The fact that the *lodgepole-spruce-fir* type retained the highest surviving tree density and basal area indicates that forest renewal in these stands should occur relatively quickly. The degree to which the epidemic will promote the dominance of Engelmann spruce and subalpine fir in these forests is variable, and will depend on the density of large sized Engelmann spruce and subalpine fir and the ability of seedlings to grow into the canopy.

Of particular interest to land managers and the public is the lodgepole-aspen forest type. Aspen is the only major upland deciduous tree species in the Southern and Central Rocky Mountains, and aspen forests support a rich and distinctive biota. Aspen forests are declining in many areas, due to recent climatic conditions, paucity of fires, and other causes (e.g., Worrall et al. 2008), but it is hypothesized that aspen will become more abundant in mixed stands where the lodgepole pine component has been largely removed

by mountain pine beetles. In this study, surviving lodgepole pine trees were abundant in the *lodgepole-aspen* type, and minor increases in the relative abundance of aspen in these forests had occurred by 2008. The fate of aspen suckers in the seedling layer of these stands is uncertain. Recent research indicates that an extremely high proportion of aspen suckers in the study area are being heavily browsed by elk, although increased growth, establishment, and density of aspen suckers was observed in areas with higher levels of beetle-induced lodgepole pine mortality (Nelson 2009).

The post-epidemic forest conditions described here serve as starting points that will influence future forest development. These initial conditions allow for informed projections of future forest structure and composition. Several unpredictable factors, however, will shape forests in the future; these are discussed in Chapter Two.

The most important insight from this study is that the bark beetle epidemic greatly reduced stand basal area and stem density, but it left almost all forests fully stocked with smaller trees that should grow well following the reduction in overstory dominance. Many of the changes associated with this epidemic are undesirable to society and command swift action, including hazard tree removal around buildings and infrastructure. In wildland settings of Rocky Mountain National Park, however, I found that surviving trees – including larger trees in the canopy and sapling layers – were generally abundant and that lodgepole pine remained a dominant species even as the epidemic was subsiding in 2008. In the absence of future disturbance or rapid changes to climate, it is likely that this lodgepole pine-dominated landscape will remain forested. Trees will be smaller for

some time, but species composition will be similar to what existed before the epidemic. This implies that proactive efforts to “restore” mountain pine beetle-disturbed forests are unnecessary in much of the Park. A second implication of the findings of this study is that, given the variability in beetle-disturbed forests both before and after the epidemic, uniform portrayals of the epidemic and one-size-fits-all management strategies are likely to be erroneous and ineffective.

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Table 1-1. Average pre-epidemic density by species for the five lodgepole pine forest types and the estimated percent of the landscape occupied by each type.

| Forest Type | Percent of Landscape (± 95% confidence interval) | -----Canopy Trees (stems/ha)----- | | | | -----Saplings (stems/ha)----- | | | | -----Seedlings (stems/ha)----- | | | |
|--------------------------------------|---|-----------------------------------|-------------------------|--------------------------|------------------------|-------------------------------|--------------------------|--------------------------|--------------------------|--------------------------------|-----------------------------|----------------------------|----------------------------|
| | | lodgepole pine | fir | spruce | aspen | lodgepole pine | fir | spruce | aspen | lodgepole pine | fir | spruce | aspen |
| Lodgepole-Sparse Understory* | 20% (±9%) | 1107 (132) | 0 (0) | 0 (0) | 0 (0) | 285 (72) | 0 (0) | 0 (0) | 0 (0) | 83 (31) | 67 (52) | 0 (0) | 0 (0) |
| Lodgepole-Lodgepole Seedlings | 20% (±9%) | 997 (107) | 0 (0) | 3 (3) | 0 (0) | 717 (181) | 7 (4) | 22 (9) | 0 (0) | 2600 (625) | 83 (40) | 50 (27) | 17 (17) |
| Lodgepole-Fir Seedlings | 28% (±10%) | 983 (118) | 15 (5) | 25 (6) | 0 (0) | 323 (80) | 42 (10) | 46 (11) | 0 (0) | 393 (101) | 1095 (212) | 214 (65) | 0 (0) |
| Lodgepole-Spruce-Fir† | 20% (±9%) | 658 (137) | 95 (22) | 193 (40) | 2 (2) | 457 (225) | 252 (51) | 208 (40) | 8 (5) | 204 (79) | 5402 (1623) | 1483 (910) | 117 (80) |
| Lodgepole-Aspen | 12% (±7%) | 488 (86) | 0 (0) | 22 (15) | 53 (22) | 456 (110) | 91 (80) | 59 (53) | 216 (114) | 375 (94) | 156 (94) | 125 (47) | 2406 (776) |
| Average | 100% | 892 (60) | 24 (6) | 49 (12) | 6 (3) | 436 (66) | 74 (17) | 66 (13) | 25 (14) | 737 (169) | 1453 (404) | 385 (192) | 287 (118) |

Note: Standard errors are in parentheses, unless otherwise noted.

*Douglas-fir is not shown here and was present in two plots.

†Limber pine is not shown here and was present in two plots.

Table 1-2. Average density (standard error) of all species combined for the five lodgepole pine forest types before the epidemic, in 2008, and with hypothetical extreme scenario mortality.

| Forest Type | -----Canopy Trees (stems/ha)----- | | | Saplings* (stems/ha) | Seedlings (stems/ha) | -----Total Canopy Trees, Saplings, and Seedlings (stems/ha)----- | | |
|--------------------------------------|-----------------------------------|---------------------------|----------------------------------|---------------------------|-----------------------------|--|-----------------------------|----------------------------------|
| | Pre-Epidemic | 2008 | Hypothetical Extreme Scenario | | | Pre-Epidemic | 2008 | Hypothetical Extreme Scenario |
| Lodgepole-Sparse Understory | 1117 (129) | 487 (113) | 10 (10) | 290 (72) | 267 (105) | 1674 (178) | 1026 (178) | 549 (145) |
| Lodgepole-Lodgepole Seedlings | 1000 (108) | 442 (78) | 3 (3) | 745 (178) | 2750 (641) | 4495 (698) | 3932 (718) | 3493 (733) |
| Lodgepole-Fir Seedlings | 1024 (114) | 504 (108) | 40 (8) | 411 (80) | 1702 (256) | 3137 (303) | 2616 (313) | 2152 (268) |
| Lodgepole-Spruce-Fir | 950 (108) | 635 (75) | 292 (52) | 928 (230) | 7206 (2265) | 9084 (2231) | 8753 (2232) | 8411 (2210) |
| Lodgepole-Aspen | 563 (92) | 325 (81) | 75 (24) | 822 (272) | 3063 (807) | 4448 (971) | 4210 (990) | 3960 (962) |
| Average | 973 (55) | 495 (45) | 81 (17) | 603 (75) | 2886 (551) | 4462 (564) | 3976 (572) | 3562 (570) |

*Pre-epidemic sapling densities are reported.

Table 1-3. Percent of the landscape (95% confidence interval) dominated by each species before the epidemic, in 2008, and with hypothetical extreme scenario mortality.

| Dominant species | Pre-epidemic | 2008 | Hypothetical Extreme scenario |
|---------------------------------|--------------|--------------|-------------------------------|
| Lodgepole pine | 93% (±6%) | 84% (±8%) | 55% (±11%) |
| Engelmann spruce-subalpine fir* | 5% (±5%) | 15% (±8%) | 39% (±11%) |
| Aspen | 0% | 0% | 5% (±5%) |
| Douglas-fir | 1% (±2%) | 1% (±2%) | 1% (±2%) |

Note: Dominance is defined as the species with the highest total basal area in the plot. Columns might not add up to 100% due to rounding.

*Engelmann spruce and subalpine fir were treated as one taxon in this analysis.

