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Survey of Disjunct Red Spruce (*Picea rubens*) Stands in North Carolina Mountain Basins

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ABSTRACT

In the southern Appalachians, disjunct red spruce (*Picea rubens*) populations persist at low latitudes at elevations above 1,370 m. However, research on the condition of these disjunct red spruce populations is limited. This study compares species composition, stem density, basal area, health, and recruitment in two of the southernmost red spruce populations in North America: the Alarka Laurel and Rich Mountain spruce bog basins in Nantahala National Forest, North Carolina. Moreover, using stand data collected at Alarka Laurel in 2007, we assessed changes in the stand and compared those data to our 2022 survey. Our findings revealed that red spruce was the dominant overstory species, comprising 24.3–25.9% of all measured overstory trees, with seedlings and saplings making up 51.0–86.2% of the red spruce population, indicating stable recruitment. Red spruce basal area declined by 48.2% from 2007 to 2022 in Alarka Laurel, with a concomitant increase in some hardwood species. However, both Alarka Laurel and Rich Mountain showed levels of sapling and seedling recruitment that were comparable to red spruce stands found in other regions. Overall, red spruce trees were healthy, particularly seedlings, representing the healthiest size category, determined through visual assessment. Our results, derived from a reassessment of Alarka Laurel and the addition of the Rich Mountain site, suggest that these stands are relatively stable but may benefit from modest management efforts that increase light availability in areas with dense evergreen shrub cover or that have an overstory dominated by red maple (*Acer rubrum*).

Key words: basal area, recruitment, southern Appalachian Mountains, spruce bog, stand dynamics

INTRODUCTION

Picea rubens Sargent (Pinaceae), known as red spruce, is a slow-growing conifer native to eastern North America, with core populations in southeast Canada and the northeastern United States (Blum 1990; Cogbill and White 1991; Nowacki et al. 2010). Red spruce occupies an ecological niche defined by cool climates, with annual temperatures ranging from 4 to 13°C, abundant rainfall (910 to 320 mm per annum), and moist soils. Its range extends southward along the Appalachian Mountains to its southern limit in North Carolina, where stands are typically restricted to elevations above 1,370 m (Whittaker 1956; Hart 1959; Blum 1990; Cogbill and White 1991; Nowacki et al. 2010). Shifts in these climatic conditions, notably elevated summer temperatures above 33°C, can limit regeneration and may contribute to range contractions of red spruces, with impacts predicted to be most pronounced at the southern extent of the species' range. Red spruce exposed to temperatures 2–4°C above average are predicted to experience a loss of >95% of their habitat by 2040 (Webb et al. 1993; Koo et al. 2015; Brown 2022). Southern peripheral stands are particularly vulnerable; their restriction to isolated peaks or basins prevents upward migration to higher elevations with more suitable climates (Ribbons 2014; Yetter et al. 2021). Presently, low-elevation basin bogs at the southern range of red

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spruce can ameliorate thermal stress, allowing red spruce to exhibit resilience; however, this resilience is likely to diminish with intensified climatic changes. (Collins et al. 2010).

Red spruce were abundant across the southern Appalachians within the Pleistocene Epoch, the last major ice age, roughly 10,000 to 20,000 years ago (Delcourt and Delcourt 1984; Schmidtling 2007; Adams et al. 2010). After the glacial maximum, as the climate became hotter and drier, the species migrated upward by 300–400 meters in elevation. During the Little Ice Age (1,600 to 1,900 C.E.), when the climate cooled, red spruce recolonized lower elevations in the southern Appalachians (Whittaker 1956). After the Little Ice Age (1850), red spruce likely declined at the southern edge of its range; this decline is expected to continue due to climate warming (Hamburg and Coghill 1988; Koo et al. 2014).

Extensive logging in the early 1900s resulted in a 50.8% decline in red spruce in the southern Appalachians (Busing 1985; Adams et al. 2010). Slash left over from clearcutting, coupled with droughts in the 1920s and 1940s, encouraged large fires, altering soil conditions and directly killing remaining spruce, which lacks the ability to resprout (Korstian 1937; Minckler 1945). Together, these factors resulted in southern spruce populations remaining only on peaks, ridges, and high mountain basins (Adams et al. 2010; Nowacki et al. 2010; Houle et al. 2012). Temperatures within these basins are cooler than surrounding areas due to cold air drainage and topography that buffers against drought (Busing 1985; Daly et al. 2010; Dobrowski 2011; Novick et al. 2016).

