

THESIS

THE ECOLOGICAL LEGACY OF THE MOUNTAIN PINE BEETLE IN THE SOUTHERN
ROCKIES: FOREST CHANGE AND DISTURBANCE INTERACTIONS

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ABSTRACT

THE ECOLOGICAL LEGACY OF THE MOUNTAIN PINE BEETLE IN THE SOUTHERN ROCKIES: FOREST CHANGE AND DISTURBANCE INTERACTIONS

Mountain pine beetle (*Dendroctonus ponderosae*; MPB) outbreaks are naturally occurring ecological disturbances in western North America, but the last two decades have seen eruptions of unprecedented severity and extent. These outbreaks have created novel conditions in lodgepole pine forests that have historically had disturbance regimes dominated by large, stand-replacing fires. Previous research has found that MPB outbreaks increase relative abundance of non-host species. I use the lodgepole pine forest on the west side of Rocky Mountain National Park to examine mechanisms in this predicted forest change and the ecological legacy of the mountain pine beetle outbreak, particularly in terms of its implications for future disturbances. The recent mountain pine beetle outbreak increased spatial heterogeneity of species composition as a result of spatial variability in mechanisms of post-outbreak forest composition. Post-outbreak variances of up to 5 times greater and patch sizes up to 7 times smaller than pre-outbreak conditions. The increase in species heterogeneity will inhibit future landscape-level bark beetle outbreaks, though projected increases in Engelmann spruce and subalpine fir may make post-MPB forests more susceptible to other disturbances, including drought and fire. The MPB outbreak has increased landscape asynchrony, which will increase resiliency to future disturbances. However, this heterogeneity is a result of more spruce and fir on the landscape, species which are less adapted to projected future climate conditions.

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INTRODUCTION

Disturbance is a key component of ecological systems, and as the global climate changes, disturbance regimes are also changing rapidly and may become profoundly different over the next century (Turner 2010). Additionally, disturbances can interact with each other to produce synergistic effects (Paine et al. 1998), which are contingent on the order and timing of the disturbances in question (Davies et al. 2009, Miao et al. 2009). For example, the ecological legacies of a wildfire's influence on forest characteristics could influence the likelihood, extent, or severity of future disturbance events (Veblen et al. 1994). It is clear that disturbances interact, often producing ecological surprises, but the ecological consequences and mechanisms of many key interactions are not well understood (Turner 2010). Consequently, improving our understanding of disturbance interactions is critical for understanding forest ecosystems in an era of rapid change, and for developing plans for managing them (Millar et al. 2009). The goal of this study was to investigate disturbance interactions preceding a recent, extensive, high-severity mountain pine beetle outbreak in the Southern Rocky Mountains and to understand the consequences of the outbreak for shaping future disturbance regimes.

Interactions among disturbances including fires, bark beetle outbreaks, avalanches, and wind blowdowns play a central role in shaping patterns of forest conditions in the subalpine zone of the Southern Rocky Mountains. These disturbances typically interact through their influences on stand age, structure, and species composition. Fire history affects the likelihood and severity of subsequent bark beetle outbreaks (Veblen et al. 1994; Bebi et al. 2003), the severity of subsequent blowdown events (Kulakowski and Veblen 2002), and the likelihood (Bigler et al. 2005) and extent (Kulakowski and Veblen 2007) of subsequent fires with more recently burned stands less susceptible to all three disturbances. Pre-fire disturbance history, in turn, can

influence fire severity, with increased burn severity in stands affected by severe blowdowns (Kulakowski and Veblen 2007). Pre-fire bark beetle outbreaks may affect fire likelihood, with a slight increase in likelihood in post-beetle forests found by Bigler et al. (2005), though Bebi et al. (2003) found no relationship between post-beetle forests and subsequent fire likelihood. Moreover, interactions can also influence post-disturbance regeneration. Sibold et al. (2007) found that lodgepole pine establishment was facilitated by higher severity disturbances that occurred in younger post-fire stands, while subalpine fir establishment was facilitated by lower severity disturbances that occurred in older post-fire stands. Kulakowski et al. (2013) found increased aspen regeneration in stands affected by blowdown then fire, as compared to stands only affected by fire.

The recent mountain pine beetle outbreak in the Southern Rockies offers another example of the importance of disturbance interactions. Forests in western North America have been extensively reshaped by this outbreak, which is unprecedented in its severity, extent, and duration (Raffa et al. 2008). The reasons behind this extreme mountain pine beetle eruption are not fully understood, but it is most likely due to the combination of a prolonged period of abnormally warm temperatures (Klutsch et al. 2009), and a homogenous landscape of large lodgepole pine. This homogenous landscape was created by the disturbance history of the region, which consisted of extensive, high-severity fires in the late 1800s, followed by decades of relatively little fire (Kipfmüller and Baker 2000; Sibold et al. 2006). As it was shaped by past disturbance history, the ecological consequences of this mountain pine beetle outbreak will also shape future disturbances in the region.

Bark beetles are key disturbance agents in forests of western North America, and mountain pine beetle (MPB; *Dendroctonus ponderosae*) is perhaps the most significant, affecting

the greatest area of any bark beetle in the region (Hicke et al. 2006). Mountain pine beetles have historically existed at both endemic and eruptive levels, but MPB outbreaks in the past 20 years have been exceptionally severe and extensive (Raffa et al. 2008). These outbreaks have affected over 25 million hectares of forest across the Western United States and Canada (Meddens et al. 2012), expanding into areas that have rarely or never been impacted by bark beetles in the past (Logan et al. 2003). The mountain pine beetle requires the concurrence of favorable climatic conditions (Bentz et al. 1991; Powell and Bentz 2009) and abundant suitable hosts (Aukema et al. 2006; Fettig et al. 2007; Hicke and Jenkins 2008) to reach eruptive levels. Given projected continued warming, it is thought that we may be moving into an era where bark beetles are the dominant forest disturbance (Bentz et al. 2010), though others argue that this era of beetles is likely to be limited to the 21st century, as the warming climate will eventually exceed suitable temperatures for mountain pine beetle outbreaks (Hicke et al. 2006).

While much recent research has focused on the importance of climate as a top-down control of mountain pine beetle outbreaks, the equally important bottom-up control of forest structure and composition has received less attention. In addition to appropriate climatic conditions, the mountain pine beetle requires abundant suitable host trees to reach epidemic levels. The importance of forest structure as a bottom-up control of potential mountain pine beetle outbreaks can be described in terms of stand susceptibility, defined as the ability of a stand to support an epidemic MPB population. This susceptibility is determined by abiotic site conditions, species composition, and tree size, age, and density (Bentz et al. 2010). Because bark beetle outbreaks can remove most susceptible host trees over extensive areas, their influences on stands conditions can limit future outbreaks until forests recover (e.g. spruce beetle; Veblen et al.

1991). Consequently, the recent outbreak may limit future outbreaks even if climate conditions favor population development to eruptive levels.

MPB primarily attacks lodgepole pine (*Pinus contorta*) in western North America, but has also been known to kill ponderosa pine (*Pinus ponderosa*), limber pine (*Pinus flexilis*) and whitebark pine (*Pinus albicaulis*) (Dordel et al. 2008). Mountain pine beetle preferentially attacks trees of larger diameter (Cole and Amman 1969; Safranyik et al. 1974) because they are more visually attractive (Amman 1977) and offer thicker phloem than small trees. Minimum size thresholds for MPB attack vary by site and by outbreak, but range between 15 cm diameter at breast height (DBH; Shore and Safranyik 1992) and 23 cm DBH (Bjorklund and Lindgren 2009). During an epidemic, trees < 12.5 cm DBH are rarely attacked by MPB, while those with a DBH > 30 cm experience close to 100% mortality (Bjorklund and Lindgren 2009). Tree age also potentially plays a role in MPB-susceptibility. Some studies have found that the most susceptible trees are between the ages of 80 and 100 years (Van Sickle 1988; Shore et al. 2000), but others suggest that any relationship between tree age and MPB attack is solely due to the correlation between age and DBH (Mitchell and Preisler 1991). Another structure-related factor in MPB outbreaks is tree density. Low-density stands produce large diameter trees, but these trees tend to be more vigorous and more able to resist MPB attacks. Conversely, high-density stands have less vigorous trees but they are typically smaller and slower-growing, so less suitable for mountain pine beetle (Shore and Safranyik 1992). Intermediate stand densities (750-1500 stems per hectare) tend to have the highest MPB-related mortality as they offer plentiful trees of a suitable size that are not so vigorous that they can effectively resist a mountain pine beetle mass attack (Shore and Safranyik 1992).

Because mountain pine beetle is species-selective in its attack, it logically follows that an MPB outbreak would increase relative abundance of non-host species, a phenomenon which has been documented over past outbreaks in the United States and British Columbia (Amman et al. 1988; Sibold et al. 2007; Astrup et al. 2008; Nigh et al. 2008). The occurrence of species shifts is well documented, but there remains a lack of quantitative understanding of the mechanisms involved and how they will affect spatial heterogeneity of the landscape. This forest change is a key part of the ecological legacy of a mountain pine beetle outbreak and has implications for both the composition of future forests in beetle-affected areas and the disturbance regimes of these forests.

