

THESIS

TO BEETLE OR NOT TO BEETLE: ASSESSING ENGELMANN SPRUCE FOREST RESILIENCE
FOLLOWING SPRUCE BEETLE OUTBREAK IN WESTERN COLORADO

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ABSTRACT

TO BEETLE OR NOT TO BEETLE: ASSESSING ENGELMANN SPRUCE FOREST RESILIENCE FOLLOWING SPRUCE BEETLE OUTBREAK IN WESTERN COLORADO

Bark beetle outbreaks are affecting millions of hectares globally. In the southern Rocky Mountains, native spruce bark beetles (*Dendroctonus rufipennis*) are a natural disturbance agent in subalpine forests, but recent outbreaks have increased in severity, resulting in landscape-scale changes in forest composition and structure. These beetles primarily affect Engelmann spruce (*Picea engelmannii*) trees larger than 40 cm in diameter. Following outbreak, post-disturbance recovery may be influenced by previous management, stand composition, and regeneration dynamics. In this study we examined three questions: (1) How do different species (e.g., Engelmann spruce, aspen) respond to treatments under varying climate conditions? (2) Under different climate scenarios, will spruce recruitment be sufficient to maintain forest structure and composition, or will other species (e.g., aspen) become dominant? (3) How do treatments affect forest structure, and how do these treatments promote long-term resilience to future disturbances (e.g., fire, drought, secondary insect outbreaks)?

To evaluate these questions, 44 repeatedly measured plots, and 66 additional inventory plots in south-central Colorado in previously managed, unmanaged, and salvaged, and no-beetle reference stand were analyzed. Future stand trajectories were

then projected using the Forest Vegetation Simulator (FVS). Regeneration responses differed among species, with aspen increasing in larger seedling height classes while spruce recruitment declined in the smallest size class (0.1- 9.9 cm; Class 1). Seedling responses to vapor pressure deficit differed by species despite no significant overall effect on seedling density. Modeled tree density differed significantly among species and disturbance history, indicating species life-history traits and beetle disturbance history were stronger drivers of projected stand structure than management history alone. Regeneration-based species composition also differed significantly among pre-disturbance, current, and future regeneration based communities, indicating continued composition shifts following disturbance.

These results suggest that post-disturbance regeneration dynamics may influence future forest composition depending on pre-disturbance species composition and species-specific life-history traits. Engelmann spruce is projected to persist on the landscape, albeit at lower densities and often with greater aspen presence. These findings indicate that disturbance history, regeneration dynamics, and management decisions interact to influence long-term forest composition, emphasizing the need to integrate adaptation strategies with long-term monitoring to support resilience in high-elevation subalpine ecosystems.

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1.1 Introduction

Bark beetles outbreaks are affecting millions of hectares globally (Canelles et al., 2021, van Lierop et al., 2015, Jaime et al., 2024). Bark beetle outbreaks are causing unprecedented tree mortality that disrupts ecosystem services, threatens forest resilience, and challenges managers to balance economic recovery with long-term forest health issues (Canelles et al., 2021, van Lierop et al., 2015). Insects are among the most important biotic disturbance agents in forests globally, and in North America bark beetles are responsible for extensive tree mortality across millions of hectares, particularly in western conifer forests (Fettig et al., 2022). The widespread mortality of conifer trees has led managers to seek strategies to extract economic value out of dead or beetle-affected trees (Mattson et al., 2019). At the same time, many managers desire to improve ecological outcomes, before, during and after outbreaks, including reducing fire hazard and promoting tree regeneration (DeRose and Long, 2010). Moreover, bark beetles operate across jurisdictional lines, altering stand structure, tree size class distribution, composition, and successional dynamics (Jaimie et al., 2024). These ecosystem-level shifts directly influence forest resistance and resilience to subsequent disturbances (Johnstone et al., 2016). Here we define resistance as a forest's ability to remain relatively unchanged after disturbances, whereas resilience refers to the capacity of a forest to recover and maintain essential functions and structure (Derose and Long 2014). As changing climatic conditions impact forest resistance and resilience there is a growing concern about post-disturbance recovery across the Rocky Mountains.

In the southern Rocky Mountains, native bark beetles (*Dendroctonus*) represent a natural disturbance regime that has historically regulated stand dynamics and succession in forested stands (Temperli et al., 2014) at endemic levels. However, recently beetle outbreaks have increased in severity, resulting in landscape wide changes in composition and structure (Bentz et al., 2010, Raffa et al., 2008). In subalpine forests, these beetles primarily effect Engelmann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*). Recent warming has increased the extent of outbreaks (Howe et al., 2024).

Subalpine forests in the Rocky Mountains, dominated by Engelmann spruce and subalpine fir (*Abies lasiocarpa*), with a smaller component of lodgepole and aspen (*Populus tremuloides*) trees in some areas span from southern Canada to New Mexico, and are typically at the highest forested elevations. Insect outbreaks occur with varying intensity in the subalpine forests, estimated to have affected over 270,000 hectares in the San Juan Mountains of Colorado (Andrus et al., 2020), with over >85% overstory mortality in subalpine stands (Deroose and Long 2014, Dymerski et al., 2001, Temperli et al., 2014). Spruce beetles (*Dendroctonus rufipennis*) most often target large-diameter, stressed Engelmann spruce trees (Hart et al., 2014), but can infest trees as small as 5 cm in diameter at breast height (DBH) during outbreak populations (Windmuller-Campione and Long 2015). Warming temperatures and drought have fueled beetle population increases throughout Colorado (Andrus et al., 2021) and have caused concern about forest recovery in the area. Although the spruce beetles are a natural part of the ecosystem, epidemic populations can have cascading effects on various parts of the ecosystem from regeneration to stand vulnerability to future disturbances (Jenkins et al., 2014; Windmuller-

Campione and Long 2015). These beetle outbreaks raise critical questions about which management strategies can best support long-term resilience.

Understanding the role of advanced regeneration is key to evaluating how subalpine forests can recover structurally after disturbance. Field studies across the southern Rocky Mountains suggest that advanced regeneration can accelerate structural recovery in subalpine forests by providing an existing cohort of seedlings and saplings that persist through disturbance and contribute to stand reestablishment (Rodman et al., 2021; Schapira et al., 2021; Hart et al., 2014; Temperli et al., 2014). These studies suggest that recovery may also be supported by the release of surviving understory trees following overstory mortality. However, recovery trajectories likely vary across the southern Rocky Mountains because regional differences in climate, disturbance severity, and tree growth rates can influence post-disturbance stand development (Hill et al., 2019). Site-specific studies are therefore needed to better understand these recovery processes and inform effective management.

Forest management in subalpine spruce-fir forests is variable. For example, silvicultural strategies like group selection and shelterwood can create canopy openings that help promote regeneration while retaining mature spruce as a seed source. However, Engelmann spruce regeneration is often slow to establish and microsite-dependent (Hill et al., 2019, Long et al., 2018), making management outcomes less predictable. In mixed-species stands, management must also account for the recruitment and persistence of co-occurring species such as subalpine fir and aspen, which contribute to stand diversity, resilience, and ecological function (Gill et al., 2017). In addition to promoting regeneration,

stand diversity, and stand composition, treatments also need to address stand conditions that influence beetle susceptibility. Since high densities of mature spruce increase infestation risk, treatments must balance the recruitment of new cohorts while reducing overstory dominance and density. Beyond proactive silvicultural strategies, post-disturbance salvage logging is a common management practice used to recover economic value from dead timber following beetle outbreaks. However, it can significantly alter forest structure, increase surface fuels, and modify understory microclimates by increasing solar radiation, which may influence natural spruce regeneration (Mattson et al., 2019; Temperli et al., 2014).

By altering stand structure, regeneration, and species composition, silvicultural treatments can influence post-disturbance recovery. These management legacies are particularly important in stands that contain aspen (*Populus tremuloides*), where recovery trajectories may differ from spruce-dominated forests (Davis et al., 2022). Aspen introduces additional uncertainty due to their vulnerability to sudden aspen decline and climate sensitivity, both of which complicate projections of future forest composition (Andrus et al., 2021, Rodman et al., 2022). However, greater tree species diversity can help reduce future susceptibility to epidemic level beetle outbreaks by limiting host availability (Roman et al., 2022; Conner et al., 2014). This may lead to a forest structure that differs from historical species dominance patterns, potentially increasing the relative abundance or persistence of aspen in areas previously dominated by spruce (Davis et al., 2022; Morris et al., 2021; Rodman et al., 2022). Because forest composition influences host availability

and tree stress, it also plays an important role in shaping the frequency and severity of spruce beetle outbreaks.

Tree vigor and forest composition strongly influence the frequency and intensity of spruce beetle outbreaks. Drought stress and high stand density increase host susceptibility and weaken defenses by creating conditions that favor beetle success (Windmuller-Campione and Long 2015, Bentz et al., 2010). In contrast, broader climate trends such as rising temperatures exacerbate tree stress across landscapes, intensifying outbreak frequency and severity (Hart et al., 2014). When outbreaks coincide with drought-stressed, mature spruce stands, widespread mortality can occur (Temperli et al., 2015; Rodman et al., 2021). As a result, the risk of higher temperatures, alongside changes in drought stress such as vapor pressure deficit (VPD) is likely to further decrease tree defenses (Hart et al., 2014). Openings created by bark beetle outbreaks will create space for non-host species like aspen and subalpine fir to establish dominance, thereby altering long-term forest composition (Temperli et al., 2015; Rodman et al., 2022; Hart et al., 2014). Over time, reduced host availability has been shown to lower the likelihood of future outbreaks (Conner et al., 2014). Forest composition and structure can influence outbreak dynamics, with stands containing greater aspen presence showing increased resistance and resilience due to increased species heterogeneity and reduced host continuity (Temperli et al., 2014; Davis et al., 2022, Rodman et al., 2021 Conner et al., 2014).

The scale and complexity of beetle-induced mortality highlight the importance of proactive management approaches to support long-term ecosystem stability. As spruce beetle outbreaks intersect with changing climatic conditions and other disturbances, it

becomes increasingly important to understand how management actions shape forest resilience. Specifically, we asked three questions: (1) How do different species (e.g., Engelmann spruce, aspen) respond to treatments under varying climate conditions? (2) Under different climate scenarios, will spruce recruitment be sufficient to maintain forest structural composition, or will other species (e.g., aspen) become dominant? (3) How do treatments affect forest structure, and how do these treatments promote long-term resilience to future disturbances (e.g., fire, drought, secondary insect outbreaks)? To evaluate these questions, we analyzed 44 repeatedly measured plots, and 66 additional inventory plots in south central Colorado and projected future stand trajectories using the Forest Vegetation Simulator (FVS). We evaluated changes in forest structure, species composition, mortality, and regeneration to assess how legacy effects of spruce beetle outbreak shape long-term resilience under different climate scenarios. We specifically assessed whether post-outbreak conditions favor spruce recovery or contribute to compositional shifts towards species such as quaking aspen.

1.2 Methods

1.2.1 Study Area

Subalpine forests in the Rocky Mountains span from southern Canada to New Mexico, typically between 2,700 and 3,700 meters in elevation at the lower latitudes. This ecosystem represents the highest-elevation forest type in the Rocky Mountains and are dominated by Engelmann spruce and subalpine fir, though lodgepole, and aspen trees can also occur in some stands. Subalpine forests are notable for their deep snowpacks and

their cool summer temperatures. Moisture accumulation occurs primarily in winter in the form of snowpack, which can persist into late summer (Bowling et al., 2018).