Historical range shifts which are determined through fossil pollen analysis demonstrate red spruces' sensitivity to climate (Davis and Shaw 2001). Elevational and latitudinal shifts due to climate change are documented for other species of conifers as well. For instance, white spruce (*Picea glauca* Vossb) in Canada are moving to higher latitudes out of their boreal biome into the tundra (Dial et al. 2022). Additionally, the southwestern white pine (*Pinus strobiformis* Engelm. In Wisl.) is expected to shift by 1,000 km north in its mean latitude and 500 m in elevation (Shirk et al. 2018). Consequently, the southwestern white pine's habitat will fragment, and the range will decline by over 60% (Shirk et al. 2018).

However, range shifts for red spruce are more nuanced and complex. For instance, in the northeastern United States, where the red spruce range is broader, the species is expanding downslope, successfully recolonizing areas following decades of deforestation (Morelli et al. 2025). In the Central Appalachians, red spruce basal area and density increased from the early 1990s to the mid-2000s and expanded into nearby hardwood-dominated stands (Rollins et al. 2010). In the southern Appalachian Mountains, overstory red spruce declined by nearly half from 1946–2004 at Mount Collins, Great Smoky Mountains National Park (Busing 2004). However, temperature and precipitation were poor predictors of red spruce growth rates based on analyses of tree cores from several red spruce stands in the southern Appalachian Mountains (Rochner et al. 2023). Overall, these findings demonstrate that individual stands of spruce are likely to be more impacted by other factors, such as southern pine beetle (*Dendroctonus frontalis* Zimmermann) outbreaks (Murphy 1917; Gan 2004; McNulty 2009), insufficient light availability (Busing 1985; Lutz 2018), and acid deposition (McLaughlin et al. 1987; Adams and Eagar 1992; Driscoll et al. 2003; Houle et al. 2012; Rochner et al. 2023).

With climate change and these additional factors in mind, this study seeks to understand the current condition of the southernmost red spruce populations. To do this, we conducted vegetation surveys of two of the southernmost red spruce stands in the eastern United States, the Alarka Laurel and Rich Mountain basins in Nantahala National Forest, western North Carolina. Our objectives were to assess the condition of the stands and determine if management actions (e.g., thinning of competing vegetation) might be needed to ensure the long-term persistence of these disjunct stands of spruce. Moreover, our observations from these sites may offer insights into the potential stressors (e.g., southern pine beetles, shading from evergreen shrubs) impacting these forests. Our surveys focused on the condition of red spruce, including overstory basal area, stem density, health, and size class distribution (seedling, sapling, and overstory tree), in addition to the composition of the overstory. In conjunction with the 2007 survey of red spruce in Alarka Laurel by Collins et al.

(2010), this study sought to assess changes of the Alarka Laurel stand over the course of 15 years. In addition, we sought to provide baseline documentation for the Rich Mountain spruce bog, as well as to compare both the Alarka Laurel and Rich Mountain spruce bogs, as they are rare communities with differing site histories.

MATERIALS AND METHODS

Study Sites

We surveyed disjunct red spruce stands at Rich Mountain and Alarka Laurel. The two stands are anomalies, located at the southernmost extent of the species' latitudinal range and either below or marginally higher than the typical minimum elevation (~1,370 m in the Southern Appalachians; Whittaker 1956). The Alarka Laurel Spruce Bog is in Nantahala National Forest, Swain County, North Carolina (35.341506°, −83.351523°) at an elevation of 1,220 m (Figure 1). Alarka Laurel is approximately 16 ha and is 18.5 km from the nearest population within the Plott Balsam Mountains. The Rich Mountain spruce bog is in Nantahala National Forest on the eastern side of Jackson County, North Carolina (35.290217°, −83.042028°) at an elevation of 1,460 m (Figure 1). The Rich Mountain spruce bog is approximately 4 ha and is 5.6 km from the nearest red spruce population at Rough Butt and Gauge Bald, which are part of the Great Balsam Mountains. The stands of red spruce at Alarka Laurel and Rich Mountain are found in high elevation hanging valleys or basins. These basins are fed by seeps and springs from surrounding ridges and form a Swamp Forest-Bog Complex (Spruce Subtype); only seven examples of these spruce bogs are known from North Carolina (Pittillo 1994; Schafale 2024). From observations and survey work, the overstory surrounding both bog basins were hardwood forests composed largely of oaks (*Quercus* spp.), maples (*Acer* spp.), tulip poplar (*Liriodendron tulipifera* L.), black and yellow birches (*Betula lenta* Du Roi and *B. alleghaniensis* Britton), and American beech (*Fagus grandifolia* Ehrh.). Within the bogs, rosebay rhododendron (*Rhododendron maximum* L.) and mountain laurel (*Kalmia latifolia* L.) dominated the shrub layer, with red spruce and hardwoods comprising most of the upper canopy.