Figure 1-1. Map of Rocky Mountain National Park showing the locations of the 38 sample sites. The sampled area is the 11,200 ha of lodgepole pine forests west of the Continental Divide.

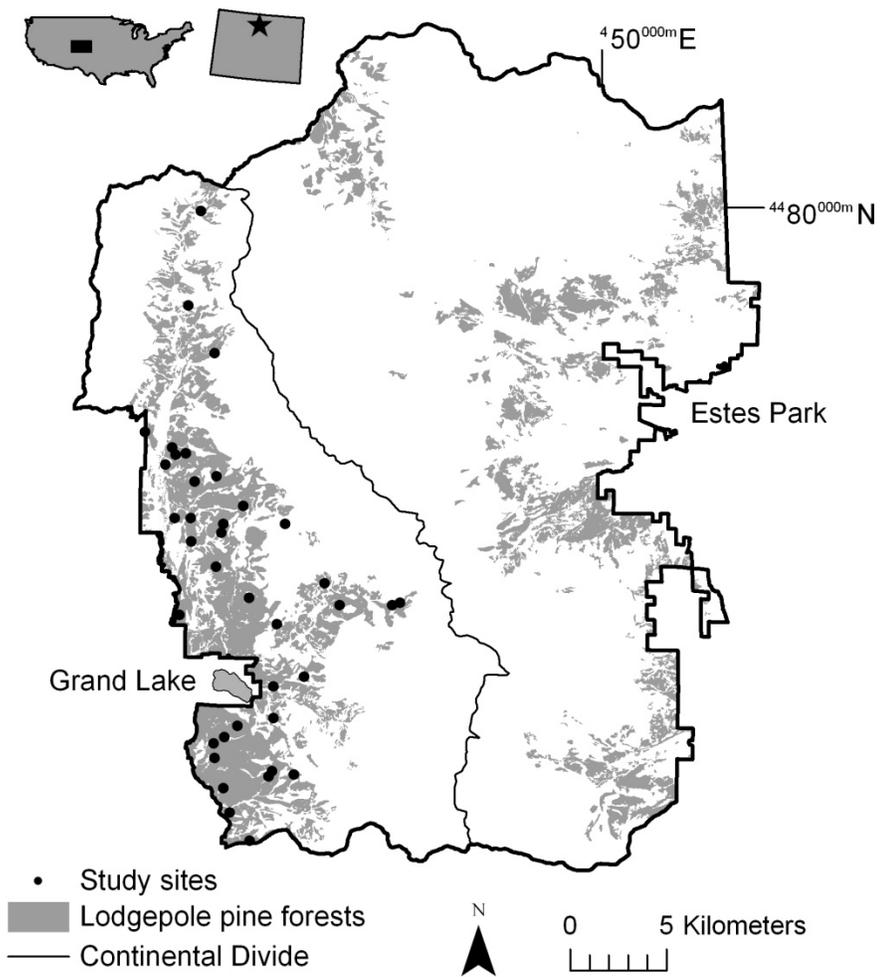


Figure 1-2. Two-dimensional NMS ordination showing the segregation of the forest types and relationships with taxon abundance. Each symbol represents a plot and is coded according to its forest type, derived from a cluster analysis. Weighted average abundances for each taxon are indicated with crosses.

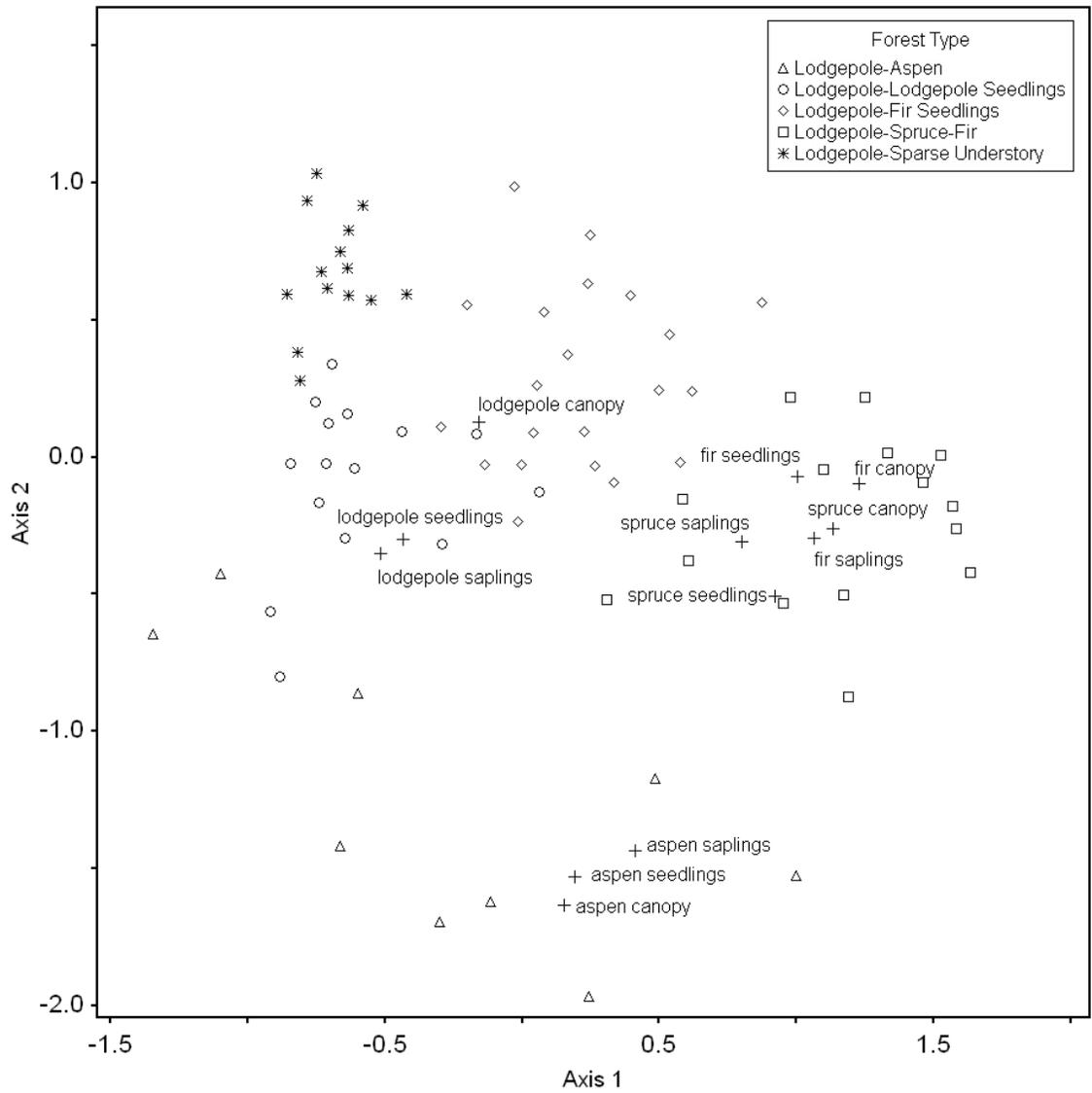


Figure 1-3. Average basal area (all species) for the five lodgepole pine forest types before the epidemic, in 2008, and with hypothetical extreme scenario mortality. Error bars show standard errors.