The sampling area consisted of three study areas located within the Grand Mesa, Uncompahgre, and Gunnison (GMUG) national forests in western Colorado, USA. One study area categorized as “post-beetle” plots are located in the La Garita Mountains east of Lake City (38.0300° N, 107.3153° W; Figure 1), while a second and third areas are categorized as “pre-beetle” plots are located within the West Elk Mountains, North-West of Gunnison, CO (38.5458° N, 106.9253° W and 38.630334° N, -107.178157° W). Epidemic beetle outbreaks began in 2009 and originated in the San Juan Mountains, spreading to the GMUG (Colorado State Forest Service, 2022).

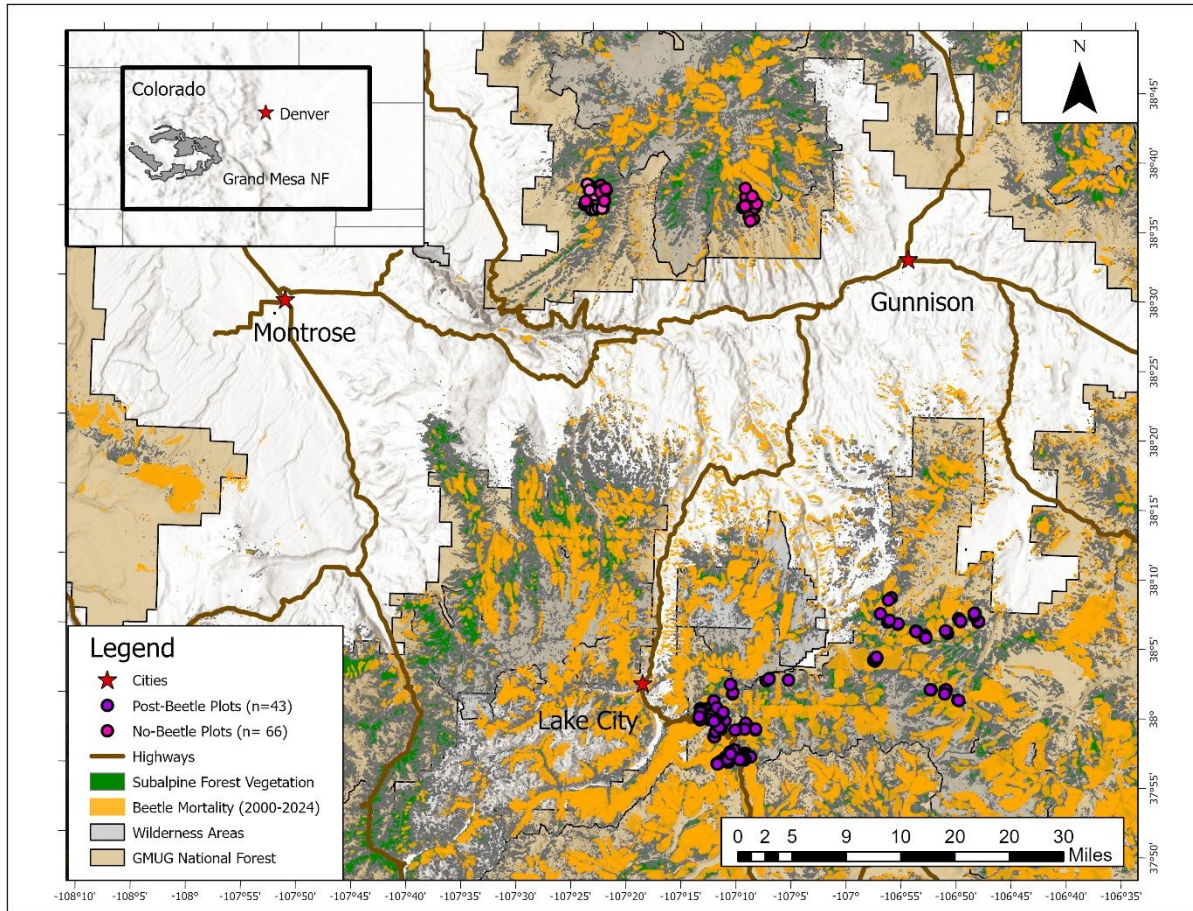


Figure 1: Map of plot locations with the Grand Mesa, Uncompahgre, and Gunnison National Forests in Colorado, USA. Map of spruce-fir vegetation layer (green) with spruce beetle outbreak extent (orange).

1.2.2 Site Establishment

Plots were established over a range of management histories and disturbance conditions to capture variability in forest structure and composition. Post-beetle plots were located in areas that were (1) previously managed, (2) unmanaged, or (3) salvaged. Pre-

beetle plots were located in areas not impacted by beetle and served as the no-beetle-presence untreated plots. Plots were further divided into Engelmann spruce dominated and spruce/aspen mixed. Managed areas were treated in the 1980s and 1990s using 2-3 step shelterwood cuts, in which only the first prep/establishment cut was completed (Davis et al., 2022). Unmanaged plots were in the La Garita Wilderness and had no known historical management. Salvage logging was conducted within the La Garita Mountain area following spruce beetle impacts and occurred from 2014 to 2018. Salvage logging operations removed dead spruce trees that were over 20 cm diameter at breast height (DBH); live trees were not logged. However, in areas of high public activity, all trees were removed regardless of size class and living versus dead; this comprised approximately 2 out of 44 of the sites (Mattson et al., 2019; Davis et al., 2022).

Plots were stratified by forest type using GIS Vegetation layers from the U.S. Forest Service (USFS) and GMUG. They were then field verified to match the relative abundance thresholds which were designated as Engelmann spruce-dominated plots where at least 75% of the basal area (BA; $\text{m}^2 \text{ha}^{-1}$) was spruce, and aspen/spruce stands were required to have a relative abundance between 5% and 75% of both species by basal area. All pre-outbreaks sites were designated as spruce dominated as there were too few plots that had aspen presence. Post-beetle plots were permanently installed and monitored from 2015-2019 and were remeasured in 2018 and 2023. Non-beetle plots were permanently installed from 2020-2024.

1.2.3 Field Sampling Methods

Plots were 0.05 ha where forest structure and composition were measured. Elevation, slope, aspect, slope position and GPS coordinates were recorded. In each plot, species, DBH (1.37 m) and status were recorded. Overstory trees were classified as 12.7 cm DBH or greater, while saplings were classified as trees that were <12.6 cm DBH and while also being ≥ 1.37 m in height. Saplings were classified into diameter classes (0.1 - 2.4, 2.5 – 4.9, 5 – 9.9, and 10 - 12.6 cm). Tree status was recorded using numeric codes. Status 1 indicated live trees, status 2 represented trees with immediate beetle presence. Statuses 3–5 were classified as snags and further differentiated by decay stage: status 3 indicated recently dead trees (gray stage with fine branches present), status 4 indicated long-dead trees (loose bark with no fine branches), and status 5 indicated downed trees resulting from recent beetle-caused mortality (spruce only). To determine beetle infestation on individual trees, field staff were trained to identify beetle-caused mortality agents such as pitch tubes, frass, beetle hole, or gallery presence. Trees smaller than 1.37m were classified as seedlings and divided further by height. Height classes were 0.1-9.9, 10-19.9, 20-49.9, and ≥ 50 cm. Seedling density counts, species, height classes, and status were recorded for all seedling trees. Furthermore, seedling density for post-beetle plots were sampled in the North-East and South-West quadrants of each 0.05 ha plot, while pre-beetle plots used five 1/250th ha subplots for each plot located at plot center, and at 6 m North, South, East, and West. Survival and growth data was also collected at post-beetle sites. A subset of ten individuals from each seedling size class (see above) were randomly chosen, tagged with numbered aluminum tags secured to the ground on the

north side of each seedling using landscape staples, and measured for initial height and basal diameter. Overstory and sapling trees were tagged and DBH, species, and height were tracked. From 2016- 2023, individual tree status was recorded as live, dead, or missing, while height and diameter were remeasured. Pre-beetle structure of these beetle impacted stands was recreated using status collected in the field in order to reconstruct stands. For pre-beetle reconstruction, statuses 1–3 and 5 were treated as live, while status 4 was assumed to represent pre-outbreak mortality.

1.2.4 Statistical Analysis

Due to the variability in forest structure and treatment types within the study area, sites were separated first by beetle presence, then habitat type (spruce-dominated and spruce/aspen-dominated), then treatment type. All analyses were conducted in RStudio (4.5.2, 2025) and tested at an $\alpha=0.05$ level. Sample sizes varied by treatment type and location. Due to expansive beetle damage, no-beetle control sites were added from the west elk range as this mountain range has similar overall composition and structure to the sites that were located near Lake City. Pre-beetle data was reconstructed to pre-outbreak forest structure to simulate post-outbreak forest structure using a repeated measures two-way analysis of variance on overstory trees.

Table 1: Sample size for analyses.

Post-Beetle Analysis		
Treatment Type	Forest Type	Plots
Unmanaged	spruce	5
	spruce/aspen	6
Previously Managed	spruce	10

	spruce/aspen	8
Salvaged	spruce	9
	spruce/aspen	6
No-Beetle Control (No recent management)	spruce	66

Pre-beetle Analysis		
Treatment Type	Forest Type	Plots
Unmanaged	spruce	43
	spruce/aspen	9
Previously Managed	spruce	35
	spruce/aspen	17

1.2.5 Field Based Data Analysis

1.2.5.1 Overstory Structure: Live vs. Dead Trees

To evaluate the differences in forest structure between beetle-impacted and non-beetle impacted areas, we summarized live and dead tree basal area and trees per hectare (TPH) for each forest type and treatment for overstory (DBH >12.7cm) and sapling trees (Height >137cm and DBH >12.7 cm). Tree-level measurements were aggregated to the plot level using plot-specific expansion factors, and mean BA and TPH were calculated across plots within each treatment. Analyses focused on current field data and were used to characterize structural differences associated with the mortality and management history. Differences in overstory and sapling BA and TPH between live and dead trees were further evaluated using linear models and analysis of variance (ANOVA), with tree status, treatment, and their interaction included as predictors. To further evaluate structural differences, treatments were grouped into beetle-impacted and non-beetle impacted categories to assess if disturbance history were associated in differences in live vs. dead

trees. Two-way ANOVAs were conducted for overstory and saplings to test the effects of beetle history, tree status, and their interaction on TPH and BA.

1.2.5.2 Climate Drivers of Regeneration (Vapor Pressure Deficit)

To address how climate variables affect regeneration, we used vapor pressure deficit (VPD) data obtained from PRISM Climate Group gridded climate dataset, which provided spatially interpolated climate estimates at approximately 4-km resolution across the United States. Climate variables including precipitation, temperature (minimum, average, and maximum), VPD (minimum and maximum) were extracted for each study site and summarized across growing season (May-September) for each year from 2016-2023. Mean growing season VPD was then joined to annual seedling post-beetle monitoring data by plot and year. To quantify incoming regeneration, seedlings in height class 1 were summed by plot, year, species, treatment, and habitat. Seedling density was expressed as $\log(\text{count} + 1)$. We used a linear mixed-effects model (Bates et al., 2015) to test the effects of species, treatment, habitat, year, and growing season VPD on seedling density, with plot included as a random intercept to account for repeated annual measurements. Fixed effects included species, treatment, habitat, year, and VPD, with species x VPD interactions included to evaluate species-specific climatic responses. Separate species-level models were also fit for Engelmann spruce and quaking aspen to further assess species-specific responses to atmospheric moisture demand.