The area encompassing Alarka Laurel was acquired by the U.S. Forest Service in the late 1990s (Gary Kauffman, USDA Forest Service, pers. comm.). There is no indication of former logging (Gary Kauffman, USDA Forest Service, pers. comm.), and the oldest spruce cored by Collins et al. (2010) dated to 1855, suggesting that the stand may have never been logged. More recently, it was noted that there were large trees in the basin that were impacted in the early 2000s by pine beetle outbreaks (Gary Kauffman, USDA Forest Service, pers. comm.).

Conversely, the Rich Mountain stand was owned and managed for timber resources by the Mead Paper Company until it was acquired as public land in 1980–1981. It is estimated that the area was logged from the 1920s to the 1940s. This is indicated by stumps found along the bog's periphery and notes from previous USFS surveys conducted in the 1990s, which documented stumps in and around the site, indicating former logging activity (Gary Kauffman, USDA Forest Service, pers. comm.).

Field Data Collection

Our methods are based on those used in the 2007 survey of red spruce in Alarka Laurel by Collins et al. (2010). We established five 10 m wide belt transects at each site, with the length of each transect corresponding to the width of the spruce stands. Each transect was composed of 10 × 10 m plots. Every 10 meters along the transect center line, the point was flagged to mark the end of the plot, and the coordinates were recorded using a GPS. We used a measuring tape or hypsometer to measure 5 m on either side of the center line at the start and end points of the plot. These points were flagged, marking the corners of the plots.

At the Alarka Laurel site, the transects were at approximately 100 m intervals, going west to east through the basin (Collins et al. 2010). In the Rich Mountain site, the transects were at approximately 70 m intervals going north to south. The transects had different lengths due to variations in the width of the bogs. We chose the transect intervals to ensure representative samples, distributed evenly across the approximate site widths of 480 m at Rich Mountain and 750 m at Alarka Laurel.