Western forests are subject to many types of disturbances, including wildfire, insects, diseases, drought, and blowdown. Prior to the recent mountain pine beetle outbreak, the lodgepole pine forest type throughout the southern Rocky Mountains was primarily shaped by a disturbance regime of infrequent high-severity, stand-replacing fires (Kipfmüller and Baker 2000; Buechling and Baker 2004; Sibold et al. 2006), which initiated single-cohort stands of lodgepole pine (Logan and Powell 2001; Sibold et al. 2007; Axelson et al. 2009). Bark beetles have existed at endemic and eruptive levels in the past, but the recent outbreak is unprecedented in its severity and extent. As such, we have little understanding of how the ecological legacy of this MPB outbreak will interact with future disturbances.

To address key questions surrounding forest change resulting from the recent MPB outbreak and the ecological consequences of this change for future patterns of disturbance, I quantified recent forest change in the field and used ecological modeling techniques to investigate mechanisms of forest change and project future forest conditions to address the following questions:

1. How has the forest landscape changed as a result of the recent MPB outbreak and what are the mechanisms driving forest change?
2. How will the post-MPB landscape develop through time and interact with future disturbances?

METHODS

Study Area

I addressed these questions in the lodgepole pine forest type in Rocky Mountain National Park (ROMO). The park covers 108,000 ha and spans elevations from 2240 to 4350 on both sides of the Continental Divide in the Rocky Mountains in Colorado. My study was focused on the lodgepole pine cover type west of the divide, which constitutes approximately half of the forest cover and was severely affected by the recent mountain pine beetle outbreak. The nearest weather station to the study area in Grand Lake, CO records an average yearly minimum temperature of -17.5° C in January and average yearly maximum temperature of 24.6° C in July. Average annual precipitation is 48.26 cm, and average annual snowfall is 350.26 cm (Western Regional Climate Center 2012).

The recent mountain pine beetle outbreak in the region first appeared in western RMNP in 2002, and subsided in approximately 2008 after exhausting most suitable host trees. Prior to the outbreak, the disturbance regime of the lodgepole pine cover type in RMNP was dominated by infrequent, spatially-extensive stand-replacing fires (Sibold et al. 2006). The pre-outbreak forest generally regenerated following widespread fires in the second half of the nineteenth century, although some areas regenerated after fires in the 1600s and 1700s. No significant fires occurred in the study area in the 1900s (Sibold et al. 2006). These large, high-severity fires created a fairly homogenous forest characterized by expansive single-cohort patches of predominantly lodgepole pine at elevations from 2500-3300 m (Sibold et al. 2006; 2007). Higher elevation and more mesic sites at lower elevations, such as north-facing slopes, are dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*).

Field methods

I randomly selected sampling sites stratified by abiotic variables (elevation, aspect) from a digital elevation model (Gesch et al. 2002), time since fire (Sibold et al. 2006), and distance to spruce-fir forest (Salas et al. 2005). At each site I quantified forest conditions in two 20 x 20 m plots, which were separated by 100 m in a random direction. Because plots at the same site often exhibited very different species composition and size structures, I treated each plot as an independent sample in analysis.

At each plot all trees were assessed for species, DBH, and status (live, dying, recently dead, long dead) and species, height, and status were recorded for seedlings. Recently dead (<10 years before present) and long dead trees (>10 years before present) were differentiated based on the amount of fine fuels that remained on the tree and how intact the bark was. I also estimated seedling age based on terminal bud scar counts (Urza and Sibold 2013). Seedlings with five or fewer distinguishable bud scars were assigned an age equal to the number of scars. I found that most seedlings did not have more than six clear bud scars, so all seedlings with at least six scars were assigned an age of > five. Some seedlings did not show any bud scars, but displayed other traits indicating old age including thick bark and gnarled growth patterns. These seedlings were assigned to the > five year age group. For analysis, seedlings \leq five years were considered post-beetle regeneration, while seedlings > five years were considered pre-beetle. As 5-year-old seedlings would have initiated in 2007, this delineation may slightly underestimate post-beetle regeneration.

In addition to recording all trees and seedlings, we cored five live trees at breast height in each plot to obtain data about pre and post-outbreak growth rates. Cored trees were selected to represent the distribution of tree sizes and species in the plot. Increment cores were prepared

using standard dendrochronological methods (Stokes and Smiley 1968) and annual rings were counted and measured using a stereomicroscope, slide-bench micrometer, and the MeasureJ2X tree-ring measuring program.

Data analysis

The ecological legacy of the mountain pine beetle outbreak is defined by both immediate post-outbreak forest conditions and by how this post-disturbance forest landscape influences future forest conditions. While immediate post-outbreak conditions can be described with summary statistics, a mechanistic understanding of the ecological processes underlying these conditions is essential for making meaningful future predictions and applying knowledge to other sites and situations.

To investigate the ecological processes shaping post-outbreak forest conditions and trajectories, I developed Bayesian regression models for several response variables of interest, including: outbreak severity, pre- and post-outbreak seedling density of lodgepole pine, Engelmann spruce, and subalpine fir, and post-outbreak overstory species composition. I chose a Bayesian statistical approach to allow for intuitive interpretation of parameter estimates and credible intervals and for greater flexibility of inclusion of regression coefficients. Posterior probability distributions for regression parameters were estimated with Markov Chain Monte Carlo methods in the statistical package JAGS (Just Another Gibbs Sampler; Plummer 2013) implemented in R (R Development Core Team 2013). To ensure convergence, I ran three chains simultaneously for 50,000 iterations after a burn-in of 5,000 iterations. Convergence was confirmed visually through trace plots and computationally with the Gelman-Rubin diagnostic (Gelman and Rubin 1992).

For each variable of interest, I first fit a model with all independent variables representing potential mechanisms of forest change. I then iterated through models with different combinations of independent variables and selected the model that optimized the deviance information criterion (DIC; Spiegelhalter et al 2002). Final predictor variables included in regression models were elevation, mean lodgepole pine DBH, stem density of lodgepole > 15 cm, time since fire, outbreak severity, total basal area, and distance from spruce-fir dominant forest, Engelmann spruce stem density, and subalpine fir basal area. All predictor variables were standardized to speed convergence and allow for easy comparison of the magnitude of covariate effects between predictors. Coefficient values represent the effect of an increase of the covariate by one standard deviation from its mean. Posterior predictive checks were computed for model fit to verify that the chosen model was appropriate for the data. This check yields a Bayesian p-value; p-values close to 0 or 1 provide evidence of lack of model fit.

I used a negative binomial regression model with a log link for total and post-outbreak seedling regeneration. The model statement is as follows:

$$\mathbf{y} \sim \text{NB}(\boldsymbol{\lambda}, N)$$

$$\log(\boldsymbol{\lambda}) = X\boldsymbol{\beta}$$

$$\boldsymbol{\beta} \sim \text{N}(\boldsymbol{\mu}_\beta, \boldsymbol{\Sigma}_\beta)$$

$$N \sim \text{IG}(r, q).$$

The posterior distribution is denoted:

$$[\boldsymbol{\beta}, \sigma | \mathbf{y}] \propto [\mathbf{y} | \boldsymbol{\beta}, \sigma][\boldsymbol{\beta}][\sigma].$$

Seedling density (\mathbf{y}) is drawn from a negative binomial distribution with dispersion parameter N and with λ modeled as an log-linear function of the standardized covariates ($\boldsymbol{\beta}$). An uninformative normal prior was specified for the covariates with a mean of zero and a variance matrix (Σ_{β}) of $1000 * I$. An uninformative inverse gamma prior was specified for N with $r = 0.0001$ and $q = 0.0001$.

I used a beta regression model with logit link for outbreak severity, and post-outbreak species composition, as they are both measured as proportions on the interval $[0,1]$. The model statement is as follows:

$$\mathbf{y} \sim \text{beta}(\mathbf{a}, \mathbf{b})$$

$$\mathbf{a} = \frac{\mu^2 - \mu^3 - \mu\sigma^2}{\sigma^2}$$

$$\mathbf{b} = \frac{\mu - 2\mu^2 + \mu^3 - \sigma^2 + \mu\sigma^2}{\sigma^2}$$

$$\text{logit}(\mu) = X\boldsymbol{\beta}$$

$$\boldsymbol{\beta} \sim N(\mu_{\beta}, \Sigma_{\beta})$$

$$\sigma \sim \text{IG}(r, q).$$

The posterior distribution is denoted:

$$[\boldsymbol{\beta}, \sigma | \mathbf{y}] \propto [\mathbf{y} | \boldsymbol{\beta}, \sigma][\boldsymbol{\beta}][\sigma].$$

Outbreak severity and species proportions (proportion of basal area represented by each species) (\mathbf{y}) are drawn from a beta distribution with μ modeled as a logistic function of the standardized

covariates (β). An uninformative normal prior was specified for the covariates with a mean of zero and a variance matrix (Σ_β) of $1000 * I$. An uninformative inverse gamma prior was specified for σ with $r = 0.0001$ and $q = 0.0001$.