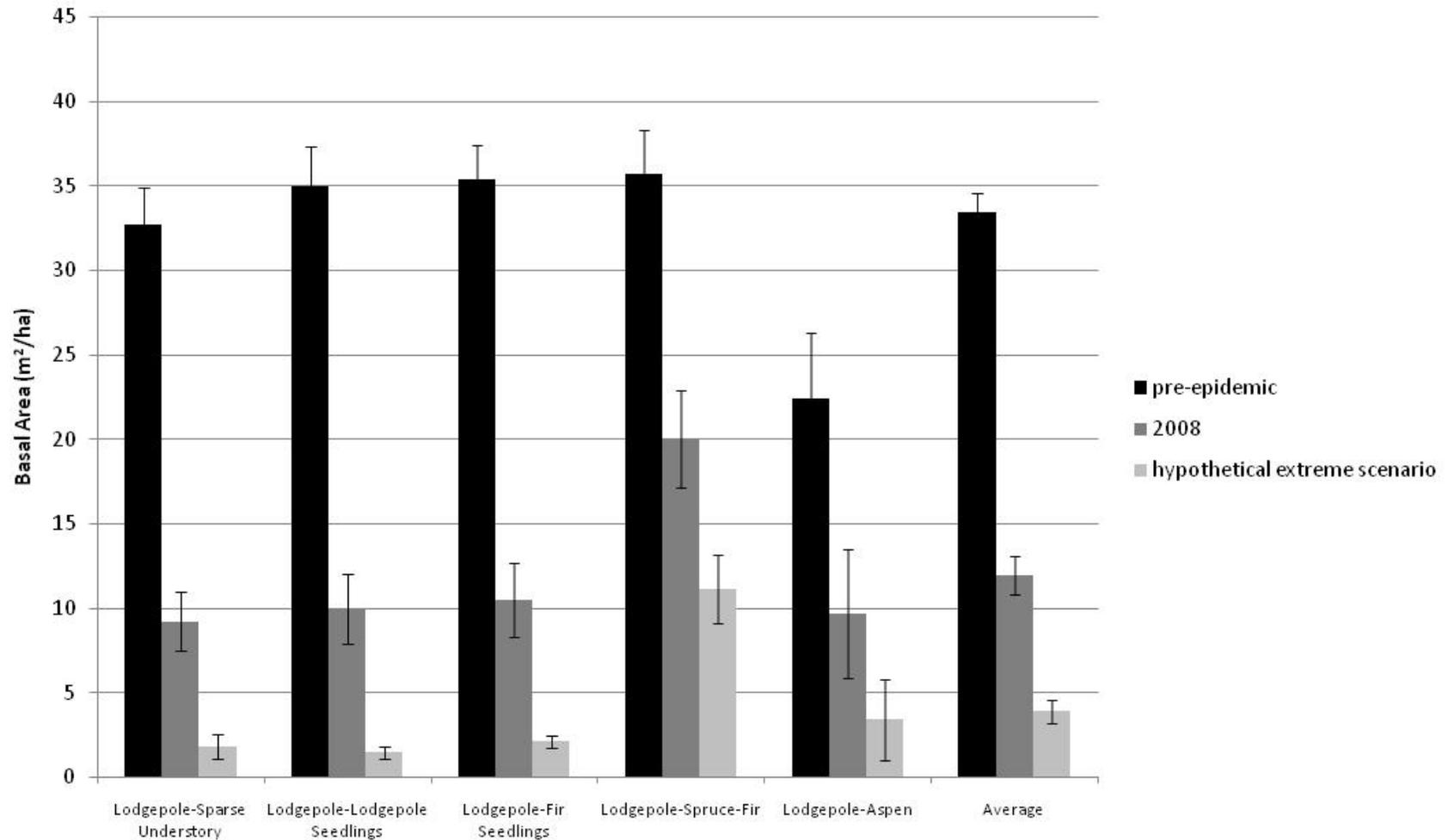
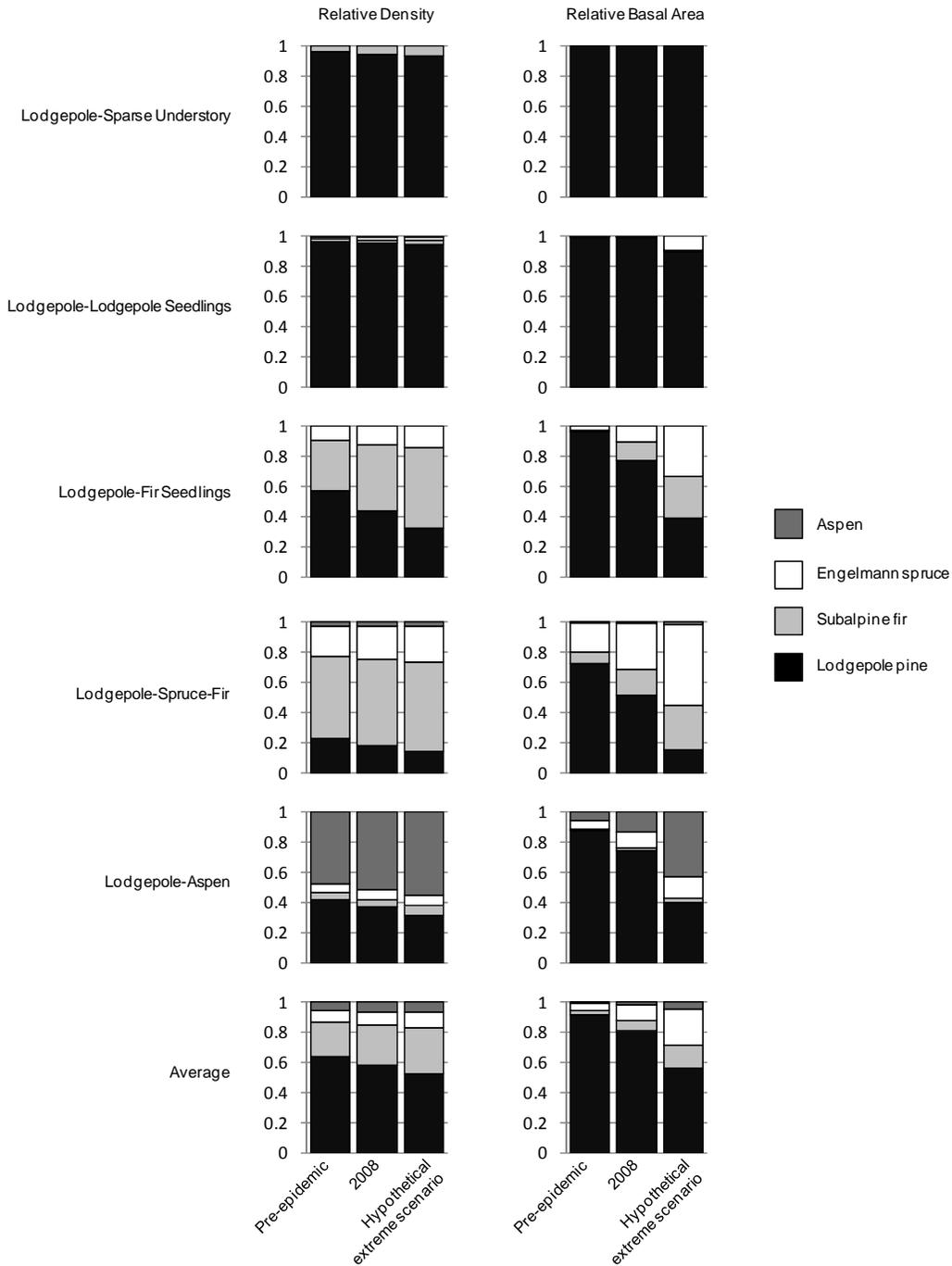


Figure 1-4. Relative species composition of the five forest types before the epidemic, in 2008, and with hypothetical extreme scenario mortality. The graphs on the left show the relative density by species of the combined canopy, sapling, and seedling layers, and the graphs on the right show the relative basal area by species of the combined canopy and sapling layers. Not included are Douglas-fir (present in two plots in the *lodgepole-sparse understory* forest type) and limber pine (present in two plots in the *lodgepole-spruce-fir* forest type).