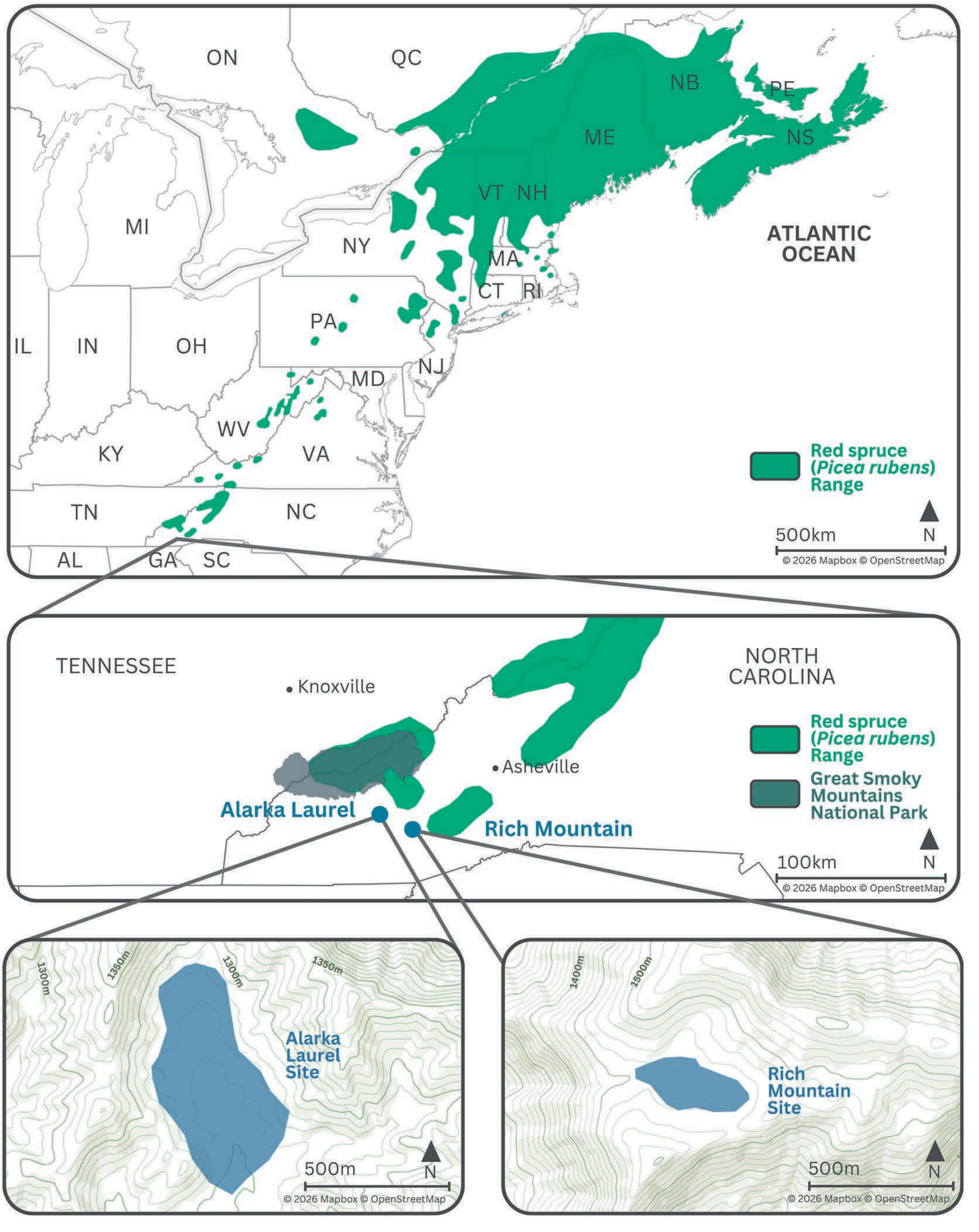

Figure 1. Red spruce study site locations in western North Carolina. Top panel: Current red spruce range across eastern North America (USDA 1999), showing distribution in the Appalachian Mountains and northeastern regions. Middle panel: Regional context of Alarka Laurel and Rich Mountain spruce bog study sites relative to the Great Smoky Mountains National Park (gray shaded area) and regional red spruce distribution (green shaded areas). Bottom panels: Topographic detail of each study site with red spruce stand boundaries delineated in blue.

By dividing the total widths by seven to allow for equal buffer zones from the basins' edges, we calculated and rounded to 70 m and 100 m increments, respectively. This approach ensured the transects traversed the width of the spruce stands while maintaining a consistent distance between transects to provide a reliable assessment of the basins' forest composition. Although we used a compass to ensure the same direction was followed in each transect, it was sometimes difficult to navigate through the thick vegetation, so in some cases our transects were not perfectly parallel to one another.

The Alarka Laurel spruce stands were surveyed in late summer and early autumn of 2007 (by Collins et al. 2010) and again in 2022. The 2007 survey did not leave specific transect coordinates or permanent markers. Furthermore, the 2007 data we received are missing one of the five transects for the overstory data, so our 2007 reported results differ from those reported in Collins et al. (2010). To replicate the 2007 transects, we extrapolated starting coordinates by overlaying the 2007 transects on satellite imagery; however, it is possible that our transects did not fully overlap with those from 2007. The 2022 survey at Alarka Laurel included more plots (128 plots or 1.28 ha (~8% of the basin) than the 2007 survey (51 plots or 0.51 ha (~3% of the basin). Because of the missing transect, when we re-analyzed the overstory and sapling data, there were only 39 plots or 0.39 ha (~2.4% of the basin), though the seedling data from 2007 still contained all 51 plots. To traverse the Alarka Laurel basin completely, our transects ranged from 170–346 m, compared to 80–120 m in the previous study. This increased survey area allowed for analysis of the basin's edge. The surveys of Rich Mountain spruce stands were conducted during the late summer and early autumn of 2023. The Rich Mountain transects encompassed 0.69 ha (69 plots) representing 17% of the basin.

We conducted three surveys within each plot: the overstory, saplings, and seedlings. First, we surveyed overstory vegetation to assess the composition, basal area (BA), and stem density of the overstory trees, and to compare the composition of overstory tree species between the basins. For this survey, we measured the diameter at breast height (DBH) of every overstory tree, defined as those ≥2 m in height and with a DBH ≥10 cm as measured 1.37 meters from the ground on the uphill side of the tree to the nearest 0.1 cm. The DBH measurements were converted into BA (cm^2 or m^2) for analysis. Nomenclature follows Weakley (2023). Next, we surveyed spruce saplings (≥2 m in height, with a DBH <10 cm) and seedlings (<2 m in height) to assess recruitment. We measured the DBH of saplings and the height of seedlings. Our seedling counts may be a slight underrepresentation of the true quantity of red spruce seedlings in the basin due to the dense understory that, at times, made accurate surveying difficult.