To reconstruct pre-outbreak conditions (hereafter referred to as 2002 forest conditions), I removed all post-outbreak seedlings from the data set and reclassified all recently dead trees as live. Though this does not yield an exact representation of pre-outbreak conditions, it does provide a useful approximation for comparison with post-outbreak forests. To project future forest conditions and the long-term legacy of the MPB outbreak, I used the Central Rockies variant of the Forest Vegetation Simulator (Dixon 2002). FVS is an individual-tree, distance-independent forest growth and yield model that predicts stand development over time. Field data from 2012 was entered into FVS to project forest structure and composition for each plot at decadal cycles through 2112. Projected tree growth was calibrated by species using tree-ring measurements from 1980-1999. FVS model output was based on current climate conditions. While the assumption of static climate is almost certainly incorrect, tree growth in the study area appears to be relatively buffered from drought. Whereas projected 21st century climate will be warmer and drier (IPCC 2007), the general muted response of radial tree growth in the study area to the extreme drought year of 2002, which was similar to projected average mid-century climate conditions, suggests that growth rates might not be significantly changed. Specifically, ring widths in 2002 were on average 0.9 times the mean ring width from 1990-2001, with 69% of trees displaying narrower rings in 2002, and 31% of trees showing wider rings in 2002. To model seedling establishment and recruitment in all plots I used the REPUTE extension to FVS. REPUTE uses a yield-based approach to estimate natural regeneration based on existing

vegetation state (size and density class) as each projection cycle is completed (Vandendriesche 2010).

I predicted potential future MPB outbreak severity for modeled future forest conditions with the outbreak severity model developed from the recent outbreak. The model predicts the proportion of lodgepole pine stems killed; because this model was fit based on a forest that was lodgepole pine dominant, this proportion was equal or nearly equal to the proportion of total stems killed. However, future forest species composition is expected to be considerably more mixed. To address this change, I calculated predicted outbreak severity as both the proportion of lodgepole pine stems killed (the existing model), and the proportion of total stems killed (existing model \times proportion of lodgepole stems).

To evaluate the amount and scale of landscape heterogeneity pre- and post-outbreak, and for modeled future forest conditions, I generated empirical semi-variograms for species composition (proportion of basal area for lodgepole pine, Engelmann spruce, and subalpine fir) and selected the model semi-variogram that best fit the data using AIC (Reich 2008). In all cases a Gaussian semi-variogram model provided the best fit. I compared sill and range values generated from the model semi-variograms to assess changes in heterogeneity. The sill represents the amount of variance in the variable, and the range is the distance at which data are no longer spatially autocorrelated, which can be interpreted as patch size.

RESULTS

Pre and post outbreak forest composition and structure

I sampled 218 plots at 109 sites on the west side of Rocky Mountain National Park during summer, 2012. The recent MPB outbreak killed an average of 53% of lodgepole pine stems and 75% of lodgepole pine basal area within these plots. Outbreak severity was highly variable across the landscape, with plot-level mortality ranging from 3% to 100%. Mean lodgepole DBH decreased from 16.2 to 11.0 cm pre and post outbreak, and percent lodgepole (by basal area) decreased from 92% to 76% and percent lodgepole by stem density decreased from 84% to 74%. Engelmann spruce and subalpine fir showed corresponding increases in percent composition by basal area and stem density. Pre-outbreak Engelmann spruce made up 5% of the landscape by basal area and 8% of the landscape by stem density, with post-outbreak increases to 16% for basal area and 13% for and stem density. Pre-outbreak subalpine fir made up 2% percent of the landscape by basal area and 7% by stem density; post outbreak it increased to 6% by area and 11% by density.

Seedling density for all species combined nearly doubled from the pre- to post-outbreak periods from 1145 stems/ha to 2098 stems/ha. Seedling species composition also shifted from the pre- to post-outbreak with subalpine fir seedlings dominant pre-outbreak and fir and lodgepole seedlings co-dominant post-outbreak (Table 1). Plot-level seedling density was highly variable with pre-outbreak ranges from 0 to 8250 stems/ha, and post-outbreak ranges from 0 to 21750 stems/ha (Table 1). Aspen (*Populus tremuloides*), Douglas fir (*Pseudotsuga menziesii*), and limber pine (*Pinus flexulis*) were also found during sampling but did not appear in numbers great enough to support a statistical analysis and are not expected to form a significant portion of the canopy in future years.

Outbreak severity

Elevation, mean lodgepole DBH, and density of lodgepole stems ≥ 15 cm DBH had a strong relationship with outbreak severity (defined as the percentage of lodgepole pine stems killed in the outbreak) (Table 2). Mean lodgepole DBH had the strongest effect on outbreak severity ($\beta = 0.69$) with elevation and lodgepole stems ≥ 15 cm showing negative and positive effects of equal magnitude ($\beta = -0.12$ and $\beta = 0.12$, respectively). Regression residuals (based on median values for each coefficient) were spatially correlated (Moran's I = 0.07, p-value = 1E-06) with clustering of high-severity outbreak irrespective of forest conditions. A posterior predictive check of model fit had a Bayesian p-value of 0.46, indicating no lack of fit.

Seedling regeneration

Seedling density of lodgepole pine, Engelmann spruce, and subalpine fir all increased after the outbreak. Both pre- and post- outbreak seedling density for individual species was highly variable across the landscape with variances ranging from 1000 – 5000 times larger than the mean depending on the species and time period (Table 1). Despite this high variability, regression models were useful in illuminating some important mechanisms shaping patterns of seedling regeneration. All species showed a regeneration response to the MPB outbreak (Table 3), with post-outbreak lodgepole, spruce, and fir seedling abundances having significant positive relationships with outbreak severity, patterns of regeneration were complex.

The importance of individual mechanisms that shaped patterns of regeneration varied by species and by pre- and post-outbreak time periods (Table 3, Table 4). The model for pre-outbreak lodgepole pine seedling abundance included only basal area of all species as a predictor ($\beta = -0.68$). However, post-outbreak lodgepole pine seedling abundance responded to both

elevation ($\beta = -1.55$) and outbreak severity ($\beta = 1.03$). Posterior predictive checks for pre- and post-outbreak models indicate no lack of fit with p-values of 0.26 and 0.68, though the wide distributions of covariates suggest that seedling abundances are highly variable, which is confirmed by examination of the data.

Similarly to lodgepole pine, post-outbreak Engelmann spruce seedlings (Table 3) responded to outbreak severity ($\beta = 0.45$) and elevation ($\beta = -0.69$). However, they also respond to Engelmann spruce stem density ($\beta = 0.23$) and distance to spruce-fir dominant forest ($\beta = -0.62$). Pre-outbreak spruce seedling abundance (Table 4) was related only to Engelmann spruce stem density ($\beta = 1.00$). Posterior predictive checks showed no lack of fit for both pre- and post-outbreak regeneration models ($p = 0.58$ and 0.59).

Post-outbreak subalpine fir seedling abundance had similar relationships as spruce with responses to elevation, outbreak severity, and distance from spruce-fir dominant forest (Table 3). Unlike the spruce regeneration model, fir seedling abundance showed a very strong relationship with subalpine fir basal area ($\beta = 0.71$). Pre-outbreak subalpine fir seedlings were positively related to both fir and spruce adult stem density ($\beta = 0.72$ and $\beta = 0.40$; Table 4).

Overstory species composition and future forests

In 2002, the landscape was 93% lodgepole pine, 5% Engelmann spruce, 2% subalpine fir, and <1% other species (aspen, Douglas fir, and limber pine) by basal area, with a mean basal area of 42.3 m²/ha; in 2012 it was 76% lodgepole pine, 16% Engelmann spruce, 6% subalpine fir, and 3% other species (aspen, Douglas fir, and limber pine) with a mean basal area of only 12.6 m²/ha. Using the post-outbreak landscape conditions as a starting point to model future forest conditions, FVS projected that by 2112 the landscape will have nearly recovered to pre-

outbreak basal area, with a mean basal area of 41.5 m²/ha. Species composition is projected to be quite different, however, with 56% lodgepole pine, 25% Engelmann spruce, 14% subalpine fir, and 5% other species by basal area (Figure 2).

Mechanisms in post-outbreak overstory species composition are consistent across species, though the direction of relationships vary (Table 5). Post-outbreak lodgepole pine proportion had a negative relationship with time since fire ($\beta = -0.38$), elevation ($\beta = -0.35$), and outbreak severity ($\beta = -0.56$). In contrast, Engelmann spruce responded positively to time since fire ($\beta = 0.35$), outbreak severity ($\beta = 0.45$), and elevation ($\beta = 0.035$), and had an additional response to distance from spruce-fir forest ($\beta = -0.30$). Post-outbreak subalpine fir proportion showed positive relationships with time since fire ($\beta = 0.26$), outbreak severity ($\beta = 0.12$), and elevation ($\beta = 0.15$). Model residuals for all species were spatially correlated, indicating that there were spatial relationships in species composition not explained by predictor variables.

Spatial heterogeneity of species composition

Post-outbreak forest conditions (2012) and FVS model projections both predicted substantial changes in species composition in the next century. These results suggest that changes will happen across multiple spatial scales. Forests will be more diverse at both a landscape level (Figure 2) and a plot level (Figure 3). Plot-level basal area proportions by species showed a distinct change in species composition. Specifically, the mean plot-level proportion of lodgepole pine decreased post-outbreak, and the distribution of means became much broader. Engelmann spruce and subalpine fir showed a corresponding increase in mean proportion post-outbreak and broader distributions of means as well. Semi-variograms of species composition (Figure 4) corroborate this pattern. Pre-outbreak (2002) proportion of lodgepole pine had a sill of

0.012 and range of 6988 m, while post-outbreak (2012) proportion of lodgepole pine had a sill of 0.075 and a range of 1176 m (Figure 4, Table 6). This trend of increasing sill and decreasing range is projected to continue through 2112 when lodgepole pine proportion is predicted to have a sill of 0.13 and range of 841 m. Though the magnitude of change varied somewhat, the same trends of increasing sill and decreasing range were evident in the semi-variograms of spruce and fir proportions (Figure 4, Table 6). In terms of species composition, post-beetle forests had higher variance and smaller patches of similar forest, and FVS projections indicated that this trend towards greater variance and smaller patch size will continue as forests recover from the outbreak.