1.2.5.3 Changes in Height Class Regeneration Structure

For the beetle-impacted plots, plot-level changes in regeneration between 2018 and 2023 were summarized for each species, treatment, and height class. Seedling counts were tallied for every plot in both years, and counts were converted to TPH using the 1/40-ha subplot expansion factor. We then modeled changes in regeneration density (Δ TPH) using a linear mixed-effects model, with Species, Height Class, and Habitat as fixed effects and Plot ID included as a random intercept. Models were fit by restricted maximum likelihood (REML), and significance of fixed effects was evaluated using Satterthwaite's approximation for degrees of freedom.

1.2.6 FVS Analysis

1.2.6.1 Forest Vegetation Simulator Methods and Parameters

The Central Rockies Variant of the Forest Service Vegetation Simulator (FVS), version FS25025.2, was used as a deterministic growth and yield model that simulates growth, mortality, and other processes involved in stand development (Dixon, 2002; Keyser & Dixon, 2008). FVS was used to project future stand trajectories following spruce beetle outbreak and evaluate potential changes in forest structure and species composition over time. All simulations were conducted using the FVS Complete software package (April 2025 version). For use in FVS, tree and stand lists were developed using no-beetle and post-beetle outbreak field measurements of trees, saplings, and seedlings (see Field Sampling Methods). Stands were assigned a forest type code 205 corresponding to spruce-fir model type (type 4) on the Gunnison National Forest. FVS was used to estimate tree

height, crown length, and crown ratio. No automatic growth calibration was applied because no increment records were available for scaling in the FVS application statistics output. All recently dead and beetle affected trees were labeled as status code “6”, while live trees received a status code of “1”. Seedlings were assigned a diameter of 0.1, and a median height based on field height classes (See Field Sampling Methods). To account for difference in regeneration plot sizes, trees, saplings, and seedlings were scaled to individual tree records to a density acre^{-1} . FVS simulations were run in imperial units and converted to metric units where appropriate for reporting in R. Regeneration during simulation was represented by these measured seedlings included in the input tree lists, and no additional regeneration events were added during simulations. This assumes that future stand development is driven by survival and growth of the established regeneration cohort and does not account for subsequent recruitment. Due to different measurement years, all stands were ran through FVS from the year of post-outbreak field surveys, to a common starting year of 2025 using an initial three-year cycle, after which projections were conducted in 10-year time steps.

To constrain model behavior, species-specific upper diameter limits were applied based on maximum observed tree sizes in the dataset. For aspen, DBH was limited to 63.5 cm (Perala, 1990; Silvics of North America). For Engelmann spruce and subalpine fir, DBH was limited to 83.8 cm, which is slightly above the maximum observed diameter in the dataset (83.0 cm for subalpine fir and 80.1 cm for Engelmann spruce). These thresholds ensure inclusion of all measured trees, while excluding rare, exceptional individuals that could exert disproportionate influence on model results. Although individual Engelmann

spruce and subalpine fir may occasionally exceed these diameters elsewhere in the species' ranges (Alexander, 1990; Alexander & Shepperd 1984), such sizes were not observed in this dataset. Therefore, diameter limits were treated as site-specific modeling parameters.

Projected stand outputs were summarized at 10-year intervals to quantify changes in live basal area ($\text{m}^2 \text{ha}^{-1}$), live tree density (trees ha^{-1}), and species composition over time. To evaluate differences in projected stand trajectories among treatments and species, live basal area and tree density were analyzed using factorial analysis of variance (ANOVA), with treatment and species as fixed effects. Species composition trajectories were evaluated to assess projected shifts in stand dominance and recovery patterns across unmanaged, previously managed, salvaged, and no-beetle controls.

1.2.7 Community Composition Analyses

1.2.7.1 Pre-Disturbance, Current, and Regeneration-based Future Composition

Comparisons

To test differences pre-disturbance, current, and regeneration-based future species compositions, species percentages were calculated for overstory trees in reconstructed pre-beetle plots and current post-beetle plots (i.e. only plots in the La Garita area), and compared these to current regeneration percentages as a proxy for future forest composition. Composition was summarized by treatment to evaluate whether management history influenced compositional trajectories among unmanaged, previously managed, salvage, and no-beetle reference stands. For beetle-affected plots, pre-beetle

conditions represented reconstructed overstory structure, post-beetle conditions represented current live overstory structure, and future conditions were represented by current regeneration. For No-beetle reference plots, current overstory represented current compositions stages and regeneration represented future stages.

Differences among states and treatments were evaluated using permutational multivariate analysis of variance (PERMANOVA; *adonis2*, *vegan*). Bray–Curtis dissimilarity was used as the ecological distance metric, and significance was assessed using 999 permutations:

Community ~ Stage.

Pairwise PERMANOVA comparisons were then used to identify which stand stage transitions (PRE–POST, PRE–FUT, POST–FUT) differed significantly.

1.2.7.2 NMDS Ordination

To visualize multivariate differences in species composition among stages and habitats, we performed a non-metric multidimensional scaling (NMDS) ordination using Bray–Curtis dissimilarities (*metaMDS*, *vegan*). NMDS was run in two dimensions ($k = 2$) with 200 random starts to ensure a stable solution. Site scores from the ordination were plotted by Stage and faceted by Habitat to assess whether community trajectories differed among forest types and to complement the PERMANOVA results with a visual representation of compositional patterns.

1.3 Results

1.3.1 Current Forest Structure and Regeneration Responses

1.3.1.1 Overstory and Sapling Structure

To better understand the overstory ($\text{DBH} \geq 12.7 \text{ cm}$) and sapling ($\text{height} > 137 \text{ cm}$ and $\text{DBH} \leq 12.6 \text{ cm}$) structure, we compared live and dead basal area (BA) and tree density (TPH) across treatments (Table 2). Overstory tree density differed significantly among treatments ($F=16.15, p < 0.01$) and between live and dead trees ($F= 81.42, p < 0.01$). with live and dead differences varying across treatments ($F= 53.98, p < 0.01$). Post-hoc comparisons showed that no-beetle stands had significantly higher live overstory TPH than all beetle-affected treatments. Dead overstory TPH was significantly higher in unmanaged and previously managed treatments than in no-beetle and salvage treatments.

Overstory basal area also differed significantly among treatments ($F = 63.73, p < 0.01$) and between live and dead trees ($F = 178.82, p < 0.01$), with live and dead differences varying by treatment ($F = 96.50, p < 0.01$). Post-hoc comparisons showed that live overstory BA was highest in no-beetle stands, while dead overstory BA was highest in unmanaged and previously managed treatments. Salvage treatments had the lowest live and dead overstory BA overall.

Sapling tree densities differed significantly among treatments ($F= 15.24, p < 0.01$) and between live and dead saplings ($F = 68.75, p < 0.01$), with live and dead differences varying across treatments ($F = 9.63, p < 0.01$). Post-hoc comparisons indicated that live

sapling densities were higher in all post-beetle stands compared to no-beetle stands. Dead sapling TPH showed less separation among treatments.

For sapling trees, BA differed significantly among treatments ($F= 14.21, p < 0.01$) and between live and dead trees ($F= 61.47, p < 0.01$), with live and dead BA differences varying by treatment ($F= 4.98, p < 0.01$). Post-hoc comparisons indicated that live sapling BA was significantly higher previously managed treatments than in other treatment groups, while dead sapling BA showed substantial overlap among treatments. Overall, sapling structural differences were present across treatments but were less pronounced than overstory patterns.

Table 2. Forest metrics for overstory trees (≥ 12.7 cm DBH) and saplings (0.1- 12.6 cm DBH) for all stands. Treatment include beetle-impacted unmanaged, previously managed, salvaged, and no-beetle areas. Letters denote post-hoc Tukey groupings among treatments within each canopy and live/dead status group.

		Forest Metrics			
CANOPY	Treatment	Live TPH	Dead TPH	Live BA (m ² /ha)	Dead BA (m ² /ha)
Overstory	No beetle	566 $\pm$ 25 a	149 $\pm$ 15 b	24.472 $\pm$ 0.782 c	5.82 $\pm$ 0.576 a
Overstory	Previously managed	230 $\pm$ 35 b	391 $\pm$ 40 a	3.968 $\pm$ 0.792 a	11.381 $\pm$ 1.501 b
Overstory	Salvage	137 $\pm$ 31 b	121 $\pm$ 17 b	2.368 $\pm$ 0.599 a	1.699 $\pm$ 0.276 a
Overstory	Unmanaged	235 $\pm$ 34 b	524 $\pm$ 85 a	3.879 $\pm$ 0.722 a	12.276 $\pm$ 2.085 b
Sapling	No beetle	649 $\pm$ 74 b	124 $\pm$ 15 c	0.096 $\pm$ 0.011 a	0.026 $\pm$ 0.003 c
Sapling	Previously managed	2336 $\pm$ 341 a	408 $\pm$ 67 a	0.19 $\pm$ 0.017 b	0.072 $\pm$ 0.014 ac

Sapling	Salvage	2377 ± 744 a	180 ± 37 bc	0.054 ± 0.011 ac	0.043 ± 0.008 ac
Sapling	Unmanaged	1858 ± 412 a	367 ± 100 ab	0.102 ± 0.017 a	0.079 ± 0.021 ac

1.3.1.2 Regeneration Density and Change in Spruce Beetle Impacted Stands

Analysis in seedling density change from 2018 to 2023 indicated no significant effects of treatment or species, density (Type III ANOVA; treatment: $X^2 = 3.10$, $p = 0.21$; species ($X^2 = 0.78$, $p = 0.68$) and the treatment $\times$ species interaction was also not significant ($X^2 = 3.55$, $p = 0.47$). Pairwise comparisons among treatments within species similarly showed no significant differences in regeneration density (Appendix A). These results suggest that overall regeneration density was highly variable across plots and did not differ strongly among treatments. However, total regeneration density alone did not capture differences in regeneration dynamics among species and regeneration size classes.

Regeneration change (Δ TPH) was tested to evaluate whether treatments altered species-level regeneration patterns across height classes (Figure 2). Regeneration differed significantly among species ($F = 20.26$, $p < 0.01$) and among seedling height classes ($F = 7.55$, $p < 0.01$), while treatment did not have a significant main effect ($F = 0.55$, $p = 0.58$). However, the species $\times$ height class $\times$ treatment interaction was significant ($F = 1.95$, $p = 0.03$), indicating that regeneration responses varied among species and size classes across treatments. Across all treatments, Class 1 (0.1- 9.9 cm) spruce regeneration generally declined, while larger spruce size classes often increased, particularly in unmanaged stands, suggesting recruitment into taller size classes, especially Classes 3 (20-49.9 cm)

and 4 (>50 cm) with the largest increases occurring in unmanaged and salvaged stands. Aspen exhibited the strongest increases in regeneration, particularly within Classes 3 and 4, with several unmanaged and salvaged contrasts showing significant positive increases. For subalpine fir, regeneration changes were more variable, with smaller increases and decreases across height classes and treatments. Although many observed changes were not statistically significant, overall patterns indicated species-specific differences in recruitment dynamics. Habitat-specific analyses showed similar overall regeneration patterns, although aspen increases were more pronounced in spruce-aspen dominated stands, particularly within larger regeneration size classes (Appendix B).