In addition to measuring DBH, every red spruce tree (overstory, saplings, and seedings) was given a health score, determined through visual assessment. A score of "0" indicated the tree was dead, and we recorded snags (standing or leaning dead trees ≥10 cm DBH). A score of "1" was given to trees that had a few live branches and/or showed severe signs of insect infestation. Trees given a "2" had a few dead branches and/or some signs of insect infestation. For trees with minimal dead branches or no signs of insect infestation, a health score of "3" was recorded.

Statistical Analysis

We conducted all statistical analyses using R software version 4.5.2 (R Core Team 2025). We used an alpha level of $p<0.05$ as the rejection criteria. All data were evaluated for normality using the Shapiro-Wilks test and equality of variances using Levene's test. Given that the data violated normality with unequal variances, we used generalized linear models (GLMs) with appropriate error distributions. To evaluate differences in forest structure, we analyzed total plot BA, red spruce BA, total plot density, red spruce density, sapling BA, sapling density, seedling height, and seedling density by comparing Alarka Laurel 2007 to Alarka Laurel 2022 and Alarka Laurel 2022 to Rich Mountain. We fitted GLMs with a Gamma distribution and log link for total plot BA and seedling height; we used Tweedie GLMs for red spruce BA and sapling BA. Total plot density, red spruce density, sapling density, and seedling density variables were analyzed using zero-inflated negative binomial models.

We calculated 95% confidence intervals and *p*-values for the mean difference to compare saplings, seedlings, and overstory red spruce health and size within and between the stands. Means and standard deviations were calculated using RStudio. Figures (maps and graphs) were created in Tableau 2022.2 and 2025.2, Microsoft Excel, or RStudio. Data are archived in the Environmental Data Initiative: **https://portals.edirepository.org/nis/mapbrowse?scope=edi&identifier=2088**.

RESULTS

Overstory Alarka 2007 and Alarka 2022

We found that total overstory plot density was 20.6% higher in Alarka 2022 than Alarka 2007 (GLM estimate = 0.273 ± 0.130, p=0.035) and there was a trend for higher spruce density in Alarka 2022 than Alarka 2007 (GLM estimate = 0.423 ± 0.225, p=0.060; Table 1). We found no significant difference in total overstory BA (GLM estimate = −0.069 ± 0.199, p=0.729) or spruce BA (GLM estimate = −0.657 ± 0.411, p=0.110) between the two years, even though the average overstory BA of red spruce declined 48.2% from 2007 to 2022 (Table 1, Figure 2A and B); this was likely because the largest red spruce in 2007 was 2.3 times larger than the largest tree in 2022.

With the decline in overstory red spruce BA, the basal area of other deciduous tree species, such as red maple (*Acer rubrum* L.), white oak (*Quercus alba* L.), and American serviceberry (*Amelanchier arborea* (F. Michx.) Fernald), increased in Alarka Laurel from 2007 to 2022 (**Supplementary Figure 1**).

Tree diameter distributions were skewed toward smaller diameters for non-spruce overstory trees at Alarka 2007 and Alarka 2022 (Figure 3A–B). However, the diameter distributions for red spruce differed between Alarka 2007 and Alarka 2022, with Alarka 2007 having a more even distribution of size classes, including spruce >55 cm DBH, which Alarka 2022 lacked. Like non-spruce diameter distributions, red spruce diameter distributions for Alarka 2022 were skewed toward smaller diameter trees.

Overstory Alarka 2022 and Rich Mountain

Overall, the stand on Rich Mountain had a 6.9% larger overstory red spruce BA than in Alarka Laurel (GLM estimate = 0.744 ± 0.341, p=0.029; Table 1, Figure 2B). However, there was no difference in mean total overstory BA (GLM estimate = 0.212 ± 0.164, p=0.197), total overstory plot density (GLM estimate = −0.067 ± 0.111, p=0.547) or spruce density (GLM estimate = −0.097 ± 0.188, p=0.606; Table 1, Figure 2A).

Red spruce was the most abundant tree species and had the greatest basal area in both basins, followed by white oak, American serviceberry, red maple, and northern red oak (*Quercus rubra* L.; Table 1, **Supplementary Figure 2**). Alarka Laurel basin had a higher overstory species richness compared to Rich Mountain (Table 1, **Supplementary Figure 2**). The basal area of red spruce snags were similar between the two basins, though there were nearly three times more snags in Rich Mountain compared to Alarka Laurel (Table 1).