Severity of future mountain pine beetle outbreaks

Potential severity (percentage of stems killed for all species) of future MPB outbreaks in projected forest landscapes dropped significantly after the 2002 outbreak, and continues to decrease through 2062 and 2112 (Figure 5). Over this century, median predicted total mortality remains below that of median predicted total mortality in 2002 and the distribution of predicted total mortality increases. In 2002, predicted total mortality was high (median = 0.43) and fairly homogenous (variance = 0.019); by 2112 it will be both lower (median = 0.13) and more heterogeneous (variance = 0.035) than both 2002 and 2012 (median = 0.17 and variance = 0.016). To better understand the unique ecological legacy of the recent MPB outbreak on the severity of future MPB outbreaks, I estimated future mortality from an MPB outbreak for a post-fire forest that I developed based on forest characteristics in 2 plots that were burned in a high-severity prescribed fire in 2002. In the post-fire forest development scenario, median post-fire

predicted outbreak severity (0.21) in 2062 surpasses predicted median severity for post-beetle forests (0.15, variance = 0.20).

Median predicted lodgepole mortality from MPB outbreaks returns to pre-beetle levels by 2112 (2112 median = 0.63, 2002 median = 0.52; Figure 5), though the distribution of predicted lodgepole mortality is wider than pre-outbreak conditions by 2062 (variance = 0.038, 2002 variance = 0.021), and continues to grow through 2112 (variance = 0.056). Spatial semi-variograms for predicted lodgepole mortality show greater homogeneity immediately post-outbreak in 2012, but greater heterogeneity (higher variance and smaller patch sizes) by 2062 that continues to increase through 2112 (Table 6, Figure 6).

DISCUSSION

My results confirm insights from previous mountain pine beetle research on relationships between forest conditions and outbreak severity (e.g. Amman and Baker 1972; Berryman 1982, Shore and Safranyik 1992) and post-outbreak species composition changes. The recent MPB outbreak is exceptionally severe and extensive (Raffa et al. 2008), but it is mechanistically similar to past outbreaks. Although this outbreak has killed more trees over a greater area than past recorded outbreaks (Meddens et al. 2012), pine beetles are still responding to the same factors that they have historically – lower elevation (i.e. warmer and drier) sites with more large diameter lodgepole pine are more susceptible to MPB (Table 2). Furthermore, while pine beetles have successfully attacked trees <15 cm in diameter, that threshold still has a strong effect on outbreak severity. Nonetheless, positive spatial autocorrelation of regression residuals suggests that regardless of forest characteristics, proximity to a highly susceptible stand increases susceptibility (Table 2).

In the context of post-outbreak regeneration, my results illustrate a significant shift in forest conditions from stands dominated by single cohorts of lodgepole pine to stands that are generally characterized by increased diversity in age classes and species composition. These results stress the importance of the outbreak in increasing resources and creating opportunities for new establishment. While some studies have identified the importance of MPB outbreaks in providing opportunities for new establishment (Sibold 2007; Pelz and Smith 2012), other studies (Nigh et al. 2008; Diskin 2011; Kayes and Tinker 2012) have stressed the importance of advanced regeneration as the primary mechanism for forest renewal following bark beetle outbreaks. A possible reason for the discrepancy is in the timing of sampling. Studies that identified strong pulses of post-outbreak regeneration sampled later after outbreaks (Sibold 2007;

Pelz and Smith 2012, this study) while other studies sampled during the outbreak (Nigh et al. 2008) and two years after the outbreak ended (Diskin et al. 2011; Kayes and Tinker 2012). Moreover, studies that identified post-outbreak establishment dated establishment in contrast to assuming that seedlings preceded outbreaks. Advanced regeneration may be more important for silviculture, as larger trees will enhance the recovery of basal area and will make it more likely that stocking requirements are met. From an ecological perspective, however, density and species composition of seedling regeneration will play an important role in defining the ecological legacy of the outbreak.

How has the forest landscape changed as a result of the recent MPB outbreak and what are the mechanisms driving forest change?

My results confirm that post-MPB species shifts described in previous research (Amman et al. 1988; Sibold et al. 2007; Astrup et al. 2008; Nigh et al. 2008) are also occurring after the MPB outbreak in Rocky Mountain National Park. Immediate post-outbreak forest change is a product of overstory composition, but seedling establishment will play an important role in the longer-term trajectories of post-MPB forests. Seedling regeneration is highly variable and difficult to model, perhaps because of inherent stochasticity in regeneration, or factors not addressed in my study such as soil type and depth, microsite conditions, or whether lodgepole pine cones at a site are open or serotinous.

Despite this variability, there is a consistent positive response among post-outbreak seedling abundance of all species to MPB outbreak severity, indicating that the initiation of new seedlings plays an important role in post-outbreak forest structure (Table 3). Seedlings of all species also showed a negative relationship with elevation, suggesting that lower elevations

generally provide more favorable conditions for establishment. While lodgepole pine seedling abundance is related only to these two variables, post-outbreak spruce and fir seedlings also showed dependence on seed sources, with significant relationships to distance to spruce-fir dominant forest and in-plot seed sources, represented by spruce stem density for spruce seedlings and subalpine fir basal area for fir seedlings.

Mechanisms of post-outbreak seedling regeneration stand in contrast to those for pre-outbreak seedling regeneration (Table 4). Pre-outbreak lodgepole pine seedling abundance only responded (negatively) to total basal area, indicating that light availability was the primary driver for lodgepole establishment. Spruce and fir seedlings were more dependent on seed source and favorable site conditions, represented by adult stem density of their respective species. Spruce seedling abundance also showed a negative relationship with adult fir stem density, implying that competition from subalpine fir may play a role in spruce seedling establishment.

The MPB outbreak provided opportunities for new seedling establishment for all species and dispersal for spruce and fir. Within-plot seed sources were not a prerequisite for spruce and fir regeneration. Sixty-four percent of plots with no adult fir had fir seedlings, and 32% of plots with no adult spruce had spruce seedlings, demonstrating that spruce and fir moved into new areas that were previously dominated by lodgepole pine, and that today stands and the landscape are more diverse than pre-outbreak forests in terms of seedling composition.

Taken together, these relationships illustrate that forest change resulting from the mountain pine beetle outbreak is contingent on several factors and is creating highly diverse stands at the landscape scale. For example, younger (<130 years old) post-fire stands could show little change in species composition, even with relatively high outbreak severity. On the other end of the spectrum, older stands with spruce and fir present before the outbreak could

immediately shift to spruce-fir dominant forest if affected by high outbreak severity. Between these two scenarios lies a wide range of post-outbreak forest change possibilities dependent on stand age, outbreak severity, stand location, and available seed sources. The spatial variability of these mechanisms of forest change is reflected in increased spatial heterogeneity of species composition across the post-outbreak landscape (Figure 4, Table 6).

Thus, disturbance interactions between pre-outbreak fire history (stand age), outbreak severity, and landscape position operate synergistically to shape post-outbreak species composition. In the context of disturbance interactions, the recent mountain pine beetle eruption can be thought of as a prism that magnifies differences in species composition due to the timing and extent of pre-outbreak fire events found in pre-outbreak forests (Figure 7). Just as past disturbance interactions influenced the post-MPB landscape, the ecological legacy of this outbreak will affect the likelihood, severity, and extent of future disturbances in Rocky Mountain National Park. These interactions will primarily be through the lens of MPB-facilitated forest change and the resulting increase in spatial heterogeneity of species composition.

How will the post-outbreak landscape develop through time and interact with future disturbance?

The recent MPB outbreak initiated a change in species composition, and FVS model projections indicate that this change will set forests on a trajectory towards a greater proportion of Engelmann spruce and subalpine fir (Figure 2). This prediction is corroborated by Pelz and Smith (2012), who found that in the 30 years after a 1980s MPB outbreak, lodgepole pine stem density and basal area increased significantly in lodgepole-only stands, but did not increase in lodgepole-spruce-fir stands that experienced similar levels of mortality, indicating that

immediate post-outbreak species composition is a good indicator of future species composition. Spatial semi-variograms of projected forest conditions in 2062 and 2112 indicate that the post-outbreak trend towards higher variance in species composition at finer scales will continue as post-outbreak forests develop, with future forests exhibiting greater spatial heterogeneity than 2002 and 2012 forests (Figure 4, Table 6). This trend has important implications for future disturbance interactions.

Mountain pine beetle – bark beetle interactions

In terms of total mortality, post-beetle stands are markedly more resistant to future mountain pine beetle outbreaks than post-fire stands (Figure 5). This resistance can be attributed to forest change facilitated by the MPB outbreak – with fewer lodgepole pine on the landscape, mountain pine beetle caused mortality is much more limited. Post-beetle stands are more resistant in terms of total mortality, but they may be less resistant than post-fire stands in terms of lodgepole-only mortality. Predicted lodgepole mortality remains lower in stands developing following fire than in stands developing following the recent MPB outbreak through 2112 (Figure 5), which is to be expected as post-fire stands initiate from seedlings and post-beetle stands have an existing stock of small diameter lodgepole trees to recruit from. Though it's not evident in this 100 year projection, we would expect that post-fire predicted lodgepole mortality would eventually surpass post-beetle predicted lodgepole mortality, due to faster growth rates of post-fire lodgepole pine (Kashian et al. 2011).