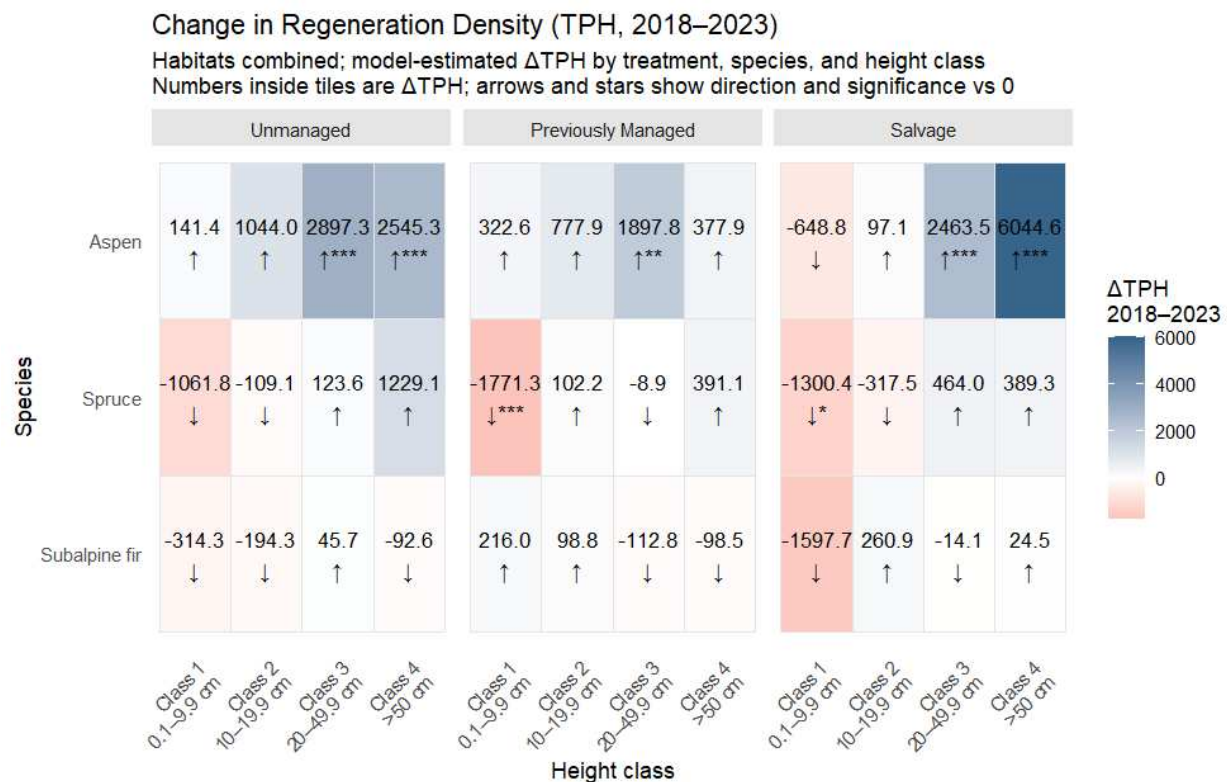


Figure 2: Change in regeneration density (Δ TPH) between 2018 and 2023 across species and treatments by seedling height class. Tiles show measured changes in TPH, where blue

indicates increases and red indicates decreases in regeneration density. Arrows indicated direction of change and asterisk denote significance.

1.3.1.3 Climate Effects on Regeneration Establishment

To evaluate how VPD influenced recent regeneration patterns, seedling density was modeled as a function of VPD, species, year, treatment, and habitat (Figure 3). The mixed-effects model explained a moderate proportion of the variation in seedling density (marginal $R^2 = 0.14$, conditional $R^2 = 0.70$), with Engelmann spruce maintaining higher seedling densities than aspen. Vapor pressure deficit also did not have significant effect on seedling density ($\chi^2 = 2.20$, $p = 0.14$), and no significant differences were detected among treatments ($\chi^2 = 0.06$, $p = 0.97$) or habitats ($\chi^2 = 1.25$, $p = 0.26$). However, a significant species x VPD interaction ($\chi^2 = 6.87$, $p < 0.01$) indicated that the relationship between VPD and seedling density differed between spruce and aspen.

Across the study period, spruce and aspen exhibited contrasting responses to with increasing VPD (Figure 3). Spruce Class 1 seedling density showed a generally positive relationship with increasing VPD, whereas aspen Class 1 seedling density declined with increasing VPD. Because this analysis was limited to the smallest seedling size, these patterns likely reflect differences in new seedling establishment rather than overall regeneration success. In contrast, aspen showed strong increases in larger height classes (Figure 2), suggesting that although new establishment may be limited under higher atmospheric moisture demand, established aspen regeneration continued to grow into taller size classes.

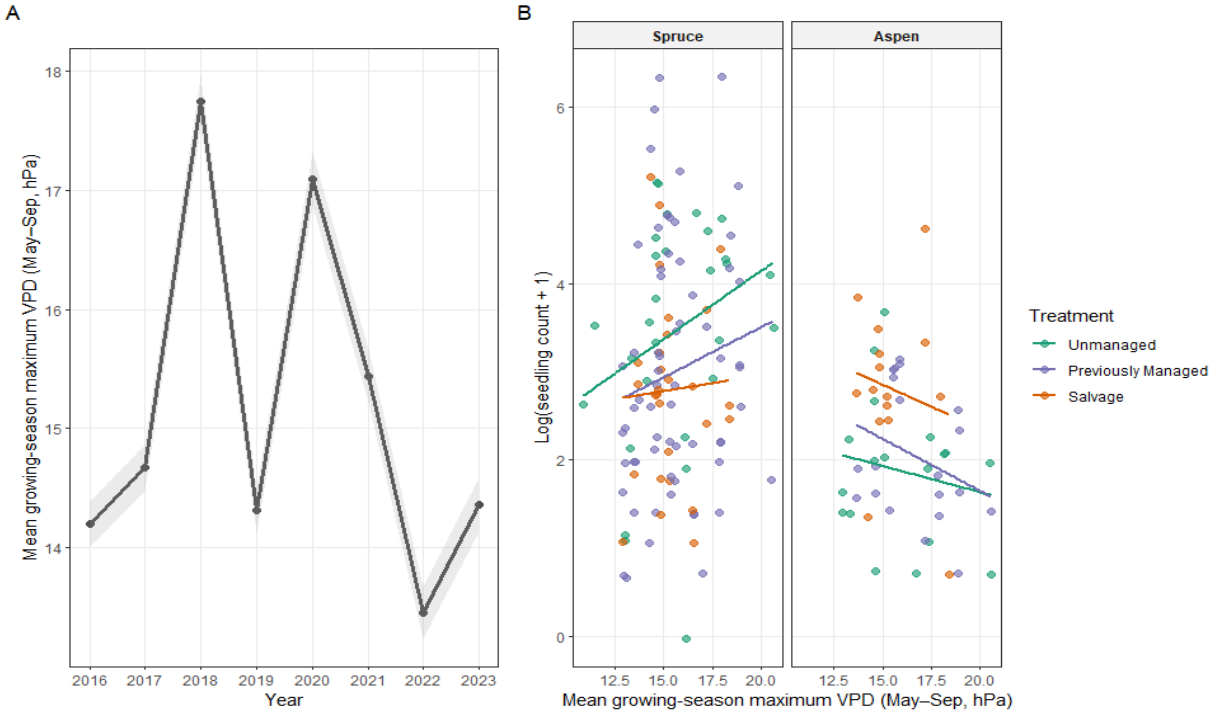


Figure 3. Relationship between summer (May through September) vapor pressure deficit (VPD) and log transformed seedling density from 2016-2023 by habitat type. Seedlings density reflects height class 1 (0.1 to 9.9 cm) Engelmann spruce and aspen with values derived from plot-level summaries.

1.3.2 Modeled Future Forest Dynamics and Species Trajectories

1.3.2.1 Simulated Stand Tree Density

To evaluate potential overstory responses to spruce beetle outbreak, we analyzed FVS-simulated tree density trajectories from 2025 to 2125 across species, and treatment groups (Figure 4). Modeled overstory tree density differed significantly among treatment groups ($F = 57.3$, $p < 0.01$), and among species ($F = 87.09$, $p < 0.01$), indicating there are strong differences in projected tree density across disturbance histories and species. A

significant treatment by species interaction was also detected ($F = 33.62$, $p < 0.01$), indicating that projected density trajectories differed among species depending on treatment type.

Tukey HSD-adjusted pairwise comparisons showed that projected spruce densities were significantly higher in beetle-affected compared to no-beetle reference stands (all adjusted $p < 0.001$), while no significant differences were detected among unmanaged, previously managed, and salvage treatments. Aspen exhibited strong increases in larger size classes were also significantly higher in beetle-affected stands relative to no-beetle reference stands, with unmanaged and salvage treatments exhibiting the highest projected densities. Aspen density was significantly lower in previously managed stands compared to unmanaged and salvage treatments (both adjusted ($p < 0.01$)). Subalpine fir densities differed less among treatment groups, with no significant differences between no-beetle and beetle-affected stands.

Modeled overstory tree density exhibited species-specific responses that were more closely associated with beetle disturbance history than with differences among management treatments. Spruce maintained the highest projected densities across all beetle-affected treatments and remained relatively stable over time, indicating that spruce is projected to remain a dominant component of post-outbreak stand structure. Aspen showed the strongest disturbance response of all species, with projected densities dramatically higher in beetle-affected stands than in no-beetle reference stands, particularly in unmanaged and salvage treatments. In contrast, subalpine fir maintained relatively similar projected densities across treatments, suggesting a more limited

response to disturbance history. Minor species such as lodgepole pine, Douglas-fir, and bristlecone pine occurred at lower projected densities and contributed little to overall stand structure. However, lodgepole pine and Douglas-fir showed modest increases over time, suggesting that minor non-host conifers may increase locally following disturbance, although they remained in substantially lower densities than spruce and aspen across all treatment groups.

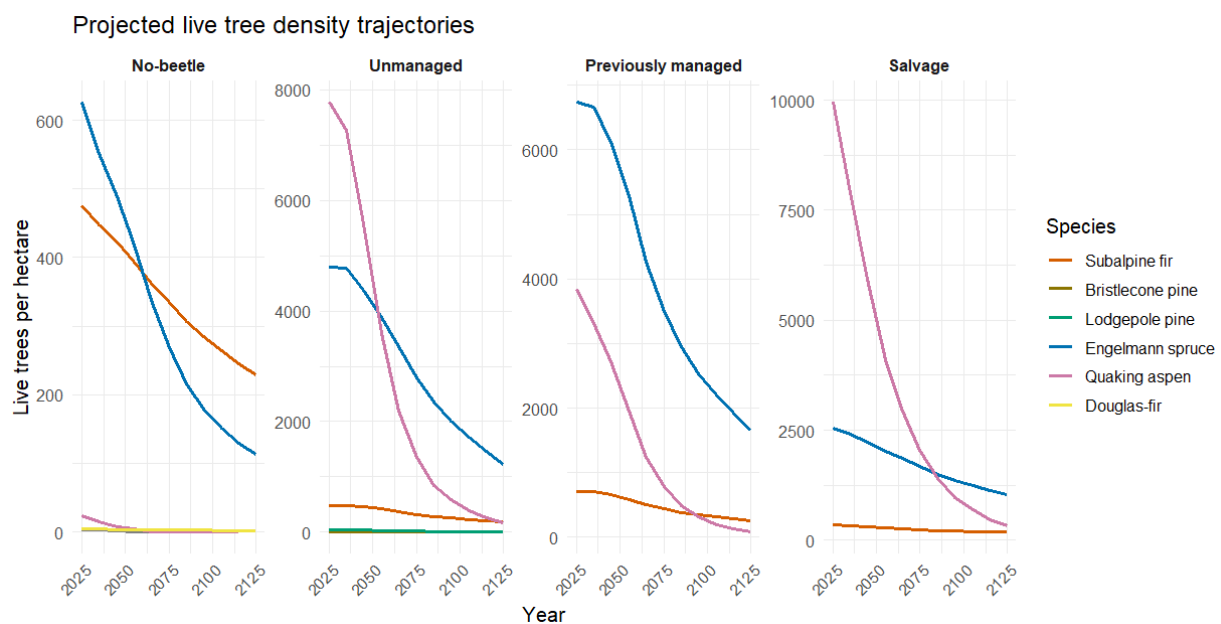


Figure 4. Simulated tree density (TPH) from 2025 to 2125 based on FVS outputs, shown by species and separated by group type (No-beetle, Unmanaged, Previously managed, and Salvage).