Like Alarka 2022, the non-spruce diameter distributions were skewed toward smaller diameter trees (Figure 4B–C). Unlike Alarka 2022, red spruce at Rich Mountain had a more even distribution of diameters across all size classes, including red spruce >55 cm DBH.

Overstory red spruce BA and density were highest in the center of the basins, particularly along the midpoints of the middle transects (**Supplementary Figures 3 and 4**). Corresponding with this pattern, most plots with low red spruce BA are at the ends of the transects and in the edge transects (1 and 5), leaving most red spruce biomass towards the center of the basins.

Recruitment Alarka 2007 and Alarka 2022

Red spruce saplings and seedlings were distributed throughout both basins (Table 2, Supplementary Figure 5). There was a 367% increase in mean sapling BA from Alarka 2007 to Alarka 2022 (GLM estimate = 1.448 ± 0.541, p=0.007; Figure 4A, Table 2), and there was 426% increase in sapling density from 2007 to 2022 (GLM estimate = 0.714 ± 0.258, p=0.005; Table 2). There was an increasing trend when assessing seedling density from 2007 to 2022 (GLM estimate = 0.454 ± 0.255, p=0.075; Table 2) and there was no difference in seedling height (GLM estimate = 0.095 ± 0.097, p=0.329; Table 2, Figure 4B).

Table 1. Red spruce stand characteristics by year and site for the overstory (±SE).

	2007 Alarka Laurel	2022 Alarka Laurel	2023 Rich Mountain
Total no. plots (n)	39	128	69
Total no. overstory tree species	13	18	10
Total overstory density/ha	230.8 ± 27.3	283.7 ± 24.7	285.5 ± 30.6
Red spruce overstory density/ha	59.0 ± 15.5	69.0 ± 16.0	73.9 ± 15.3
Red spruce relative overstory density	25.6%	24.3%	25.9%
Total overstory basal area (m^2/ha)	16.47 ± 2.92	15.37 ± 1.48	19.01 ± 2.58
Red spruce overstory basal area (m^2/ha)	8.12 ± 2.59	4.21 ± 0.92	8.86 ± 2.35
Red spruce overstory relative basal area	49.2%	27.4%	46.6%
Red spruce overstory importance value[a]	37.4	25.9	36.3
No. and (%) of plots with overstory red spruce	15 (38.5%)	37 (28.9%)	24 (34.8%)
Red spruce snag overstory basal area/ha	No data	1.99 ± 0.68	1.77 ± 0.63
Red spruce snag overstory density/ha	No data	10.9 ± 3.3	30.4 ± 13.9

[a]Importance value = (relative basal area + relative abundance)/2

Recruitment Alarka 2022 and Rich Mountain

The red spruce sapling BA at Rich Mountain was 129% lower than Alarka Laurel 2022 (GLM estimate = −1.416 ± 0.474, p=0.002; Table 2, Figure 4A). Rich Mountain had a 117% lower sapling density (GLM estimate = −0.606 ± 0.203, p=0.002) and 109% lower seedling density (GLM estimate = −0.664 ± 0.213, p=0.001; Table 2, Figure 4A-B). The two sites had similar seedling height ranges, with no statistically significant differences (GLM estimate = −0.068 ± 0.096, p=0.475; Table 2, Figure 4B).

Health

There were significant differences in the trees' visual health between size categories in both Alarka Laurel and Rich Mountain (Figure 5). In Alarka Laurel in 2022, we found no significant differences in seedling and sapling health (p=0.115). Seedlings and saplings were, however, significantly healthier than overstory spruce (seedlings: p<0.001, CI: [0.291, 0.710]; saplings: p=0.001, CI: [0.149, 0.618]). In Rich Mountain, we found that the seedlings had significantly higher health scores than the saplings (p=0.002, CI: [0.397, 1.421]). Seedlings also had significantly higher health scores than overstory spruce (p=0.001, CI: [0.273, 1.037]). Overstory spruce had no significant health difference between saplings (p=0.384).

In Alarka Laurel, saplings and seedlings were significantly healthier than overstory spruce in general, whereas in Rich Mountain, seedlings were healthier than overstory spruce and saplings (Figure 5). Saplings were also healthier in Alarka Laurel in 2022 than Rich Mountain (p=0.006, CI: [0.260, 1.272]), causing red spruce at Alarka Laurel as a whole to be healthier than the stand at Rich Mountain (p=0.018, CI: [0.037, 0.394]), though there was no significant difference between the stands for overstory (p=0.525) and seedling health (p=0.762).