Additionally, when accounting for future mountain pine beetle risk we must consider the variance of predicted mortality, not just the median. Although median predicted lodgepole mortality in 2112 surpasses that of 2002, the variance in predicted lodgepole mortality is nearly 3

times greater in 2112 than in 2002 (Figure 5). Semi-variogram analysis indicates that this increase in variance is accompanied by an increase in spatial heterogeneity with smaller patches of similar forest and greater within-patch variance (Figure 6, Table 6). This increase in variance and decrease in patch size has important implications for constraining future MPB eruptions, as stand and landscape level mountain pine beetle outbreaks are facilitated by landscape homogeneity (Raffa et al. 2008). Although post-beetle lodgepole mortality is predicted to be higher than post-fire lodgepole mortality, the increased temporal and spatial variance in predicted mortality means that another extensive MPB eruption at the scale of the 2002 outbreak is unlikely. Assuming that future climate will be exceptionally favorable for MPB, it is possible that the future will be characterized by smaller outbreaks that erupt on portions of the landscape as they become susceptible.

The predicted shift in species composition to more mixed stands of lodgepole pine, Engelmann spruce and subalpine fir will make post-beetle forests less susceptible to mountain pine beetle outbreaks, but it will increase susceptibility to other bark beetle outbreaks, namely spruce beetle (SB; *Dendroctonus rufipennis*) and western balsam bark beetle (WBBB; *Dryocoetes confusus*). Future spruce beetle and western balsam bark beetle outbreaks are of greater concern if projected increases of Engelmann spruce and subalpine fir in the lodgepole-dominant landscape are realized. However, like mountain pine beetle, these bark beetles require stand and landscape level homogeneity for an extensive outbreak, so it is unlikely that the study area will initiate a major SB or WBBB outbreak in the future, though it is possible that a spruce beetle outbreak initiating in nearby spruce-fir dominant forest could spread to the predicted mixed-species stands in the study area.

Even accounting for SB and WBBB outbreaks, in general the post-MPB landscape will be more resistant to bark beetle outbreaks because of increased species heterogeneity. The forest is predicted to have greater variation in species and smaller patches of similar species composition than the pre-outbreak forest. This increased heterogeneity means that extensive bark beetle eruptions are less likely, as bark beetles require homogenous forests to reach outbreak levels (Raffa et al. 2008). If the forest did support an outbreak, or an outbreak spread from more homogenous stands nearby, mortality would be limited to the representation of the host species on the landscape.

Mountain pine beetle – fire interactions

Like bark beetle outbreaks, wildfire events have a strong climate forcing and are expected to increase due to warmer, drier conditions facilitated by climate change (Dale et al. 2001). We expect wildfire occurrence, severity, and extent to increase with increasing temperatures and decreasing fuel moisture. Potential interactions between bark beetle outbreaks and wildfire are more difficult to parse. For decades, the increase in dead, desiccated fuels from bark beetle-caused mortality was assumed to equate to a long-term elevated fire risk (Heinrichs 1983, Lotan et al. 1985, Schmid and Amman 1992). However, recent research suggests the actual relationship is considerably more complex. This relationship is likely a function of time at two scales; an immediate post-outbreak response where fire behavior changes due to changes in the quantity and arrangement of live and dead fuels, and a longer-term response where fire behavior changes based on changes in species composition and seedling and sapling density.

The short-term post-beetle fire risk is difficult to predict. Simard (2011) asserts that red and gray-stage post-beetle stands are less likely to sustain an active crown fire than undisturbed

stands, while Schoennagel (2012) contends that active crown fire is more likely in red and gray-stage stands than undisturbed forests. Their contradictory results are likely a product of different assumptions regarding the importance of low canopy moisture levels in fire behavior. Other research postulates that by 4 years after an outbreak (mid-gray stage), there are no fine fuels left to facilitate fire spread in the canopy, so risk of fire is likely lower than pre-outbreak risk (Page and Jenkins 2007, Jenkins et al. 2008, Klutsch et al. 2009)

Longer-term post-beetle fire risk is expected to be influenced by predicted shifts in species composition. Subalpine fir and Engelmann spruce typically have lower crowns and more tightly packed branches than lodgepole pine, which will increase the crown fire hazard (Rothermel 1972, VanWagner 1977, Scott and Reinhardt 2001). When sampling stands 20-30 years after an MPB outbreak, Pelz and Smith (2012) found greater vertical continuity of fuels in mixed conifer stands than lodgepole dominant stands due to higher density of understory trees and lower crown base heights, which also leads to a greater risk of crown fire.

Significant uncertainty remains in the nature of interactions between MPB outbreaks and fire. However, there is a consensus that the occurrence of fire in Rocky Mountain subalpine forests is primarily driven by climate, not fuel conditions (Despain 1991; Turner and Romme 1994; Veblen 2000; Baker 2003). Thus, any potential future interactions between post-MPB forests and wildfire will be controlled by the presence of fire-conducive weather conditions (e.g. severe drought and high winds).

Mountain pine beetle – drought interactions

Climate change is expected to lead to more persistent weather patterns, which in turn will lead to an increase in probability of extreme weather events that result from prolonged

conditions, including drought (Francis and Avrus 2012). In western forests, drought has often been a proximate cause of forest mortality through its relationship with other disturbances, including bark beetle outbreaks and fire (Romme and Despain 1989, Bebi et al. 2003, Sibold et al. 2006). Drought can also be a direct cause of tree mortality, though this relationship is difficult to quantify due to its concomitant effects on tree physiological stress and biotic mortality agents (Bigler 2006). Bigler (2006) found strong drought-mortality associations for subalpine fir, significant, though weaker associations for Engelmann spruce, and no associations for lodgepole pine in both drought-affected and subsequent years in Northern Colorado. Both spruce and fir were more sensitive to the effects of early season than late season drought. Lodgepole pine has better stomatal control in dry conditions than spruce or fir, so it is a more efficient water conserver and less vulnerable to drought (Knapp and Smith 1981). However, we may see drought-caused lodgepole mortality in future years if drought events become sufficiently long and/or extreme.

Evidence of differential mortality by species due to drought indicates that post-beetle mixed-species forests will be less resistant to drought disturbances than pre-beetle forests. Future droughts are likely to cause subalpine fir mortality, and potentially Engelmann spruce mortality. If droughts are frequent and extreme enough, they may alter the current trajectory towards greater proportions of spruce and fir and shift forests back to the lodgepole-dominant conditions that existed pre-MPB.

Management implications

Managing forests in a changing climate is a difficult task made even more challenging by the associated increase in occurrence, extent, and severity of disturbances, and the potential for

novel disturbance interactions. Different strategies for managing forests in a climate change context have been suggested. Millar (2007) encourages managing for asynchrony by promoting diverse age classes, species mixes, and structures, while Keane (2009) recommends keeping forests within historic range of variability (HRV) conditions for successful adaptation to climate change. The recent MPB outbreak has created landscapes outside of HRV, but it has also created greater asynchrony in species composition at landscape and stand levels. Compared to HRV conditions that largely reflected infrequent, extensive, high-severity fires in lodgepole dominant forests, the landscape resulting from the recent MPB outbreak will have greater resistance to future MPB outbreaks, but will be more susceptible to other bark beetle outbreaks (namely spruce and western balsam bark beetle) and drought mortality. Despite this increase in susceptibility to certain mortality agents, post-beetle forests will be more resistant to future disturbances, as it will require multiple agents to cause the same level of mortality experienced in the recent mountain pine beetle eruption. A fire event has the greatest potential to cause landscape-level mortality. However, as fire occurrence in the study area is primarily controlled by climate, managing for asynchrony or HRV is unlikely to significantly impact the probability of wildfire. Thus, post-beetle forests and their associated increase in species heterogeneity are a preferable landscape for resistance to future disturbances in a climate change context, despite their existence outside of HRV.

However, the increase in spatial heterogeneity of these forests is a result of increasing quantities of and dispersal of spruce and fir on the landscape. These drought-intolerant species have moved into drier stands that were previously lodgepole-only, in opposition to predictions of species distribution models in the study area (Rehfeldt et al. 2006) and the idea that disturbances create opportunities for migration of species that are better adapted to climate conditions

(Overpeck et al. 1990). While Rehfeldt and Overpeck would expect increases in ponderosa pine, limber pine, and Douglas fir in the study area, the disturbance type and available seed sources instead favored Engelmann spruce and subalpine fir. Understanding these factors is essential for land managers' ability to anticipate future forest conditions. Furthermore, while the post-beetle increase in species heterogeneity will increase landscape resilience to future disturbances, the increase in spruce and fir may decrease landscape resilience to future climate conditions.