1.3.2.2 Simulated Stand Basal Area

To evaluate projected changes in overstory basal area following spruce beetle outbreak, FVS-simulated basal area trajectories from 2025 to 2125 were analyzed across species and treatment groups (Figure 5). Modeled overstory basal area differed

significantly among treatment groups ($F = 10.14$, $p < 0.01$) and among species ($F = 97.74$, $p < 0.01$), with a significant treatment by species interaction ($F = 61.78$, $p < 0.01$), indicating that projected basal area differed among species depending on treatment history. Basal area patterns largely mirrored projected density trends, but differences among treatments were more pronounced. Spruce maintained the highest projected basal area across the treatments, although basal area was significantly lower in salvage treatments compared to no-beetle reference ($p < 0.01$) and previously managed stands ($p < 0.01$). Aspen exhibited higher projected basal area in all beetle-affected areas relative to no-beetle reference stands (all adjusted $p < 0.01$), reflecting greater starting abundance in post-outbreak stands, with highest projected basal area occurring in unmanaged and salvage treatments (both adjusted $p < 0.01$).

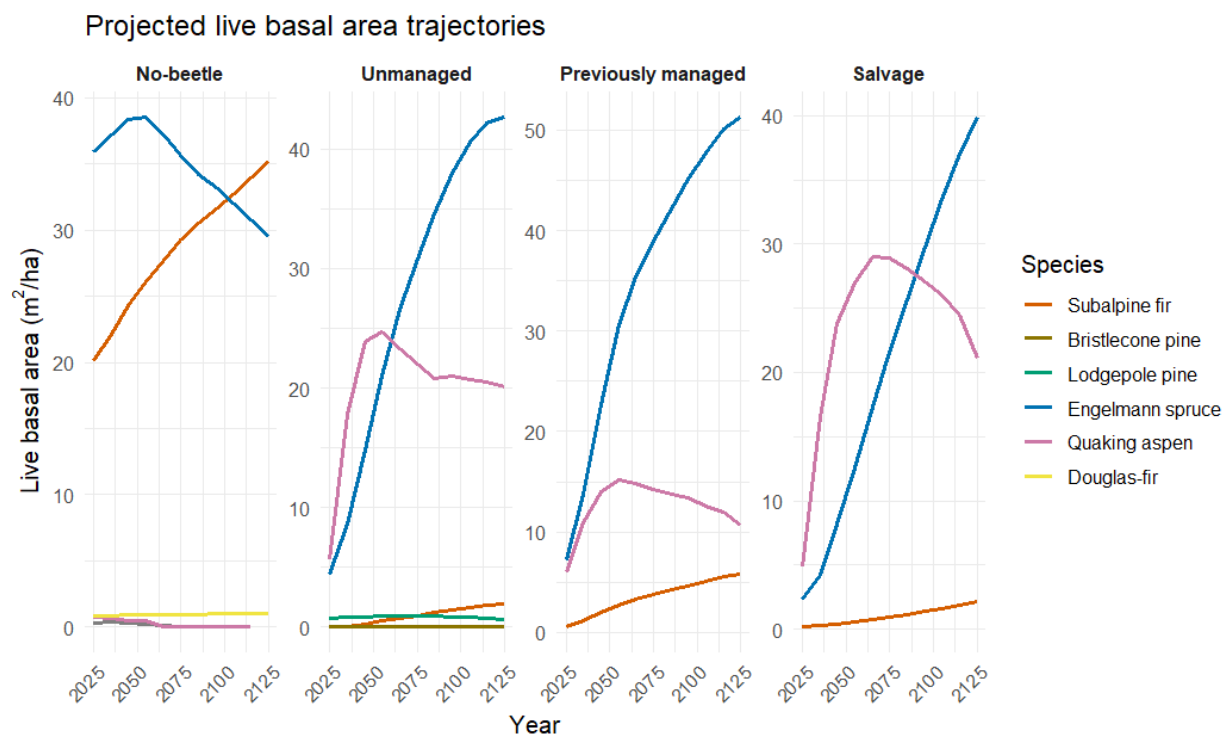


Figure 5. Simulated basal area (BA) from 2025 to 2125 based on FVS outputs, shown by species and separated by group type (No-beetle, Unmanaged, Previously managed, and Salvage).

1.3.3 Treatment Effects on Forest Structure and Long-Term Resilience

Species composition differed significantly among pre-beetle, post-beetle, and future forest conditions (PERMANOVA, Bray-Curtis; $R^2 = 0.32$, $F = 104.70$, $p < 0.01$; Figure 6). Treatment also had a significant effect on species compositions ($R^2 = 0.14$, $p < 0.01$), with a significant state by treatment interaction ($R^2 = 0.07$, $p < 0.01$), indicating that compositional trajectories differed among management histories. Pairwise comparisons indicated that the largest compositional shift occurred between pre-beetle and post-beetle communities ($R^2 = 0.36$, $p < 0.01$), with continued but reduced divergence between post-beetle and future stages ($R^2 = 0.24$, $p < 0.01$). Pre-beetle and future communities also differed significantly, although the magnitude of this difference was smaller ($R^2 = 0.15$, $p < 0.01$).

The treatment-separated trajectories showed distinct differences in projected stand development following beetle outbreak. No-beetle reference stands remained dominated by Engelmann spruce and subalpine fir across stages. In contrast, no-beetle reference stands affected area shifted toward increased aspen abundance between post-beetle and future stages. This shift was strongest in unmanaged and salvage treatments, where future compositions became dominated by aspen relative to Engelmann spruce. Previously managed stands also exhibited increases in aspen abundance, although

Engelmann spruce remained a substantial component of projected future composition. Overall, these results suggest that both beetle disturbance and management history influenced future compositional trajectories, with beetle-affected areas shifting toward greater dominance of non-host species over time.

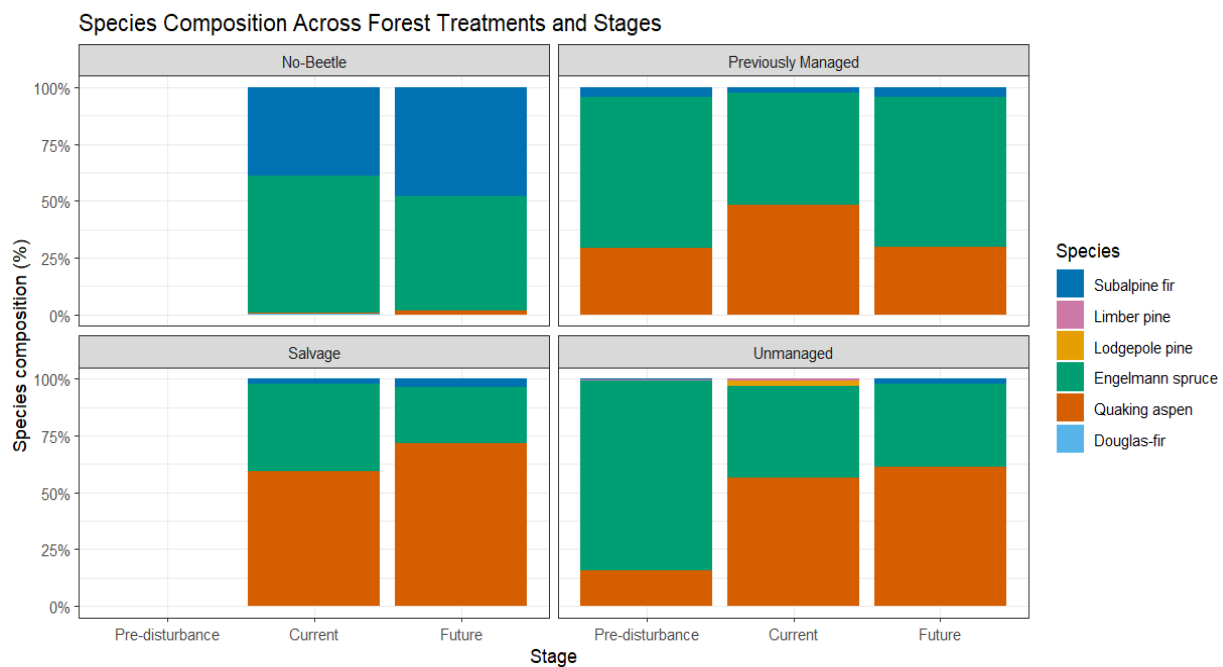


Figure 6. Species composition (%) across pre-disturbance, current, and future regeneration based composition stages by treatment group and no-beetle reference stands. Pre-disturbances composition was reconstructed from field measurements. No-beetle reference stands lacked post-disturbance mortality. Additionally, salvage stands lacked pre-disturbance measurements because sampling occurred after outbreak-related mortality.

1.3.3.1 Treatment Compositional Trajectories by Stage

NMDS ordination illustrated patterns of species compositional differences among pre-disturbance, current, and regeneration-based future stages within each treatment group (Figure 7). Consistent with PERMANOVA results, compositional trajectories differed significantly among stages ($F= 105.50$, $R^2= 0.32$, $p < 0.01$), among treatment groups ($F= 30.71$, $R^2= 0.14$, $p < 0.01$), and across the stage x treatment interaction ($F= 12.14$, $R^2= 0.07$, $p < 0.01$), indicating that compositional trajectories differed among management histories. No-beetle reference stands showed relatively little directional change among stages compared to beetle-affected stands. In unmanaged and salvage stands, current and regeneration-based future communities shifted away from pre-disturbance composition, indicating that future composition differed from historical overstory structure. Previously managed stands also showed compositional shifts among stages, although there was greater overlap among pre-disturbance, current, and future communities. Overall, regeneration-based future communities differed from historical and current overstory composition across treatment groups, indicating shifts in projected stand trajectories following disturbance. Habitat-specific analyses showed overall regeneration patterns, although aspen increases were more pronounced in spruce-aspen dominated stands, particularly within larger regeneration size classes (Appendix C).