Chapter 2. After the 2000's Mountain Pine Beetle Epidemic: Projected Future Forest Conditions in Lodgepole Pine Forests of Rocky Mountain National Park

Abstract

Future forest conditions in areas impacted by a severe mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemic are projected over a 100 year time period in Rocky Mountain National Park using an established forest growth model, the Forest Vegetation Simulator. This analysis builds off of the post-epidemic survivorship reported in Chapter One and uses the five lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) forest types I defined to describe variability in future basal area, quadratic mean diameter, and relative species composition. Although basal area and quadratic mean diameter declined substantially following the epidemic, these forest attributes recover within 40-100 years in the projected future forests in most areas. Pure lodgepole pine forests with low post-epidemic survivorship were the exception to this rule and could be slower to recover, depending on the abundance of future tree seedling establishment. The results indicate that the release of surviving trees, rather than the establishment of new seedlings will be the most important mechanism for forest renewal. Lodgepole pine, which was dominant in all sampled stands prior to the epidemic, remains the dominant species on approximately 40% of the landscape, but Englemann spruce (*Picea engelmannii* Parry ex Engelm.)-subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and quaking aspen (*Populus tremuloides* Michx.) become dominant in the remaining areas.

Introduction

Subalpine forests in Colorado are changing rapidly due to high levels of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) mortality caused by a widespread mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemic. Approximately half a million hectares of forests have been affected by the epidemic in Colorado since 1996, and it is expected that most large lodgepole pine trees in the state will die by the time the epidemic fully subsides (Colorado State Forest Service 2009). The legacies of this severe disturbance will determine the trajectories of forest development in the coming decades. In this study, I describe possible future forest conditions in Rocky Mountain National Park using an established forest growth model, the Forest Vegetation Simulator.

With such rapid, high levels of mortality, land managers and the public are curious about if and when we can expect these forests to recover, and what these areas might look like in the future. To address these concerns, I sought answers to the following questions: 1) How long will it take forests to recover pre-epidemic basal area? 2) How will basal area, quadratic mean diameter, and relative species composition change in the future? To answer these questions, I used the Forest Vegetation Simulator to project future forest conditions over a 100 year period.

This analysis builds off of the results I reported in Chapter One, in which I described survivorship immediately following the epidemic in the Park. A major finding from

Chapter One was the delineation of five different lodgepole pine forest types that had variable species composition and levels of survivorship, setting the stage for different forest regeneration trajectories. My projections in the current analysis will emphasize variability in future forest conditions using these five forest types. The results from Chapter One showed that although the epidemic had greatly reduced basal area and canopy tree density, most (though not all) stands remained fully stocked due to abundant seedlings and saplings and some larger trees that survived the epidemic. Because of these high levels of survivorship, I expect that the landscape will remain forested in my projections of future conditions, and that future forest development will be determined largely by the release of surviving trees, as opposed to post-epidemic seedling establishment. This pattern of post-epidemic forest development has been observed elsewhere following bark beetle-induced mortality (Veblen et al. 1991, Hawkes et al. 2004, Astrup et al. 2008).

Lodgepole pine remained the dominant species in most of the study area in the immediate post-epidemic forests described in Chapter One, despite modest increases in the relative abundance of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and quaking aspen (*Populus tremuloides* Michx.) in some areas. The species composition of the five forest types indicates two different trajectories for future forest development. I expect that lodgepole pine will remain dominant in the forest types that were nearly pure lodgepole pine prior to the epidemic, and I expect non-lodgepole pine species to release and gain dominance over time in the forest types where they were abundant in the understory at the time of beetle-induced

mortality. These two different forest development trajectories have been shown elsewhere in studies of lodgepole pine and mountain pine beetle epidemics (Moir 1969, Amman 1977, Sibold et al. 2007).

Methods

I used the data describing post-epidemic survivorship in the five different lodgepole pine forest types reported in Chapter One to project future forest conditions in 11,200 ha of beetle-disturbed forests in the western portion of Rocky Mountain National Park.

Canopy trees, saplings, and seedlings were measured in 74 randomly located 20 m x 20 m plots. Diameter at breast height (dbh) and species were recorded for each tree in the plot taller than 1.4 m. Live and beetle-killed lodgepole pines were both measured, allowing descriptions of pre-epidemic conditions. Trees shorter than 1.4 m and at least one year old were measured in a 2 m x 20 m transect that ran through the center of the plot. Height, species, and age were recorded for each tree measured in the transect. Age, up to five years old, was estimated using a combination of the following criteria: 1) the presence of branch whorls; 2) color differentiation along the stem; 3) differentiation in the density of leaf scars; and 4) the presence of bud scale scars. Further details about the study area and data collection methods can be found in Chapter One.

Data analysis

I used the Central Rockies variant of the Forest Vegetation Simulator (FVS) to project forest conditions over a 100 year period in the Park beginning with 2008 (Dixon 2002, Forest Vegetation Simulator Staff 2010). FVS is a forest growth model that uses locally developed relationships among abiotic site conditions, tree attributes, and stand characteristics to predict forest stand development over time. Five different model types with different growth equations for some species are contained within the Central Rockies variant; the lodgepole pine model type was used in this analysis. Site index, heights for trees taller than 1.4 m, and local growth rates were not measured; therefore, the FVS default values were used for the projections included in this study.

Future forest conditions were projected for each individual plot that was measured. For each plot, species and dbh was entered for every tree taller than 1.4 m, and species and height was entered for every tree shorter than 1.4 m. Results were compiled by, and are reported for, each of the five lodgepole pine forest types I defined in Chapter One. These five forest types are found on roughly equal proportions of the landscape and are differentiated mainly by the prevalence of spruce, fir, and aspen, and the abundance of seedlings (Table 2-1). They resemble community types from a previous classification system completed nearby (Peet 1981), but were only weakly associated at best with the environmental and stand characteristics I measured (age of stand initiation, elevation, slope, aspect, Topographic Convergence Index, equinox radiation, non-serotinous canopy percent, vegetation cover, and open canopy percent).

To describe how long it takes the forests to recover pre-epidemic basal area, I report the percentage of plots in each forest type that meet or exceed their pre-epidemic basal area 20, 50, and 100 years in the future. Projected future basal area, quadratic mean diameter, and relative species composition are also reported separately for each of the forest types.

I used a range of scenarios to describe the “starting condition” for the projection and future seedling establishment. Two starting condition scenarios, reflecting mortality observed in 2008 and the hypothetical extreme scenario described in Chapter One, were used to initiate the projections. The “observed 2008 scenario” starting condition reflects survivorship observed in 2008, and the “hypothetical extreme scenario” accounts for maximum potential levels of future mortality by removing all lodgepole pine trees greater than 10 cm dbh. Three different future seedling establishment scenarios were used to span the likely range of possible future regeneration across my plots (Table 2-2). With “zero” seedling establishment, no seedlings were added to the model in the future. The “low” seedling establishment rate is based on the average density and species composition of 1-5 year old seedlings for each forest type that was observed in 2008. This density of seedlings was added at five year intervals starting five years in the future for the first 20 years and was unique for each forest type. Because the low seedling establishment rate does not account for an expected pulse of tree establishment following mortality, I also used a “high” seedling establishment rate. The high seedling establishment rate also adds seedlings at five year intervals 5-20 years in the future and is unique for each forest type. The density added at each five year interval was one quarter

of the average establishment density reported for the 20 years following a previous mountain pine beetle epidemic that occurred in the Park in the late 1970s (Sibold et al. 2007). Although the establishment density was assumed to be the same for each forest type, the species composition was dependent on the forest type and was proportional to the average basal area of each species in the type. High seedling establishment was not used in the two forest types that had high levels of aspen or spruce-fir because Sibold et al. (2007) did not measure these forest types. The lack of a future pulse of seedling establishment in these forest types might be realistic, because the generally dense surviving understory of spruce-fir and aspen would likely compete strongly with any new tree germinants.