Table 1. Pre- and post-outbreak seedling density, variability, and species composition

	Pre-outbreak	Post-outbreak
Mean seedling density (stems/ha)		
Lodgepole pine	342	857
Engelmann spruce	186	260
Subalpine fir	508	858
Seedling density variance		
Lodgepole pine	620211	4209185
Engelmann spruce	202128	347632
Subalpine fir	1114501	3580439
Seedling density range (stems/ha)		
Lodgepole pine	0-7250	0-21500
Engelmann spruce	0-2750	0-15000
Subalpine fir	0-8000	0-14500
Seedling species composition (%)		
Lodgepole pine	30	41
Engelmann spruce	16	12
Subalpine fir	44	41

Table 2. Outbreak severity: Mean and standard deviation of estimated regression coefficients and the corresponding probability of an opposite or nonexistent effect

Parameter	β mean	σ	$P(\beta \neq 0)$
Intercept	0.17	0.043	0
Elevation	-0.12	0.044	0
Mean lodgepole pine DBH	0.69	0.053	0
# Lodgepole pine stems \geq 15 cm DBH	0.12	0.046	0
Posterior predictive check ¹			
Fit	0.46		
Spatial correlation of residuals			
Moran's I	0.07		
P-value	1E-06*		

Coefficient values represent the effect on outbreak severity of an increase of the predictor variable by one standard deviation from its mean

Bold text denotes the coefficient with the greatest magnitude effect on seedling density per model

¹A value of 0.5 indicates a perfect model fit, while values of 0 or 1 indicate no model fit

* indicates a statistically significant p-value for Moran's I; i.e. residuals *are* spatially auto correlated

Table 3. Post outbreak seedling regeneration: Mean and standard deviation of estimated regression coefficients and the corresponding probability of an opposite or nonexistent effect

Parameter	Lodgepole pine			Engelmann spruce			Subalpine fir		
	β mean	σ	$P(\beta \neq 0)$	β	σ	$P(\beta \neq 0)$	β	σ	$P(\beta \neq 0)$
Intercept	2.07	0.15	0	0.82	0.21	0	2.11	0.17	0
Elevation	-1.55	0.2	0	-0.69	0.23	0	-0.33	0.14	0
Outbreak severity	1.03	0.18	0	0.45	0.21	0	0.43	0.18	0
Distance from spruce-fir forest	-	-	-	-0.62	0.19	0	-0.35	0.18	0.06
Engelmann spruce stem density	-	-	-	0.23	0.11	0.03	-	-	-
Subalpine fir basal area	-	-	-	-	-	-	0.71	0.26	0
Posterior predictive check ¹									
Fit	0.68			0.59			0.76		
Spatial auto-correlation of residuals									
Moran's I	0.016			0.00			0.00		
P-value	0.274			0.89			0.67		

Coefficient values represent the effect on seedling density of an increase of the predictor by one standard deviation from its mean

Bold text indicates the coefficient with the greatest magnitude effect on seedling density per model

¹A value of 0.5 indicates a perfect model fit, while values of 0 or 1 indicate no model fit

* indicates a statistically significant p-value for Moran's I; i.e. residuals *are* spatially auto correlated

Table 4. Pre-outbreak seedling regeneration: Mean and standard deviation of estimated regression coefficients and the corresponding probability of an opposite or nonexistent effect

Parameter	Lodgepole pine			Engelmann spruce			Subalpine fir		
	β	σ	$P(\beta \neq 0)$	β	σ	$P(\beta \neq 0)$	β	σ	$P(\beta \neq 0)$
Intercept	2.45	0.12	0	1.54	0.12	0	2.55	0.10	0
Total basal area	-0.68	0.14	0	-	-	-	-	-	-
Subalpine fir stem density	-	-	-	-	-	-	0.72	0.15	0
Engelmann spruce stem density	-	-	-	1.00	0.09	0	0.40	0.11	0
Posterior predictive check ¹									
Fit	0.26			0.58			0.51		
Spatial auto-correlation of residuals									
Moran's I	0.067			-0.014			0.09		
P-value	0.001*			0.65			3.9E-05*		

Coefficient values represent the effect on seedling density of an increase of the predictor variable by one standard deviation from its mean

Bold text denotes the coefficient with the greatest magnitude effect on seedling density per model

¹A value of 0.5 indicates a perfect model fit, while values of 0 or 1 indicate no model fit

* indicates a statistically significant p-value for Moran's I; i.e. residuals *are* spatially auto correlated

Table 5. Post outbreak overstory species composition: Mean and standard deviation of estimated regression coefficients and the corresponding probability of an opposite or nonexistent effect

Parameter	Lodgepole pine			Engelmann spruce			Subalpine fir		
	β mean	σ	$P(\beta \neq 0)$	β mean	σ	$P(\beta \neq 0)$	β mean	σ	$P(\beta \neq 0)$
Intercept	1.62	0.13	0	-2.22	0.15	0	-2.57	0.13	0
Outbreak severity	-0.56	0.12	0	0.45	0.12	0	0.12	0.0063	0
Time since fire	-0.38	0.10	0	0.35	0.088	0	0.26	0.095	0
Elevation	-0.35	0.18	0	0.34	0.16	0	0.15	0.10	0.05
Distance from spruce-fir forest	-	-	-	-0.30	0.16	0.03	-	-	-
Posterior predictive check ¹									
Fit	0.44			0.42			0.43		
Spatial auto-correlation of residuals									
Moran's i	0.07			0.08			0.054		
p-value	1E-06*			0*			1E-04*		

Coefficient values represent the effect on overstory species composition of an increase of the predictor by one standard deviation from its mean

Bold text indicates the coefficient with the greatest magnitude effect on seedling density per model

¹A value of 0.5 indicates a perfect model fit, while values of 0 or 1 indicate no model fit

* indicates a statistically significant p-value for Moran's I; i.e. residuals *are* spatially auto correlated

Table 6. Spatial semivariogram sill and range values for pre-outbreak (2002), post-outbreak (2012) , and FVS-projected (2062, 2112) proportion of forest by basal area for lodgepole pine, Engelmann spruce, and subalpine fir, and predicted outbreak severity

Year	Lodgepole pine proportion		Engelmann spruce proportion		Subalpine fir proportion		Predicted outbreak severity	
	Sill	Range	Sill	Range	Sill	Range	Sill	Range
2002	0.012	6988	0.013	6888	0.001	2799	0.021	471
2012	0.075	1176	0.035	1324	0.022	900	0.014	561
2062	0.112	994	0.065	1168	0.043	694	0.038	419
2112	0.130	841	0.091	1136	0.059	647	0.056	361

Sill values describe variance, range represents patch size

Bold text indicates when sill and range values show greater heterogeneity than pre-MPB conditions

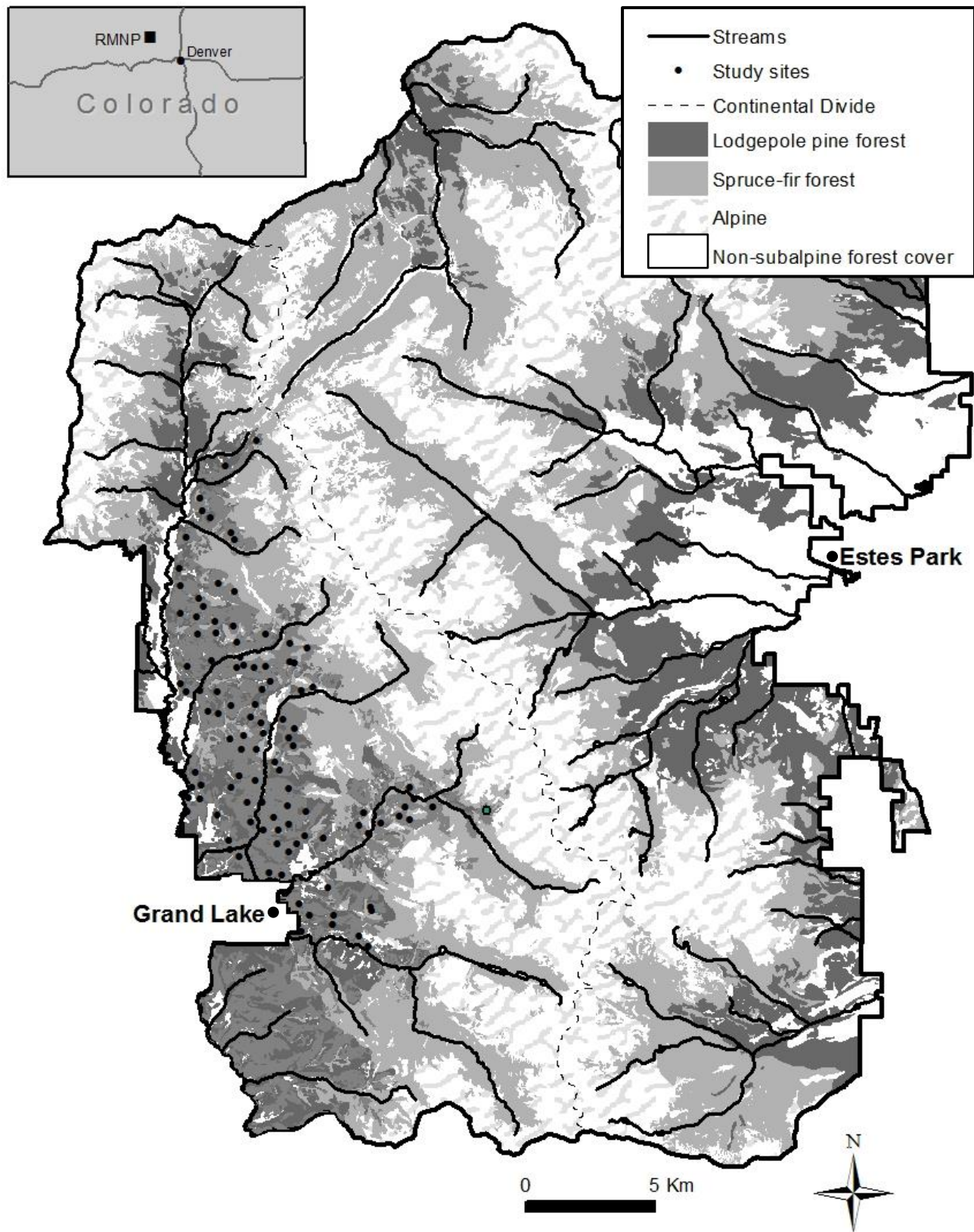


Figure 1. Distribution of study sites within Rocky Mountain National Park, Colorado, USA.