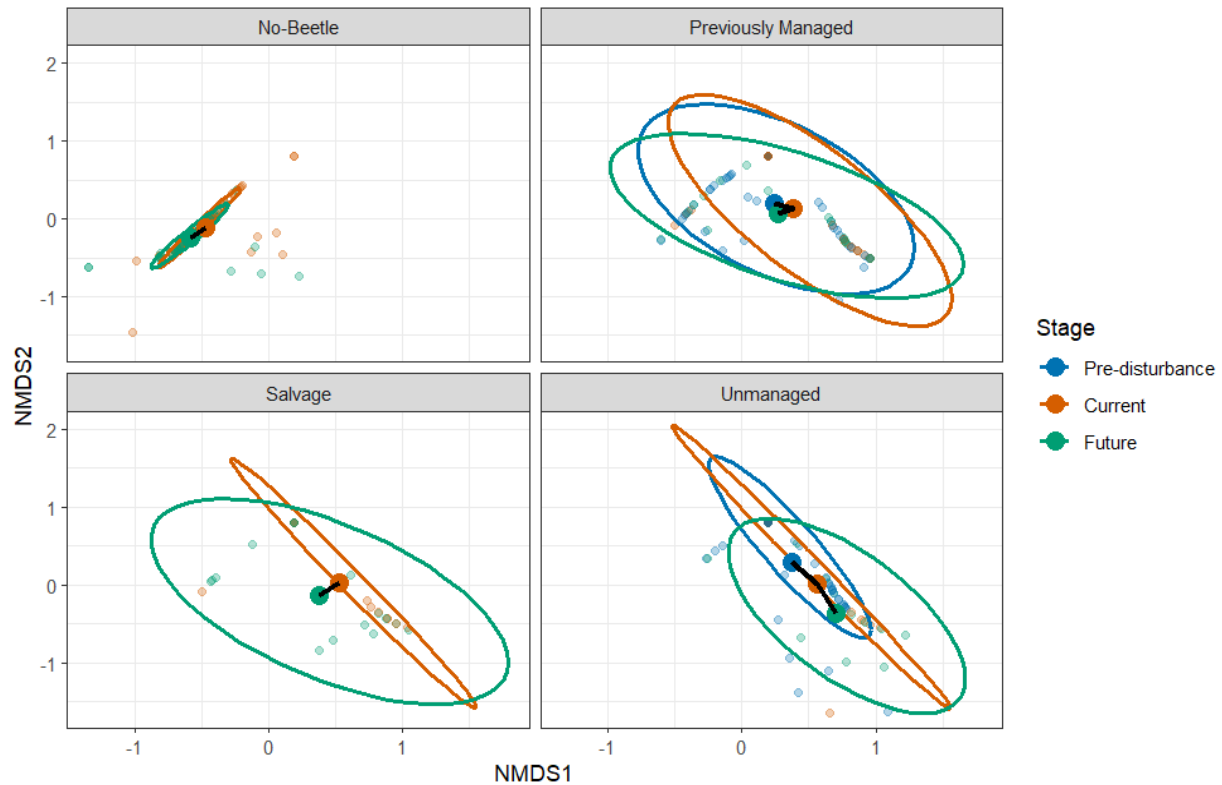


Figure 7. Non-metric multidimensional scaling (NMDS) ordination of species composition across pre-disturbance, current, and future regeneration-based stages by treatment group. Points represent plot-level community composition, ellipses represent stage-level dispersion, and larger points represent stand centroids. Ordination was based on Bray-Curtis dissimilarity.

1.4 Discussion

This study examined the tree species-specific responses to areas with and without bark beetle mortality under different forest management treatment history. We examined

future stand trajectories following disturbance and found that post-disturbance regeneration dynamics may impact future forest composition, depending on both the species present prior to beetle disturbance and species-specific life-history traits. Additionally, we found that climatic variability may further influence seedling establishment, indicating that fine-scale environmental conditions play an important role in early recruitment. Lastly, forest composition is changing, while Engelmann spruce continues to persist on the landscape, although it is at lower densities and often with higher aspen presence. Increased aspen abundance may enhance forest resilience to secondary disturbances such as beetle outbreaks as a non-host species and increase wildfire resilience (Harris et al., 2025).

1.4.1 Tree Species Response

Current forest structure reflects strong legacy effects of disturbance history and management actions, with structural differences more strongly associated with disturbance history than with ongoing treatment (previously managed-beetle, unmanaged-beetle, salvaged-beetle and no-beetle reference) effects. In beetle-affected stands, live overstory BA was lower and dead overstory BA was generally higher relative to no-beetle reference stands, indicating strong legacy effects of spruce beetle mortality on current stand structure.

This suggests that beetle outbreaks continue to strongly influence stand structure and have created forest conditions that differ substantially from areas without outbreak-related mortality (Deroose & Long 2007; Veblen et al., 1991). Additionally, overstory TPH and BA did not differ strongly among beetle-affected treatments groups. However, regeneration

responses suggested that resilience trajectories may still differ among treatments. Because we did not observe differences in TPH or BA among treatments, the question remains as to whether or not these treatments can increase resilience to beetle outbreak. Davis et al. (2022), also found that their sites did not differ significantly among treatments in stand carbon trajectories. Similarly, salvage logged areas in this study had lower live sapling densities to other beetle-affected treatments. Salvage-logged stands do not recover at the same rate as other treatments (Davis et al. 2022; Mattson et al., 2019), which was evident on these sites as live saplings varied strongly among beetle-affected treatments. Sapling density was lowest in salvage sites, indicating that without aspen presence, the existing species may experience compounded effects from both beetle mortality and salvage harvesting (Davis et al., 2022).

Seedling regeneration in post-beetle sites was influenced by pre-disturbance species composition, climatic conditions, and management treatment. Spruce and aspen regenerated at much higher densities than subalpine fir, which differed from regeneration patterns observed in northern Colorado where subalpine fir was more dominant (Schapira et al., 2021; Rodman et al., 2022). These differences may reflect variation in pre-disturbance species composition among our study areas, as many sites in the Slumgullion landscape had very low subalpine fir abundance prior to outbreak. These species-specific regeneration responses are consistent with broader evidence that recruitment patterns reflect interactions between climatic conditions and species life-history traits (Dobrowski et al., 2015). High-severity disturbances such a beetle outbreak and salvage logging, can create canopy opening and increased resource availability that favor shade-intolerant

species such as aspen, facilitating post-disturbance expansion and recruitment (Nigro et al, 2022; Andrus et al., 2021). Because aspen readily regenerates through suckering, it can rapidly occupy disturbed areas following canopy openings (Kulakowski et al., 2013).

Therefore, increased aspen abundance may improve stand resilience to future spruce beetle outbreak because aspen is a non-host species that helps facilitate tree retention on the landscape (Davis et al., 2022), which is consistent with current GMUG management objectives emphasizing adaptive management and ecological resilience under changing disturbance and climate regimes (USDA Forest Service, 2024).

VPD was associated with regeneration density, although relationships varied among species and across years. Previous work in high elevation forests has shown that regeneration dynamics are influenced by growing-season moisture availability, snow-pack persistence, and temperature conditions with seedling establishment and survival often constrained by increasing moisture stress and warmer growing conditions. (Hill et al., 2019). Similarly, Andrus et al. (2018) found that Engelmann spruce regeneration in southern Rocky Mountain subalpine forest were associated with years of high snowpack and cool, wet summer conditions, while declining snowpack and increasing summer moisture deficits reduced establishment in both Engelmann spruce and subalpine fir (Andrus et al., 2021). Although regeneration responses varied among species and years, the VPD analysis did not detect a significant overall effect of VPD on seedling density. Instead, significant species x VPD interaction suggested that responses to atmospheric moisture demand differed between spruce and aspen. In contrast, increases in larger regeneration size classes suggested that many established seedlings continued to survive and recruit into

taller height classes between 2016 and 2023. These patterns suggest that atmospheric moisture demand may influence both seedling persistence and recruitment dynamics following disturbance, although responses likely also reflect differences in seed availability, microsite conditions, and species-specific drought tolerance (Dobrowski et al., 2019; Pettit et al., 2019; Gill et al., 2017). Although previous studies have identified climate as an important driver of subalpine regeneration (Hill et al., 2019; Andrus et al., 2021), the VPD analysis in this study did not detect a significant overall effect of VPD on seedling density. This may reflect differences in the temporal extent and response variable evaluated, as this analysis was limited to recent observations of the smallest seedling size class. Additional long-term research is needed to better understand how atmospheric moisture demand influences regeneration following spruce beetle disturbance.

Treatments did not statistically change species trajectories from 2018 to 2023 in repeatedly measured post-beetle outbreak plots. Instead, regeneration patterns were primarily structured by species and size class. Across treatments, Engelmann spruce and subalpine fir were less abundant in the smallest regeneration size class, (0.1-9.9 cm; Class 1), while aspen regeneration showed the greatest increases in density in advanced height classes (20–49.9 cm and >50 cm; Classes 3 and 4) over the five year period. Notably, some species may have grown out of their original size class as survival and growth data suggest that species had an overall height growth of approximately 5-6 cm per year for spruce and 5-12 cm for aspen (Battaglia et al. *in review*). However, Engelmann spruce regeneration declined consistently at the smallest height class (1) across habitat and treatments, suggesting limited persistence during early establishment (class 1) or lack of seed source

from the dead overstory. In contrast, aspen regeneration increased substantially, particularly in taller height classes, consistent with strong growth and persistence following disturbance, likely supported in part by clonal regeneration (Nigro et al., 2022). Although some treatment-specific differences were observed, particularly within salvage treatments, regeneration patterns were more consistently associated with species-specific life-history traits than with management actions during the study period. These findings suggests that and species-specific life-history traits were stronger drivers of post-disturbance recovery than management treatment. Consistent spruce declines in the smallest regeneration size class, coupled with aspen expansion, suggest a shift toward greater deciduous tree influence in stands where aspen was present prior to disturbance, even at relatively low densities (Rodman et al., 2022), although Engelmann spruce remained a dominant component of projected future stand structure across most treatments

Species type dominated projected overstory structure outcomes, with spruce and aspen maintain higher projected overstory densities than subalpine fir or tother minor species across treatments groups, indicating that inherent demographic differences among species strongly influenced long-term stand development. (Temperli et al., 2013; Rodman et al., 2022). These results suggest that beetle-driven disturbance history, rather than management history alone, more strongly drives future trajectories, with aspen maintaining higher projected densities in beetle-affected stands than in no-beetle reference stands, while subalpine fir maintained higher densities in no-beetle plots where was more abundant (Deroose & Long, 2007; Rodman et al., 2022; Veblen et al., 1991).

Similar shifts in species composition following bark beetle outbreaks have been widely documented across subalpine forests in the Rocky Mountains, where disturbance legacies influence regeneration dynamics and long-term stand development (Derose & Long, 2007; Kayes & Tinker, 2012; Rodman et al., 2022). Although projected trajectories differed among treatment groups, Engelmann spruce remained a dominant component of future stand structure across most beetle-affected stands, while aspen abundance suggests greater deciduous influence following disturbance.

1.4.2 Climate Implications

Growth models help provide valuable insights into long-term forest dynamics, but they only represent a subset of the processes that influence forest dynamics. The Forest Vegetation Simulator is primarily an individual-tree growth-and-yield model that simulates tree growth, mortality, and stand development based on species traits and stand structure (Dixon 2002). However, bark beetle population dynamics, insect-host interaction, and future disturbance events are not explicitly represented within FVS projections and were outside the scope of this study. Instead, the model was used to examine long-term stand trajectories following disturbance based on observed regeneration patterns and current stand structure. Because bark beetle outbreaks emerge from a combination of interactions such as environmental conditions, host availability, and stand structure, predicting their timing and severity remains difficult and uncertain (Bentz et al. 2010). Therefore, projections from this study likely underestimate structural changes that could occur if additional disturbances, such as subsequent bark beetle outbreaks or wildfire, occur during stand development.