Results

Beetle-induced mortality substantially reduced basal area in all five forest types, from an average of 33 m²/ha before the epidemic to an average of 12 m²/ha in the observed 2008 starting condition scenario. Basal area was further reduced to 4 m²/ha in the hypothetical extreme scenario. Basal area then increased steadily throughout the 100 year projection period (Figure 2-1). Between 80-95% of the stands in the study area recovered pre-epidemic basal area within 100 years, depending on the starting condition scenario and seedling establishment scenario (Table 2-3). Quadratic mean diameter (QMD) followed a similar pattern as basal area, decreasing as a result of mortality, and then increasing steadily throughout the remainder of the projection (Figure 2-2). Lodgepole pine remained the dominant species throughout the 100 year projection period in two of the

forest types, but a shift to forests dominated by non-lodgepole pine species occurred in the remaining three forest types (Figure 2-3). Differences among the starting condition scenarios and seedling establishment scenarios tended to be small in the projected future forests, except in a few instances. Details about changes in basal area, QMD, and relative species composition for each forest type are discussed in the following sections.

Lodgepole-sparse understory

The *lodgepole-sparse understory* forest type recovered basal area very slowly, with only 13-40% of the area in this type recovering pre-epidemic basal area within 50 years, depending on the scenarios (Table 2-3). With zero or low seedling establishment, only 27-73% of this forest type recovered pre-epidemic basal area within 100 years, although 100% of the area recovered with the high seedling establishment scenario. Projected basal area either did not meet, or barely exceeded the pre-epidemic basal area of 33 m²/ha with hypothetical extreme scenario starting conditions and either zero or low seedling establishment (Figure 2-1). Even with observed 2008 starting conditions, average pre-epidemic basal area did not recover until 70-80 years in the future with either zero or low seedling establishment. With high seedling establishment, the average pre-epidemic basal area was attained within 60 years, and reached nearly 60 m²/ha within 100 years in all of the scenarios. The average pre-epidemic QMD of 15 cm was reached within 30-60 years in every scenario except for the two high seedling establishment scenarios, where the average QMD remained below 15 cm throughout the projection period (Figure 2-2).

Lodgepole pine dominated throughout the 100 year projection in this forest type in every scenario (Figure 2-3).

Lodgepole-lodgepole seedlings

Projected future basal area tended to be moderate in the *lodgepole-lodgepole seedlings* forest type (Figure 2-1). Depending on the scenario, 27-80% of these areas recovered pre-epidemic basal area within 50 years and 87-100% recovered within 100 years (Table 2-3). Higher levels of seedling establishment and observed 2008 starting conditions generally resulted in a greater percentage of these areas recovering pre-epidemic basal area at a given time period. Average basal area exceeded the pre-epidemic value of 35 m²/ha 50-70 years in the future (Figure 2-1). Basal area exceeded 50 m²/ha within 100 years in all of the scenarios. 40-70 years elapsed before the average pre-epidemic QMD of 10 cm was attained (Figure 2-2). This forest type remained nearly pure lodgepole pine throughout the projection period (Figure 2-3).

Lodgepole-fir seedlings

33-81% of the *lodgepole-fir seedlings* forest type recovered pre-epidemic basal area within 50 years, and 90-100% of the area recovered within 100 years in the projected future forests (Table 2-3). Higher levels of seedling establishment tended to result in higher basal area for a given time period, but differences due to starting conditions tended to be small (Figure 2-1). The average pre-epidemic basal area of 35 m²/ha was exceeded

after 60 years and exceeded 60 m²/ha within 100 years in all of the scenarios; the average pre-epidemic QMD of 12 cm was reached within approximately 40-70 years (Figure 2-2). Spruce and fir became dominant within 50 years with observed 2008 starting conditions, but became dominant immediately following mortality in the hypothetical extreme scenario (Figure 2-3). Lodgepole pine decreased in relative abundance throughout the projection, and was a very small component of these forests by the end of the 100 year period in the hypothetical extreme scenario.

Lodgepole-spruce-fir

The *lodgepole-spruce-fir* forest type retained a moderate average basal area after beetle-induced mortality (Figure 2-1), and 27-40% of this type recovered pre-epidemic basal area within 20 years (Table 2-3). At least 87% of these areas recovered pre-epidemic basal area within 50 years, and 100% basal area recovery was attained within 100 years. Projected basal area growth for this forest type was similar in the different scenarios, except that basal area tended to be higher at a given time with zero seedling establishment. The average basal area in this forest type exceeded the average pre-epidemic value of 36 m²/ha after 40 years and reached values of over 60 m²/ha within 100 years in all of the scenarios. Average QMD increased most quickly with zero seedling establishment; the average pre-epidemic value of 7 cm was reached within 30-60 years, depending on the scenario (Figure 2-2). This forest type became dominated by spruce and fir either immediately following mortality or within 20 years, with the transition occurring quicker in the hypothetical extreme scenario (Figure 2-3). By the

end of the 100 year projection period, lodgepole pine was either absent or only a very small component of these forests.

Lodgepole-aspen

Projected future basal area tended to be high in the *lodgepole-aspen* forest type, with average basal area exceeding the pre-epidemic value of 22 m²/ha after 30 years and reaching approximately 70 m²/ha within 100 years in all of the scenarios (Figure 2-1).

13-50% of this type recovered pre-epidemic basal area within 20 years, 75-100% recovered within 50 years, and 100% of the area recovered within 100 years (Table 2-3).

Basal area tended to be higher at a given time in the future with seedling establishment.

The average pre-epidemic QMD of 8 cm was exceeded within 20-40 years (Figure 2-2).

Aspen became dominant within 50 years, gaining relative abundance more quickly in the low seedling establishment scenario and with the hypothetical extreme scenario starting condition (Figure 2-3). The relative abundance of aspen either tapered off or began to decrease towards the end of the 100 year projection period.

Discussion

The projections confirm my expectations about future forest development that were based on the results from Chapter One. They support the assertion that post-epidemic stocking is adequate in most areas to regenerate forests in the future (Chapter One, Coates et al. 2006, Nigh et al. 2008). The fact that such a large percentage of stands are able to

recover pre-epidemic basal area within 50-100 years with zero seedling establishment further supports the findings from other studies that the most important mechanism for forest renewal following beetle epidemics is the release of surviving trees (Veblen et al. 1991, Hawkes et al. 2004, Astrup et al. 2008). Patterns of species composition in the future forests also followed expected pathways, shifting to non-lodgepole pine dominated forests where spruce, fir, and aspen were present in the understory, but remaining lodgepole pine dominated where it formed pure forests prior to the epidemic. Further details about the differences in forest development among the five forest types are discussed in the following paragraphs.

Forests in the *lodgepole-sparse understory* type were unique in the projections because of their slow basal area growth and sensitivity to the seedling establishment scenario. Faster basal area recovery in the high seedling establishment scenario indicates that future seedling establishment will be especially important for forest renewal in this forest type. These forests, along with the *lodgepole-lodgepole seedlings* forest type, remained dominated by lodgepole pine throughout the 100 year projection period, supporting the findings of previous studies that document this pattern on certain sites (Moir 1969, Amman 1977, Sibold et al. 2007). The *lodgepole-lodgepole seedlings* forest type, however, has faster basal area recovery, due to abundant lodgepole pine seedlings present in the understory prior to the epidemic.