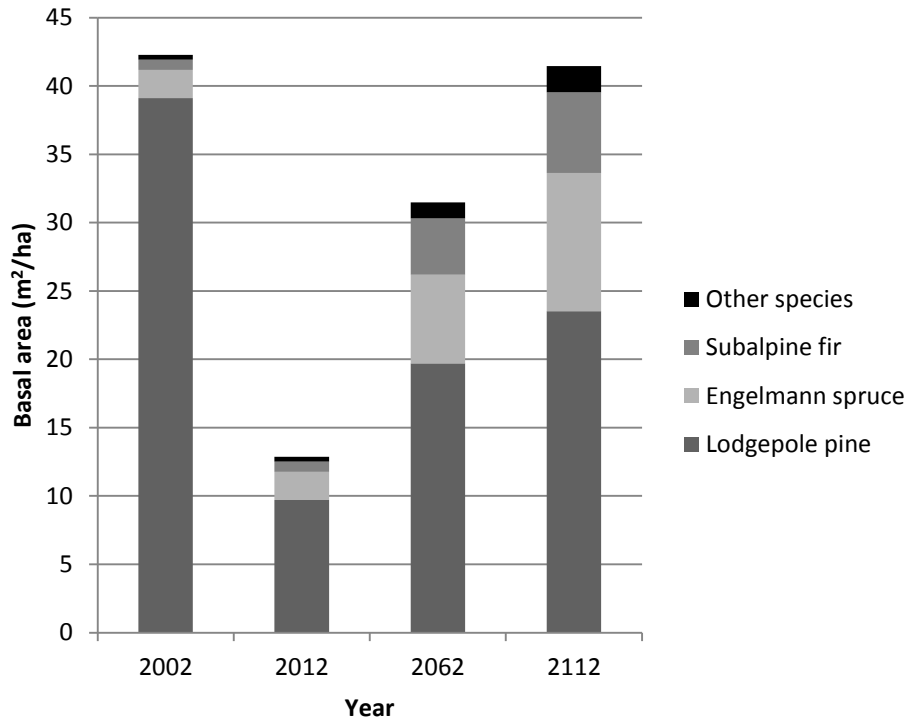


Figure 2. Pre-outbreak (2002), post-outbreak (2012), and FVS-projected (2062, 2112) landscape-level basal area by species. “Other species” includes aspen, Douglas fir, and limber pine.

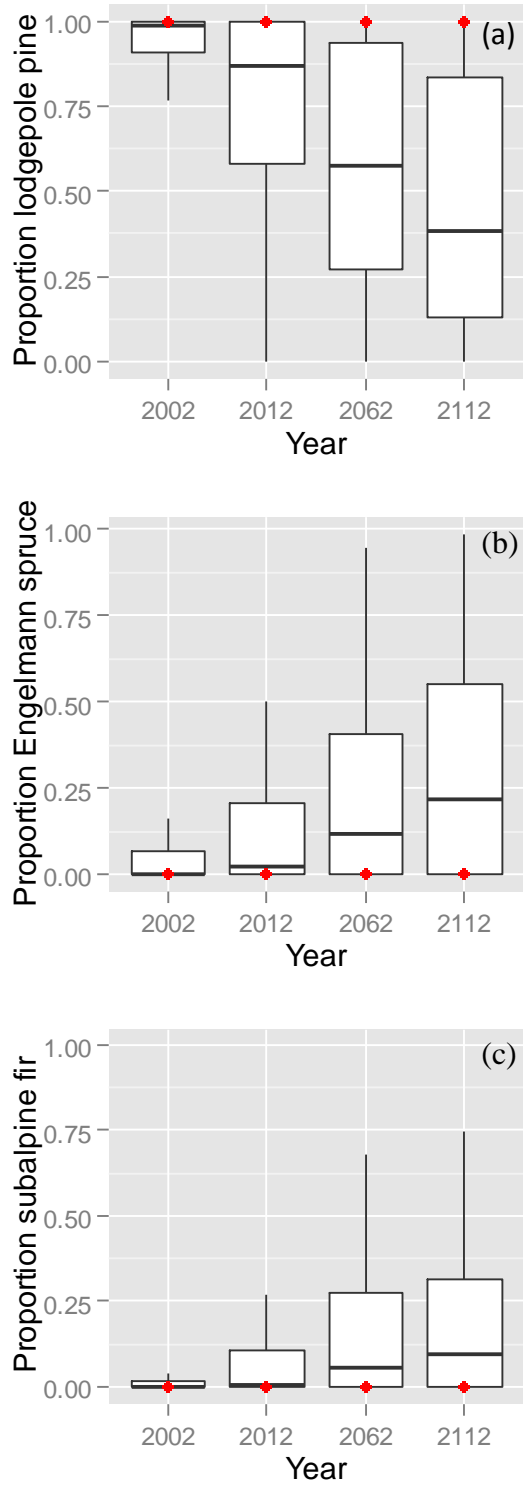


Figure 3. Pre-outbreak (2002), post-outbreak (2012) and FVS-projected (2062, 2112) plot-level species composition by basal area for (a) lodgepole pine, (b) Engelmann spruce and (c) subalpine fir. Boxplots indicate distribution of plot-level species proportions, and red points indicate median species proportions for post-fire plots.

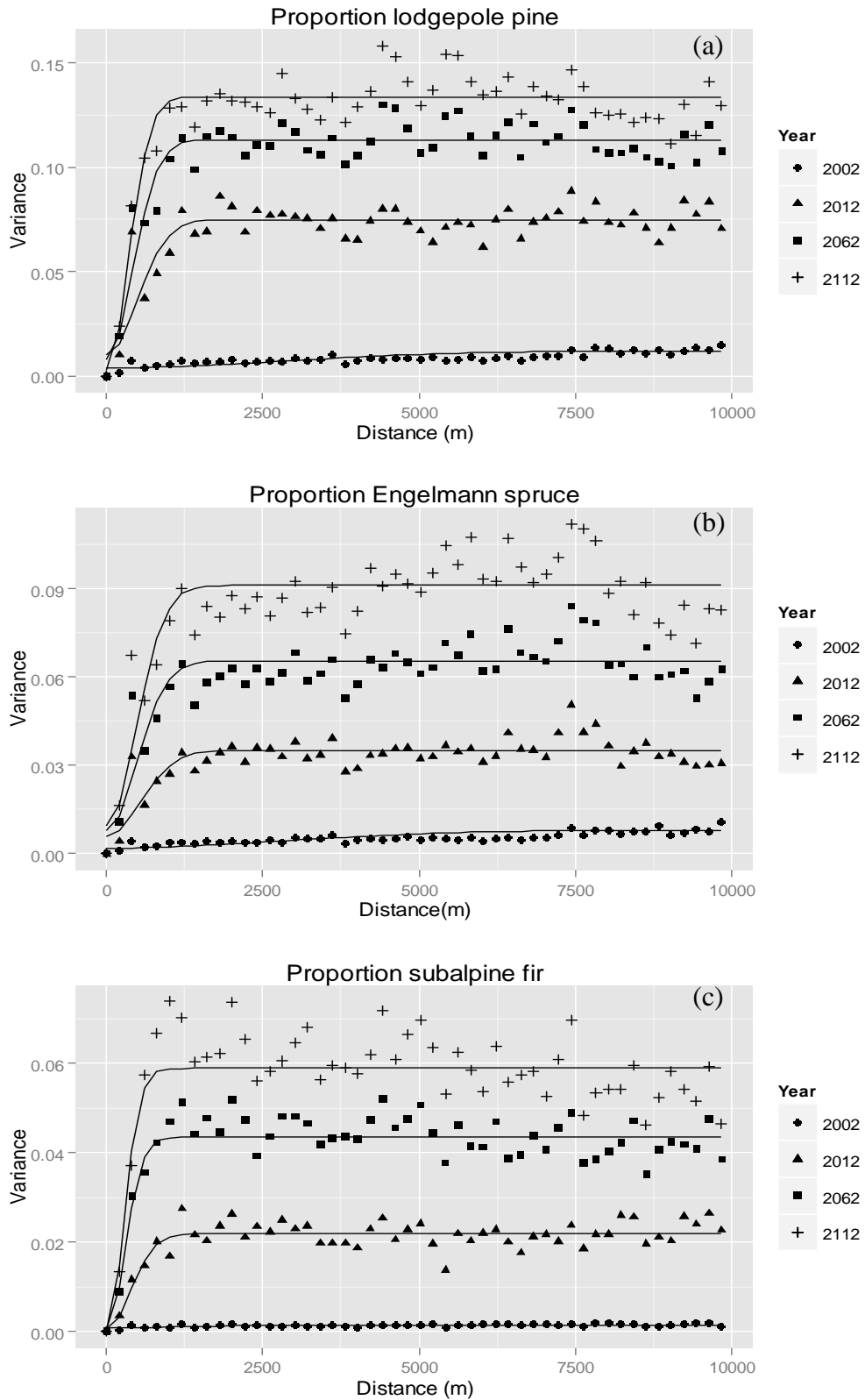


Figure 4. Spatial semi-variograms for pre-outbreak (2002), post-outbreak (2012), and FVS-projected (2062, 2112) proportion of forest by basal area for (a) lodgepole pine, (b) Engelmann spruce, and (c) subalpine fir.