Projected warming in subalpine forests of the southern Rocky Mountains is expected to alter insect-host dynamics through both direct and indirect mechanisms. Temperature directly influences bark beetle development rates, overwinter survival, and voltinism, with warmer temperatures allowing some beetle populations to shift from two-year to one-year cycles, increasing the potential for rapid population growth (Windemuller-Campione & Long 2015; Bentz et al., 2010). Rising temperatures can also increase outbreak potential, while drought stress may increase tree susceptibility to beetle infestation (Bentz et al., 2010; Hart et al., 2014). Together, these climatic mechanisms are expected to increase beetle activity and associated tree mortality across western North American forests (Pettit et al., 2020; Andrus et al., 2021; Bentz et al., 2010). As a result, future disturbance activity may produce structural changes beyond those simulated in this study (Rodman et al., 2022). Increased outbreak potential therefore remains a substantial risk, even in the absence of severe host drought stress or climate-induced mortality. Bark beetle outbreaks are likely to continue to impact these forests in the coming decades, particularly in areas that have not experienced recent outbreaks and still contain a large proportion of large diameter host trees (Temperli et al., 2014; Bakaj et al., 2016). This supports the idea that disturbances are going to continue to alter forest trajectories in the future (Rodman et al., 2021, Davis et al., 2022).

Seedling regeneration patterns suggested that climatic variability may contribute to post-disturbance recruitment dynamics and future forest structure. Seedlings are often more sensitive to microclimate variability and moisture stress than established overstory trees, particularly during early establishment and persistence (Hill et al., 2019). In this

study, regeneration responses varied among species and regeneration size classes, with smaller regeneration classes generally exhibiting lower persistence through time. Similar climatic controls on post-disturbance regeneration have been observed in other studies of post-disturbance recovery. For example, Rodman et al. (2022) documented increases in aspen recruitment on sites characterized by higher heat load index and climatic water deficits, both indicators of atmospheric and climatic moisture stress. Together these findings suggest that climatic variability may interact with disturbance history, species composition, and regeneration strategy to influence long-term forest recovery following beetle outbreak.

In addition to climate, regeneration responses are strongly associated with canopy openings that are created by disturbances (Kayes & Tinker, 2012; Veblen et al., 1991). Canopy openings following beetle outbreaks often increase light availability and can create conditions favorable for seedling establishment (Carlson et al., 2020; Kayes & Tinker, 2012). However, successful regeneration is often limited by proximity to seed sources (Carlson et al., 2020). Multiple studies have shown that seedling establishment following outbreak was strongly influenced by the distance to seed sources and the presence of existing vegetative regeneration, such as aspen root suckers (Harvey et al., 2016; Rodman et al. 2022). In addition, there are several studies that support the theory that early successional species such as aspen increase following canopy mortality, while shade tolerant conifers such as subalpine fir often increase in abundance later successional stages of recovery (Deroose & Long, 2007; Kayes & Tinker, 2012; Perovich & Sibold, 2016; Rodman et al., 2022). Disturbances often drive regeneration patterns, frequently resulting

in shifts in species composition following bark beetle outbreaks across many forests in the United States.

Subalpine systems may experience landscape-scale compositional shifts rather than abrupt structural collapse as species respond differently to disturbance history and regeneration opportunities. Across modeled trajectories, shifts toward greater deciduous influence were evident in many beetle-affected stands where aspen was present prior to disturbance. This pattern is consistent with studies showing that post-disturbance recovery in subalpine forests is often strongly influenced by pre-disturbance stand composition and the presence of advanced regeneration (DeRose & Long, 2007; Kayes & Tinker, 2012; Pelz & Smith, 2012; Pelz et al., 2015; Perovich & Sibold, 2016; Rodman et al., 2022). Following canopy mortality, shade-intolerant species such as aspen may increase in areas where vegetative regeneration or seed sources are present, while shade-tolerant conifers such as subalpine fir and spruce may gradually increase through the release of advanced regeneration (DeRose & Long 2007). These species-specific regeneration strategies can produce spatially heterogeneous recovery patterns across the landscape (Rodman et al., 2022). These findings reflect these near-term forest changes, suggesting that subalpine systems may undergo gradual compositional reorganization rather than rapid species shifts. These patterns appear to be primarily driven by disturbance history, regeneration opportunity, and species-specific life-history traits, although high-elevation subalpine systems may initially buffer some climatic stressors because of their relatively cold environmental conditions (Hill et al., 2019).

1.4.3 Management Implications

Legacy effects of spruce beetle outbreaks will continue to shape subalpine forests in Colorado. Treatments before bark beetle outbreaks did not alter spruce susceptibility to the outbreaks. In addition, the dead overstory from outbreak mortality will continue to exist on the landscape, where they will eventually fall and become coarse woody debris (Brown et al., 2003). Having these trees present on the landscape may be a delayed fuel hazard as this alters the fuel structure in beetle-affected stands and increases potential fire severity and hazardous firefighting conditions (Hood et al., 2017; Mattson et al., 2019), particularly under warmer and drier conditions.

Shifts in spruce beetle host availability have important implications for future outbreak potential. Reduced dominance of Engelmann spruce will lower subsequent potential for beetle outbreaks, but compositional changes will have altered ecosystem services such as snowpack retention, carbon storage, and wildlife habitat, which can affect management objectives (Bentz et al., 2010; Rodman et al., 2022). Managing for structural and compositional diversity, rather than focusing solely on reducing large mortality events may be warranted to increase resilience to climate effects such as drought and changes in growing season lengths. While projections suggest increased aspen dominance, aspen is susceptible to subsequent disturbances such as sudden aspen decline, browsing pressure, insects and fungal pathogens (Andrus et al., 2020; Andrus et al., 2021; Korb et al., 2014) and should be monitored in the coming decades. Additionally, studies have shown that as climate warms, increasing frequency, and large fires are already being seen in subalpine forests (Higuera et al., 2021). Continued monitoring of

stand structure and promotion of compositional heterogeneity is necessary to maintain resilience given these interacting disturbances and projected warming.

Current forest structure should be assessed and monitored, as spruce-dominated areas with large-diameter trees remain at risk of future outbreaks due to increasing spruce beetle hazard ratings over time (Schmid & Frye 1976; DeRose & Long 2014). Although density reduction treatments may provide short-term resistance under endemic conditions, they are unlikely to prevent mortality once spruce beetles reach epidemic populations as this work and others have shown (Windmuller-Campione & Long 2015; Temperli et al., 2014, Battaglia et al. *in review*). In systems where long-term bark beetle resistance is likely unsuccessful, management strategies may need to shift toward adaptive approaches that emphasize resilience and transition strategies rather than resistance alone (Nagel et al., 2017; Nagel et al., 2026). Tools such as the Vegetation Futures Tool (Hoecker et al., 2023) help provide spatial projections of potential vegetation transitions under warming scenarios and may assist managers in evaluating adaptation strategies within subalpine forest (Figure 8). Although the Vegetation Futures tool does not articulate information about future disturbance type, understanding changes in composition over time can still help managers plan for the species-specific types of disturbances that are likely to occur. Proactive silvicultural treatments that reduce host concentration while ensuring adequate Engelmann spruce regeneration can enhance stand-level resilience (Windmuller-Campione & Long 2015). Therefore, promoting stand and species heterogeneity decreases risks associated with widespread disturbances such

as beetle or climate effects as it supports regeneration continuity, reduces both beetle hazard and broader climate vulnerability (Nagel et al., 2017).

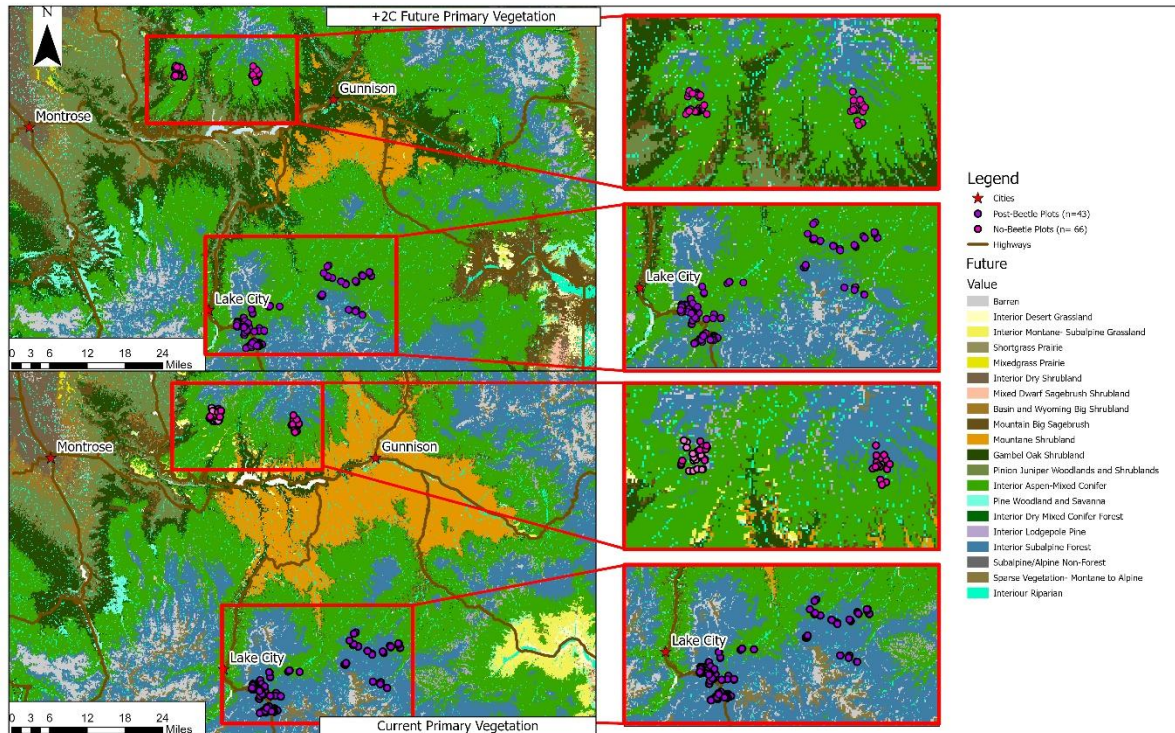


Figure 8. Projected dominant vegetation transition under current and +2 °C warming derived from the Vegetation Futures Tool (Hoecker et al., 2023). No-beetle and Post-beetle plot locations were overlaid in ArcGIS Pro to illustrate potential future compositional trajectories with the study area with zoomed in maps.

1.4.4 Limitations and Future Work

Field data included in this study were collected in sites that varied in structure and species composition. Although efforts were made to select comparable stands, the no-beetle reference sites were limited to spruce-dominated stands with a subalpine fir

component. The unique disturbance history and species composition of the study area further constrained site selection, as few locations met the criteria of aspen-spruce dominance while also lacking recent beetle mortality. Similarly, another issue was that few areas had treatment histories comparable to those located in the region that also did not have beetle-driven mortality. As a result, findings should be interpreted as most applicable to high-elevation spruce-fir systems with similar disturbance and treatment contexts. If we could improve upon the study design, we would collect additional information about microsite conditions. Specifically, we would quantify nurse objects as they are an important microsite characteristic that could help determine regeneration patterns (Hill et al. 2019). Additionally, measuring snowpack residence times and collecting soil moisture content at these sites over time would help quantify how changes in moisture content effect regeneration retention and resilience as subalpine species depend on snowpack to mediate spring and summer moisture content (Andrus et al., 2021).