A shift to forests dominated by spruce and fir occurs in both the *lodgepole-fir seedlings* and *lodgepole-spruce fir* forest types in my projections of future forests. This shift in

species composition occurs despite the only modest increases in spruce and fir relative abundance that had occurred immediately following mortality. These shade tolerant species gain dominance over time as spruce and fir present in the understory grow into the canopy and lodgepole pine trees begin to die as they grow older. Mountain pine beetle epidemics have been previously shown to release shade tolerant species present in the understory, eventually resulting in the dominance of these species (Amman 1977). My projections also show that on some sites, lodgepole pine could be entirely eliminated.

The shift to aspen dominated forests that occurs in the *lodgepole-aspen* forest type was unexpected because the effect of mountain pine beetle epidemics on aspen has not been previously studied. It is thought that on sites suitable to both lodgepole pine and aspen, aspen typically dominates immediately following a major fire, only to be eventually overtaken by lodgepole pine (Kashian et al. 2007). The mountain pine beetle epidemic appears to have reset the system, similar to a major fire, allowing the aspen suckers present in the understory to once again dominate in these areas. The end of the projections show decreasing dominance of aspen as it begins to die off and conifers once again begin to grow into the overstory. The future of these forests, though, might not be determined only by competitive interactions between conifers and aspen, as a large elk population resides in the Park and high browsing rates on aspen suckers have been recorded (Nelson 2009). It remains uncertain whether aspen suckers in the Park will be able to grow beyond the influence of elk browsing and into the canopy.

Results tended to be relatively insensitive to the starting condition or future seedling establishment scenarios, except in a few cases. If seedling establishment in the future is not high, basal area growth could be very slow in the *lodgepole-sparse understory* forest type; conversely, if establishment is high, quadratic mean diameter growth could be slow in this type. Shifts to spruce-fir forests in the *lodgepole-fir seedlings* and *lodgepole-spruce-fir* forest types occur sooner with hypothetical extreme scenario starting conditions. In the hypothetical extreme scenario and with the low seedling establishment scenario, fir could become abundant in the *lodgepole-sparse understory* forest type as well. Despite differences due to starting conditions and future seedling establishment, the qualitative results – that most areas recover pre-epidemic basal area within 100 years, that shifts in species composition will occur in some (but not all) areas, and that future forest regeneration trajectories are variable and depend on the forest type – remain the same.

The accuracy of my projections of future forest conditions depends on the degree to which FVS represents forest growth in the Park, and could be further limited by my reliance on several important FVS defaults. The point of this analysis, though, is not to necessarily exactly predict the future, but rather to generalize possible future trends in forest structure and composition in the Park. My results do just that, and successfully address questions about possible future species composition and the ability of post-epidemic forests to regenerate. Furthermore, these projections match expectations based on previous findings following mountain pine beetle epidemics elsewhere. While not intended to be perfect, my projections of future forest conditions offer a best guess of what these forest might look like using the best tools and data available.

The ultimate future of these forests will be determined by future disturbances, the ability of surviving trees to respond to increased resources, and future seeding establishment. Future disturbances, notably stand-replacing fires (Peet 2000), will likely alter forest regeneration trajectories. The effects of future fires are uncertain and highly dependent on the timing and spatial pattern of beetle killed trees. Even without fire, blowdown of surviving trees could affect forest development, and evidence from lodgepole pine harvesting operations indicates that lodgepole pine is especially susceptible to blowdown following partial canopy removal (Lotan and Critchfield 1990). On the other hand, retrospective studies of historic mountain pine beetle epidemics fail to report evidence of post-epidemic blowdown (Sibold et al. 2007, Dordel et al. 2008). Blowdown of both living and dead trees could also damage or kill trees in the understory (Griesbauer and Green 2006).

The ability to respond to increased resources (light, water, nutrients, etc.) will likely not be uniform among the surviving trees and could depend on the species, height, age, and health of the tree, although relationships are not clear (Griesbauer and Green 2006).

What is clear, though, from previous epidemics and studies of advance regeneration following timber harvests, is that surviving trees generally experience increased growth rates (Romme et al. 1986, McCaughey and Ferguson 1988, Veblen et al. 1991, Murphy et al. 1999). The spatial distribution of surviving subcanopy trees will affect their ability to replace beetle-killed trees in the canopy (Griesbauer and Green 2006). If surviving trees

are clumped in small areas, post-epidemic tree establishment could be a more important mechanism for forest renewal than indicated by summaries of stand density.

The final unknown for the future development of the Park's beetle-disturbed forests is the rate and composition of future tree establishment. I used three different seedling establishment scenarios and found that the projections tended to be relatively insensitive to future seedling establishment, except in the *lodgepole-sparse understory* forest type, which recovers basal area slowly without high levels of future seedling establishment.

Mountain pine beetle-disturbed areas in the western portion of Rocky Mountain National Park remain forested in my projections, but will look different in the future. In the near future, forests are projected to be filled with smaller diameter trees and have lower basal areas than they had before the epidemic. However, quadratic mean diameter and basal area meet or exceed pre-epidemic levels within the next 40-100 years in most cases. Forests that were previously dominated by lodgepole pine shift to spruce-fir on approximately 50% of the landscape, and aspen becomes dominant on approximately 10% of the landscape. Lodgepole pine remains the dominant species, though, on approximately 40% of the landscape. Future forest conditions are variable and depend on pre-epidemic forest structure and composition.

The results of this study indicate that active management would not be necessary to restore forested conditions in the Park. This point might not be so important in the Park, where nearly 95% of the land area is managed as a wilderness. Although my results

directly apply to only a limited area, they do suggest that the high levels of mortality associated with this epidemic do not necessarily imply the need for active management to promote forest regeneration elsewhere in the southern Rocky Mountains. Some areas with low levels of post-epidemic survivorship similar to the *lodgepole-sparse understory* type could possibly benefit from active management to promote fast basal area growth, but the majority of the study area readily regenerates on its own.

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Table 2-1. Distinguishing characteristics of the five lodgepole pine forest types used in the analysis to describe variability in projected future forest conditions.

| Forest Type | Percent of Landscape (± 95% confidence interval) | Distinguishing Characteristics |
|--|---|---|
| Lodgepole-Sparse Understory | 20% (±9%) | Nearly pure lodgepole pine; very few seedlings or saplings |
| Lodgepole-Lodgepole Seedlings | 20% (±9%) | Nearly pure lodgepole pine; abundant lodgepole pine seedlings |
| Lodgepole-Fir Seedlings | 28% (±10%) | Lodgepole pine-dominated canopy; spruce and fir present in the canopy and sapling layers; moderate density of fir seedlings |
| Lodgepole-Spruce-Fir | 20% (±9%) | Moderate abundance of spruce and fir in the canopy and sapling layers; extremely abundant spruce and fir seedlings |
| Lodgepole-Aspen | 12% (±7%) | Aspen present in the canopy and sapling layers; abundant aspen suckers |

Table 2-2. Density of seedlings by species added to the projection 5, 10, 15, and 20 years in the future under three different seedling establishment scenarios for the five forest types.

| Forest Type | Seedling Establishment Scenario | Lodgepole Pine (stems/ha) | Fir (stems/ha) | Spruce (stems/ha) | Aspen (stems/ha) | Total (stems/ha) |
|--------------------------------------|---------------------------------|---------------------------|----------------|-------------------|------------------|------------------|
| Lodgepole-Sparse Understory | Zero | 0 | 0 | 0 | 0 | 0 |
| | Low | 50 | 67 | 0 | 0 | 117 |
| | High | 1477 | 0 | 0 | 0 | 1477 |
| Lodgepole-Lodgepole Seedlings | Zero | 0 | 0 | 0 | 0 | 0 |
| | Low | 900 | 50 | 0 | 17 | 967 |
| | High | 1470 | 0 | 7 | 0 | 1477 |
| Lodgepole-Fir Seedlings | Zero | 0 | 0 | 0 | 0 | 0 |
| | Low | 60 | 643 | 24 | 0 | 726 |
| | High | 1139 | 180 | 158 | 0 | 1477 |
| Lodgepole-Spruce-Fir | Zero | 0 | 0 | 0 | 0 | 0 |
| | Low | 67 | 2787 | 400 | 117 | 3370 |
| | High* | -- | -- | -- | -- | -- |
| Lodgepole-Aspen | Zero | 0 | 0 | 0 | 0 | 0 |
| | Low | 31 | 125 | 31 | 2000 | 2188 |
| | High* | -- | -- | -- | -- | -- |

*See text for an explanation of why the high seedling establishment scenario was not used for these forest types.