DISCUSSION

Overstory

In the early 2000s, the Alarka Laurel stand experienced a southern pine beetle infestation, resulting in a considerable die-off of red spruce (Gary Kauffman, USDA Forest Service, pers.comm.). The increase in overstory spruce stem density, despite the nearly 50% decline in overall overstory red spruce basal area from 2007 to 2022, confirms that recruitment of spruce into the overstory is occurring. The DBH class distribution of red spruce corroborates this pattern, with 2022 dominated by small-diameter stems (≤15 cm DBH), in contrast to the more even size class distribution recorded in 2007, which included large individuals exceeding 55 cm DBH that were not detected in 2022. Concomitant to the decline in basal area of red spruce, non-spruce overstory basal area and

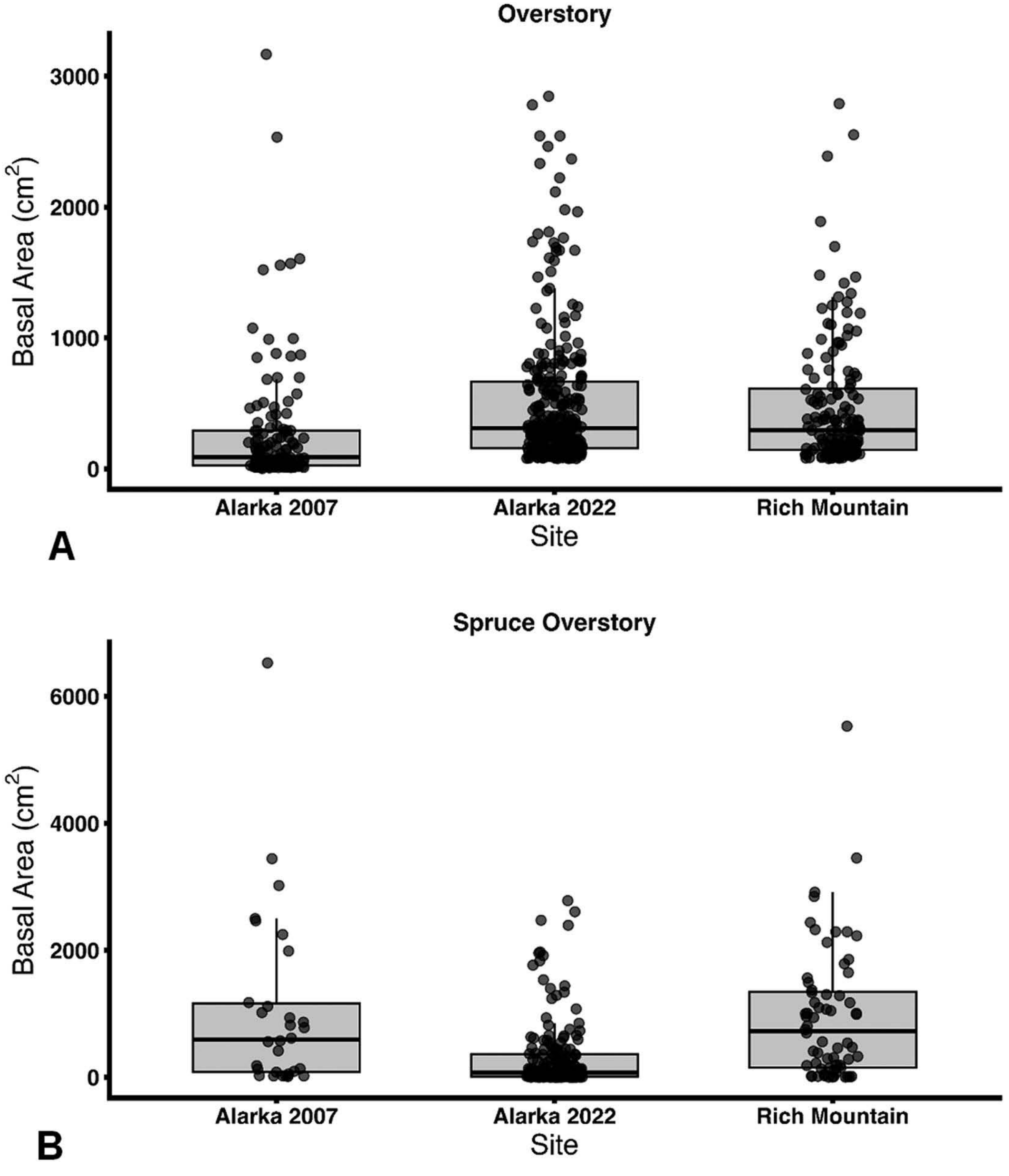

Figure 2. Comparison of **A.** total overstory BA (cm²) and **B.** overstory red spruce BA (cm²) among Alarka Laurel (2007), Alarka Laurel (2022) and Rich Mountain (2023). Points represent individual observations; light gray represents single observations and black represents overlapping observations.