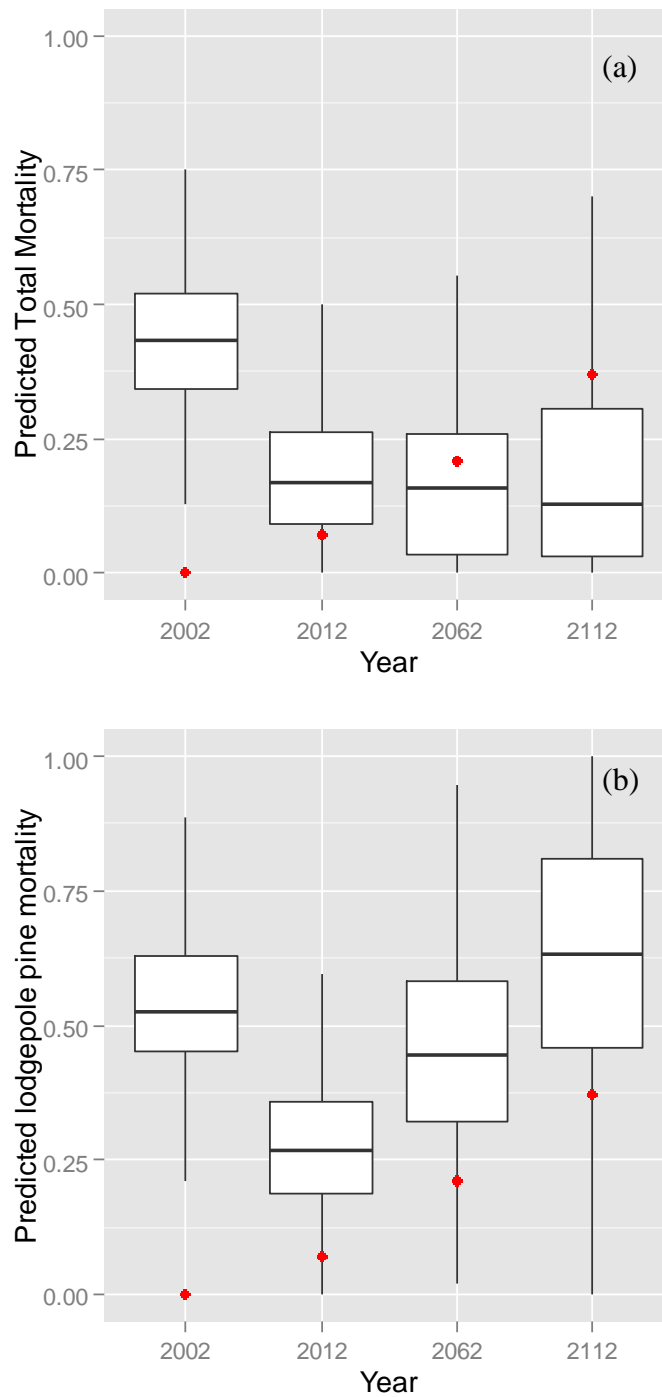


Figure 5. Predicted MPB outbreak severity for pre-outbreak (2002), post-outbreak (2012) and FVS-projected (2062, 2112) forests. Boxplots show distribution of plot-level predicted mortality as a proportion of all stems (a) and a proportion of lodgepole pine stems only (b). Red points represent median predicted mortality for post-fire plots.

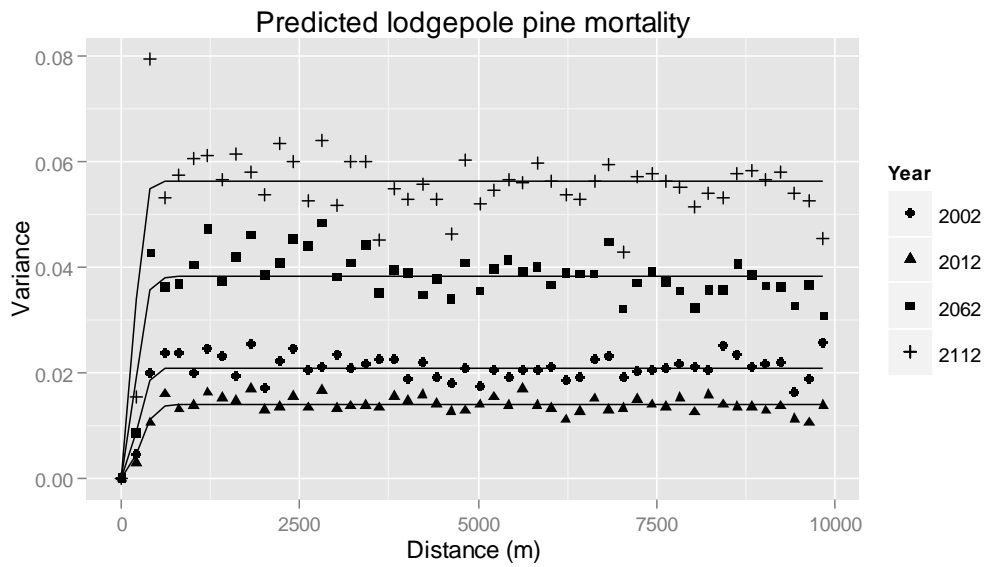


Figure 6. Spatial semi-variograms for pre-outbreak (2002), post-outbreak (2012) , and FVS-projected (2062, 2112) predicted outbreak severity, represented as the proportion of lodgepole pine stems killed.

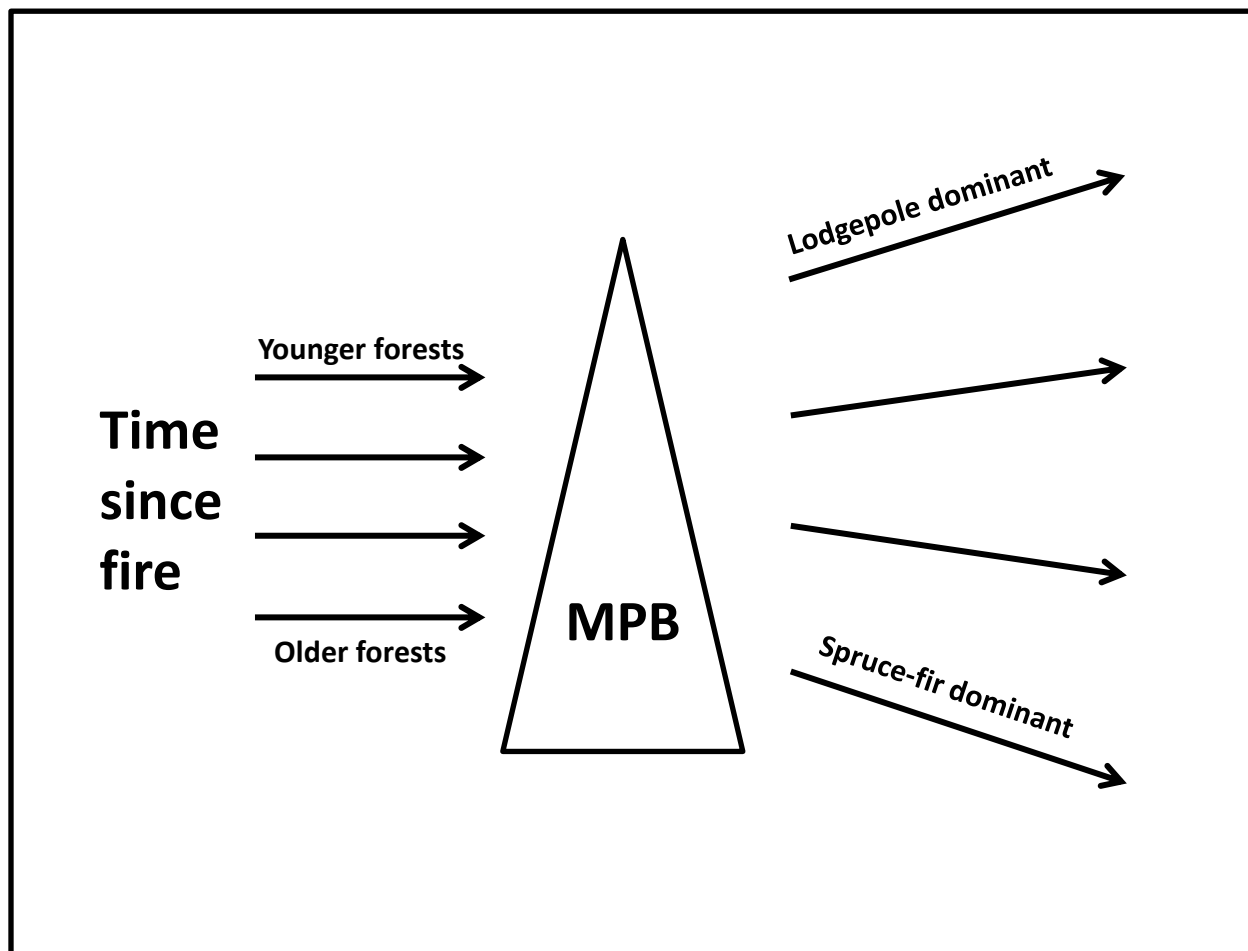


Figure 7. Conceptual diagram of disturbance interactions in species composition: the 2002 mountain pine beetle outbreak amplifies pre-outbreak differences in species composition due to time since fire.

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