Table 2-3. Percent of plots in each forest type recovering pre-epidemic basal area in the projected future forests.

| Time | -----20 years in the future----- | | | | | | -----50 years in the future----- | | | | | | -----100 years in the future----- | | | | | |
|--|----------------------------------|-----|------|-------------------------------|-----|------|----------------------------------|-----|------|-------------------------------|-----|------|-----------------------------------|-----|------|-------------------------------|-----|------|
| | Observed 2008 | | | Hypothetical Extreme Scenario | | | Observed 2008 | | | Hypothetical Extreme Scenario | | | Observed 2008 | | | Hypothetical Extreme Scenario | | |
| Starting Condition Scenario ¹ | | | | | | | | | | | | | | | | | | |
| Seedling Establishment Scenario ² | Zero | Low | High | Zero | Low | High | Zero | Low | High | Zero | Low | High | Zero | Low | High | Zero | Low | High |
| Lodgepole-Sparse Understory | 13 | 13 | 20 | 0 | 0 | 0 | 27 | 33 | 40 | 13 | 13 | 27 | 53 | 73 | 100 | 27 | 40 | 100 |
| Lodgepole-Lodgepole Seedlings | 0 | 0 | 0 | 0 | 0 | 0 | 53 | 73 | 80 | 27 | 53 | 67 | 93 | 100 | 100 | 87 | 100 | 100 |
| Lodgepole-Fir Seedlings | 5 | 10 | 5 | 0 | 0 | 0 | 57 | 57 | 81 | 33 | 62 | 81 | 95 | 100 | 100 | 90 | 100 | 100 |
| Lodgepole-Spruce-Fir | 40 | 40 | -- | 27 | 27 | -- | 87 | 87 | -- | 87 | 93 | -- | 100 | 100 | -- | 100 | 100 | -- |
| Lodgepole-Aspen | 38 | 63 | -- | 13 | 50 | -- | 88 | 100 | -- | 75 | 100 | -- | 100 | 100 | -- | 100 | 100 | -- |
| Average | 16 | 20 | -- | 7 | 11 | -- | 59 | 66 | -- | 43 | 61 | -- | 88 | 95 | -- | 80 | 88 | -- |

¹The starting condition scenario refers to the tree attributes used to initiate the FVS projections, defined by the density, dbh, and species of trees in each stand. See text for descriptions of the observed 2008 and hypothetical extreme starting condition scenarios.

²The seedling establishment scenario refers to the density and species of seedlings that are added to the model in the future. See text and Table 2-2 for descriptions of the zero, low, and high seedling establishment scenarios.

Figure 2-1. Average basal area of the five forest types in the projected future forests. The graphs show basal area development over time with two different starting conditions and three different future seedling establishment scenarios.

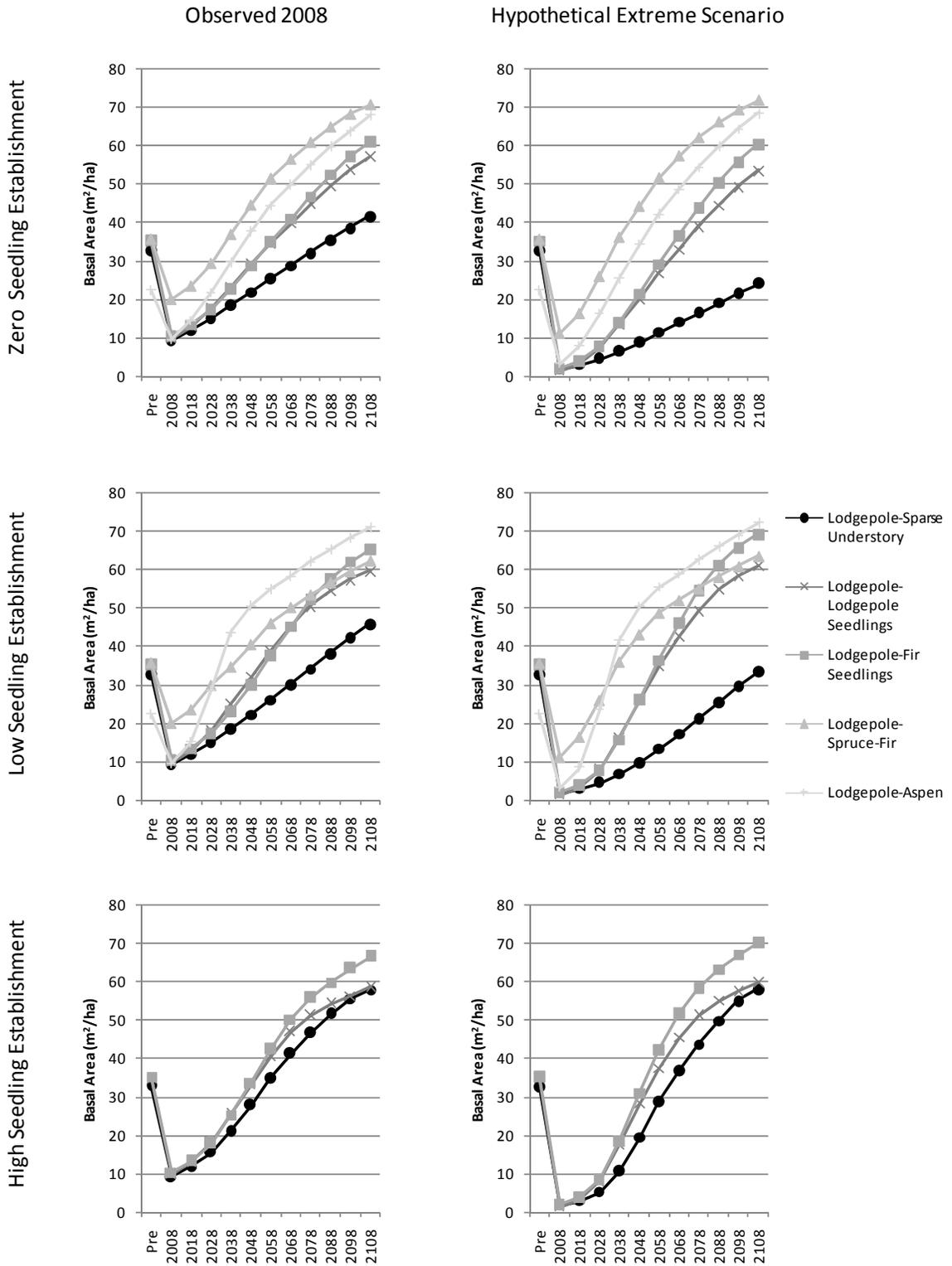


Figure 2-2. Average quadratic mean diameter of the five forest types in the projected future forests. The graphs show changes in quadratic mean diameter over time with two different starting conditions and three different future seedling establishment scenarios.