The Forest Vegetation Simulator has many model-based limitations. While FVS is widely used and accessible forest growth model, some ecological functions could not be simulated. For example, the model does not account for future disturbances, such as SAD, which is a drought induced disease that is known affect the Southern Rockies (Korb et al., 2014; Worrall et al., 2015). In addition, the potential for lodgepole pine encroachment into high-elevation spruce–fir forests could not be represented with the model framework (Rodman et al., 2022, Nigro et al., 2021). This could not be represented within the model framework. More broadly, projections from FVS are subject to uncertainty because growth, mortality, and regeneration are modeled using empirical relationships derived from

historical conditions (Crookston & Dixon 2005) responses under different climate regimes, as well as interactions with future disturbances such as drought, wildfire, or secondary insect outbreaks, may differ from simulated outcomes. Model results should be interpreted as plausible trajectories under the specified scenarios rather than precise forecasts of future forest composition and structure.

1.5 Conclusions

Species type and disturbance history were stronger determinants of structural and regeneration trajectories than projected differences among climate scenarios. Aspen expanded following disturbance, spruce exhibited early-life-stage recruitment limitations, and subalpine fir showed comparatively stable but lower regeneration and density among seedling classes. Climate influenced interannual seedling dynamics, but did not independently drive overstory density or mortality differences among simulated scenarios. Spruce recruitment appears sufficient to maintain presence in the overstory over the modeled timeframe; however, early-life-stage recruitment declines and increased aspen expansion suggest gradual shifts in species dominance for the near future. Rather than structural collapse, future change may occur through compositional reorganization toward mixed spruce-aspen stands. Some treatments influenced immediate stand structure but did not fundamentally alter long-term species trajectories relative to disturbance history. Salvage logging was associated with lower live overstory density than other beetle-affected treatments, potentially influencing structural complexity and fuel dynamics. Long-term resilience appears more strongly linked to compositional diversity and disturbance legacy than to treatment type alone.

1.6 Citations

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Appendix A: Regeneration Tables

Table A1. Observed regeneration density by treatment, species, and height class (2018 vs 2023).

Treatment	Species	Class	TPH_2018	TPH_2023	Delta_TPH
Unmanaged	Aspen	Class1	420	600	180
Unmanaged	Aspen	Class2	826.7	1884.4	1057.8
Unmanaged	Aspen	Class3	2576	5456	2880
Unmanaged	Aspen	Class4	4264	6792	2528
Unmanaged	Spruce	Class1	2727.3	1665.5	-1061.8
Unmanaged	Spruce	Class2	2130.9	2021.8	-109.1
Unmanaged	Spruce	Class3	1883.6	2007.3	123.6
Unmanaged	Spruce	Class4	945.5	2174.5	1229.1
Unmanaged	Subalpine fir	Class1	600	560	-40
Unmanaged	Subalpine fir	Class2	1080	1160	80
Unmanaged	Subalpine fir	Class3	280	600	320
Unmanaged	Subalpine fir	Class4	0	80	80
Previously Managed	Aspen	Class1	434.3	800	365.7
Previously Managed	Aspen	Class2	900	1700	800
Previously Managed	Aspen	Class3	1912	3832	1920
Previously Managed	Aspen	Class4	3400	3800	400
Previously Managed	Spruce	Class1	5280	3510.6	-1769.4
Previously Managed	Spruce	Class2	3084.4	3186.7	102.2
Previously Managed	Spruce	Class3	2142.2	2133.3	-8.9
Previously Managed	Spruce	Class4	1746.7	2137.8	391.1
Previously Managed	Subalpine fir	Class1	160	342.9	182.9
Previously Managed	Subalpine fir	Class2	253.3	306.7	53.3
Previously Managed	Subalpine fir	Class3	491.4	354.3	-137.1
Previously Managed	Subalpine fir	Class4	1000	906.7	-93.3
Salvage	Aspen	Class1	1831.1	1191.1	-640

Salvage	Aspen	Class2	2700	2830	130
Salvage	Aspen	Class3	4392	6856	2464
Salvage	Aspen	Class4	4462.2	10515.6	6053.3
Salvage	Spruce	Class1	2034.3	737.1	-1297.1
Salvage	Spruce	Class2	1542.9	1228.6	-314.3
Salvage	Spruce	Class3	1045.3	1509.3	464
Salvage	Spruce	Class4	613.3	1002.7	389.3
Salvage	Subalpine fir	Class1	2613.3	986.7	-1626.7
Salvage	Subalpine fir	Class2	208	528	320
Salvage	Subalpine fir	Class3	148.6	228.6	80
Salvage	Subalpine fir	Class4	114.3	217.1	102.9

Table A2. Type III ANOVA summary for regeneration change model.

Effect	df	F	p-value
Species	2	20.26	<0.01
Size class	3	7.55	<0.01
Treatment	2	0.55	0.58
Species × Size class × Treatment	12	1.95	0.03

Appendix B: Habitat Regeneration Density and Change by Habitat

Habitat-separated analyses were also conducted to evaluate regeneration responses within spruce and spruce-aspen stands independently. Overall patterns were consistent with the pooled analysis presented in the main text, although aspen increases were more pronounced in spruce-aspen habitats, particularly within larger regeneration size classes. Habitat-specific heatmaps and associated model outputs are provided below.

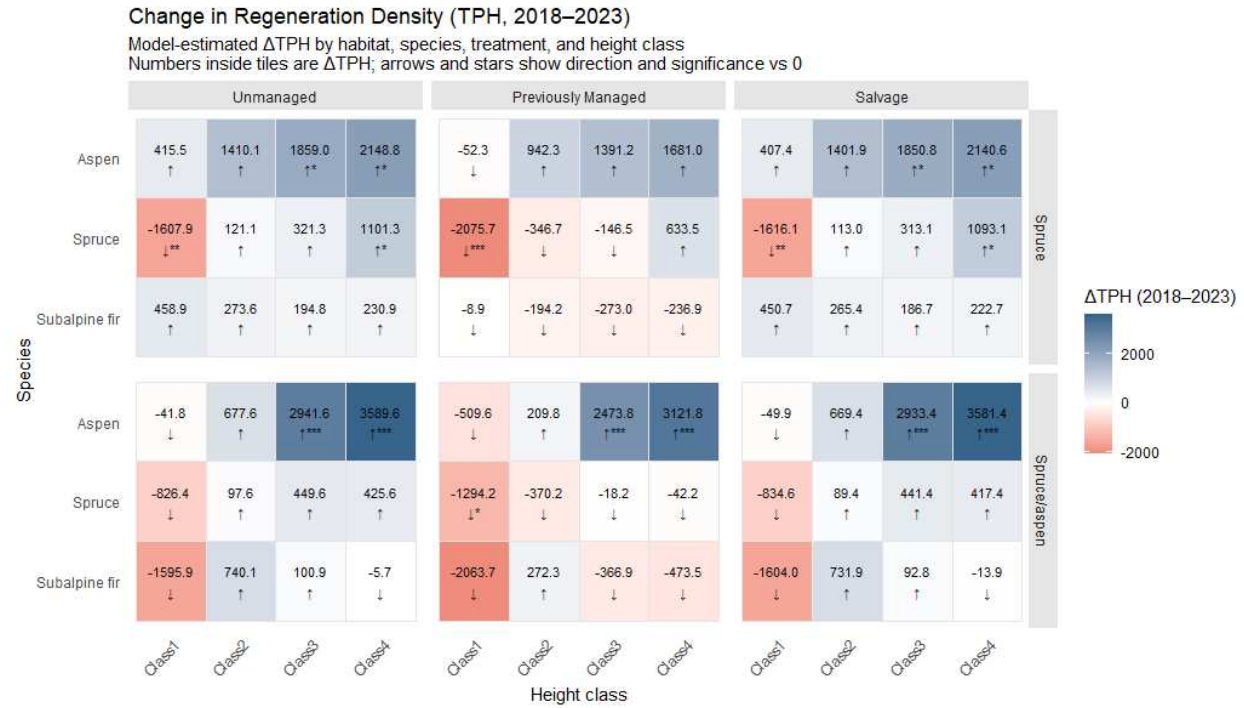


Figure B1. Change in regeneration density (Δ TPH) between 2018 and 2023 across species, habitat types, treatments by seedling height class. Tiles show measured changes in TPH, where blue indicates increases and red indicates decreases in regeneration density. Arrows indicated direction of change and asterisk denote significance. Size Class 1: 0.1–9.9cm; size Class 2: 10–19.9cm; size Class 3: 20–49.9, and size Class 4: 50–137 cm.

Appendix C: Habitat-Specific Compositional Trajectories

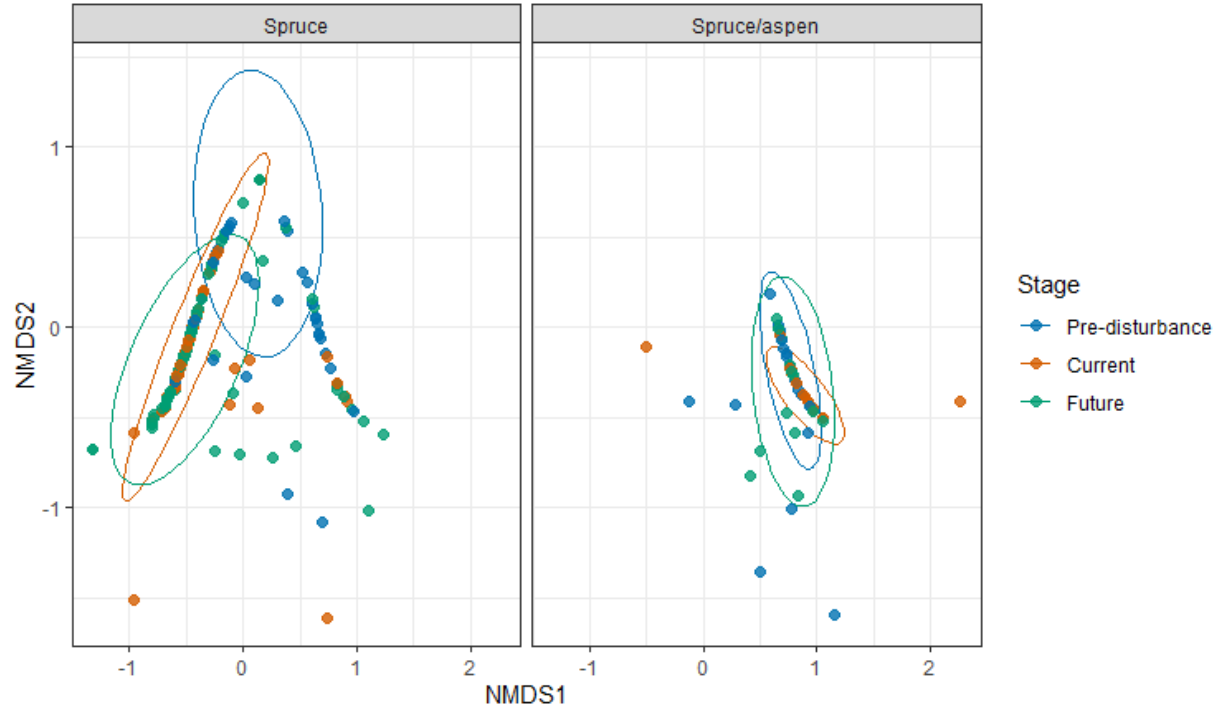


Figure C3. Non-metric multidimensional scaling (NMDS) ordination of species composition across pre-disturbance, current, and future regeneration-based stages by habitat type. Points represent plot-level community composition, ellipses represent stage-level dispersion, and larger points represent stand centroids. Ordination was based on Bray-Curtis dissimilarity.