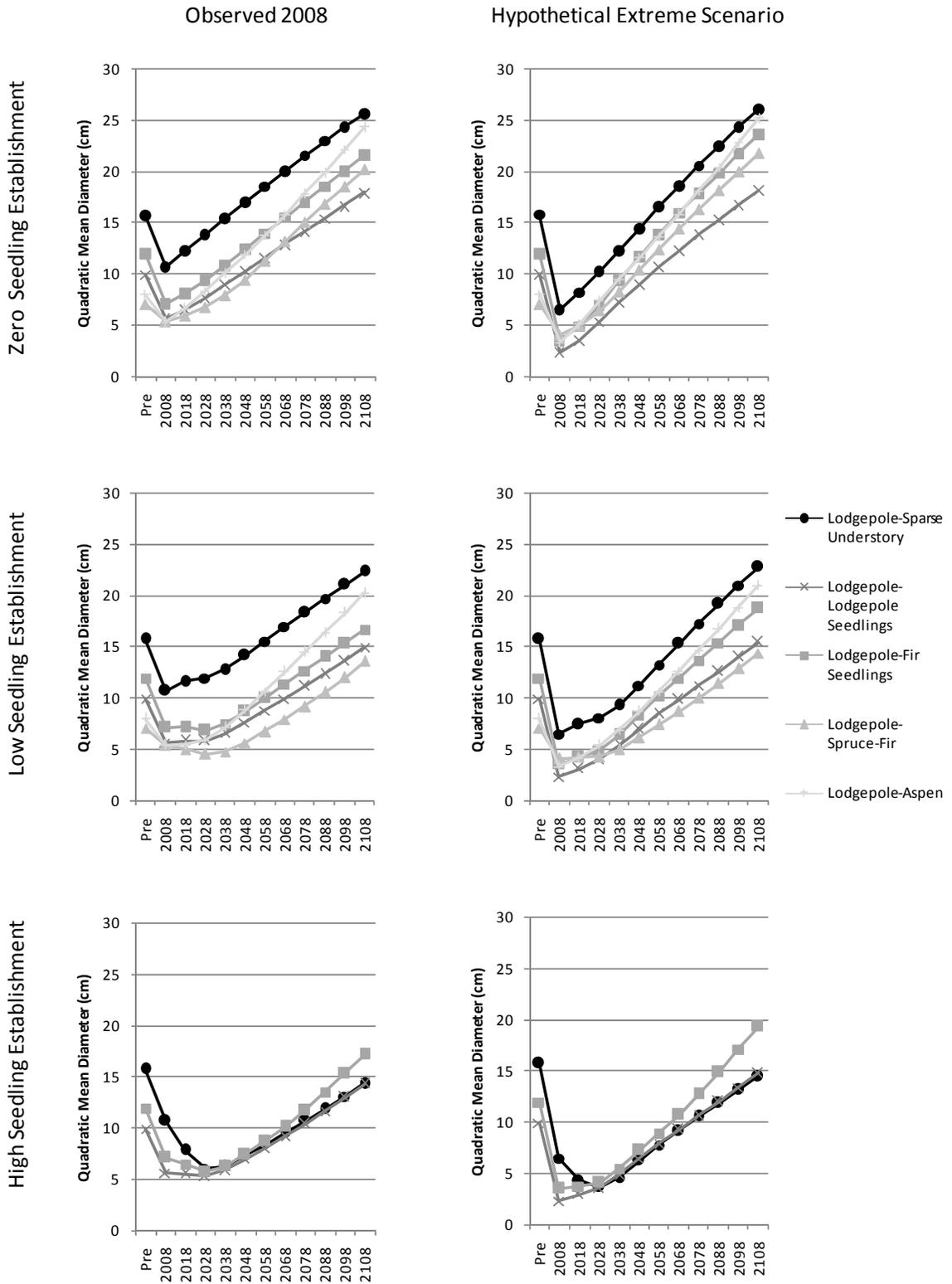


Figure 2-3. Average relative species composition of the five forest types in the projected future forests. The graphs show the relative basal area by species with two different starting conditions and three different future seedling establishment scenarios.

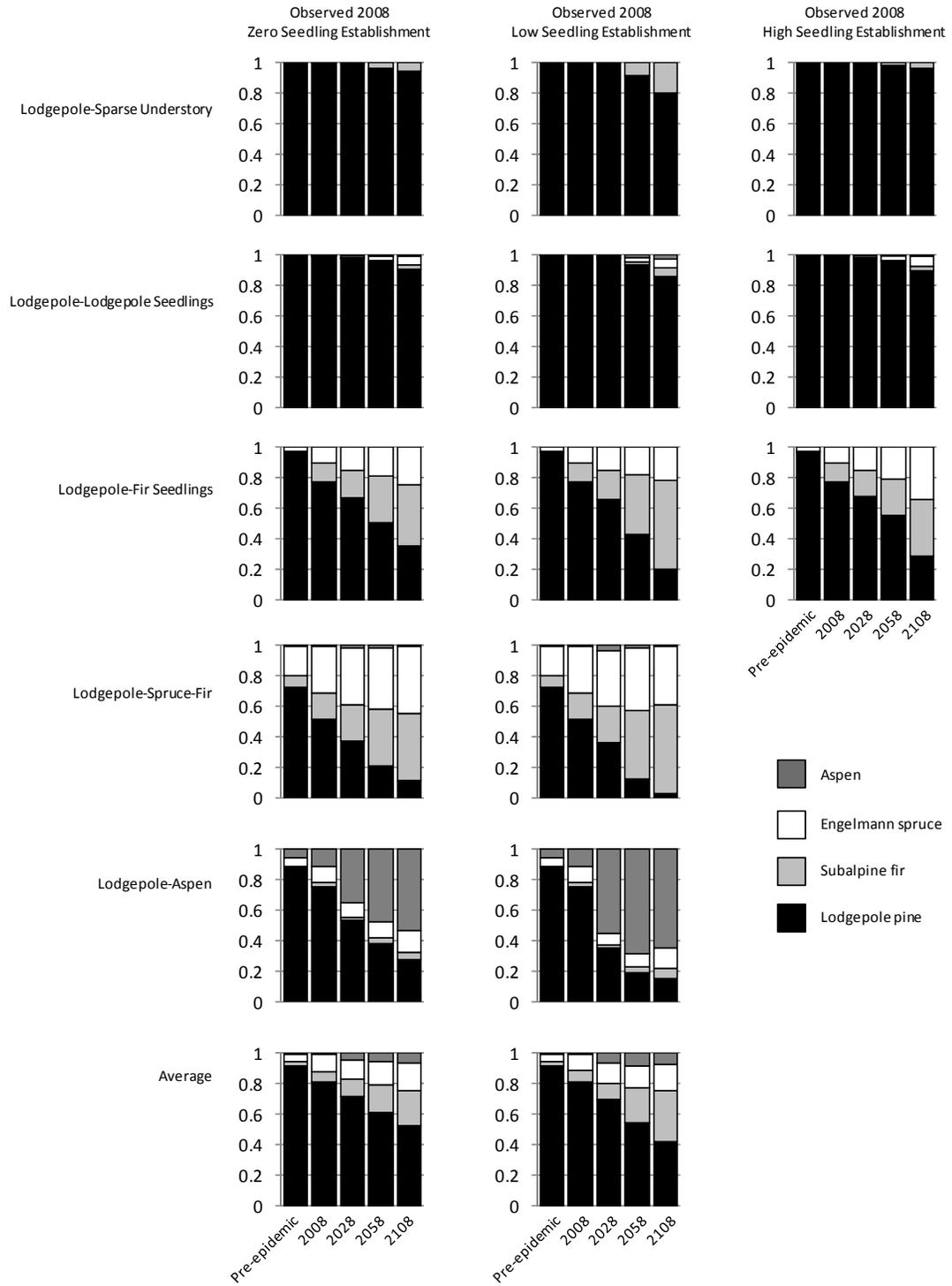


Figure 2-3 (continued). Average relative species composition of the five forest types in the projected future forests. The graphs show the relative basal area by species with two different starting conditions and three different future seedling establishment scenarios.