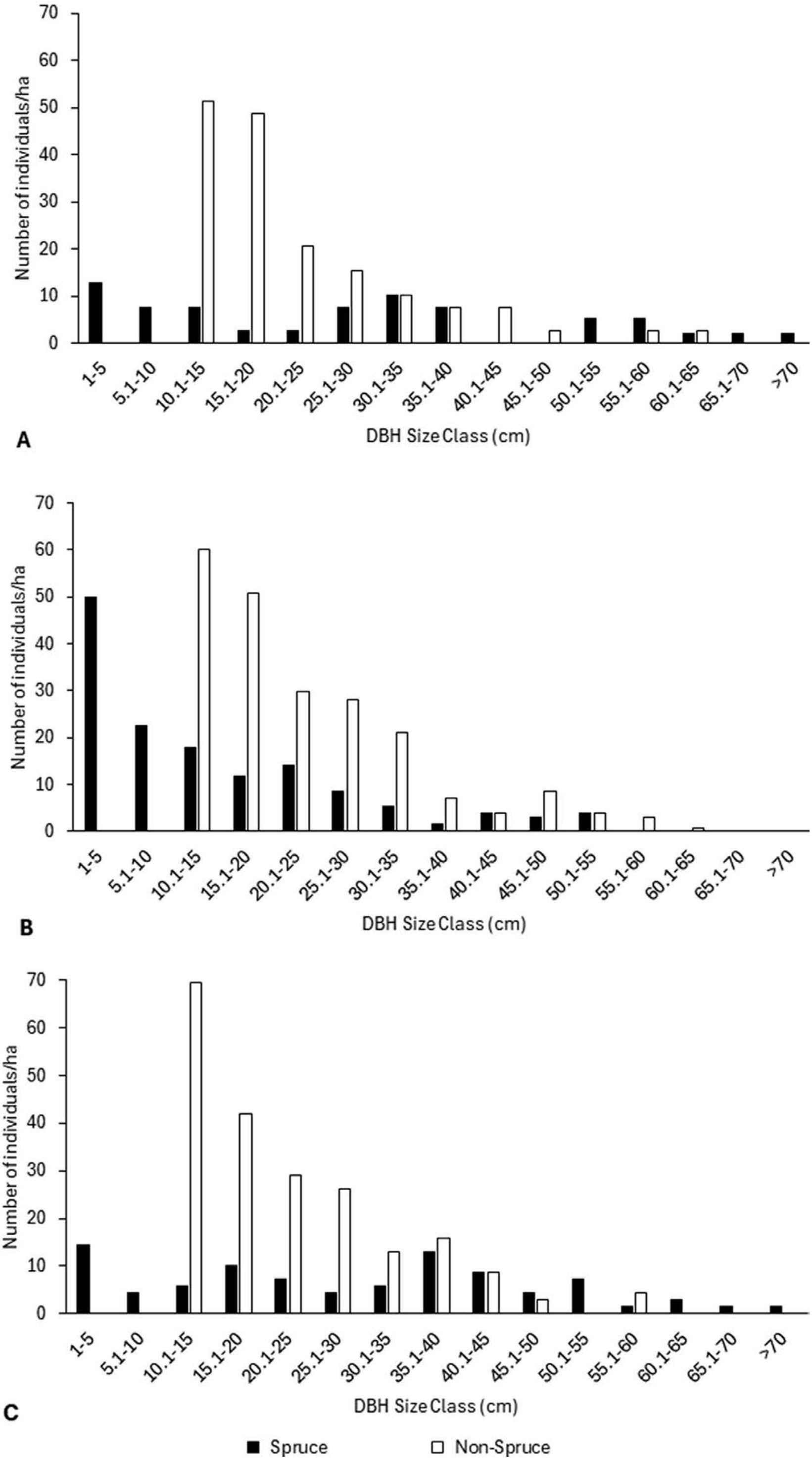

Figure 3. Diameter size classes for red spruce and non-spruce overstory trees and saplings for **A.** Alarka 2007, **B.** Alarka 2022, and **C.** Rich Mountain 2023. Note that we did not collect DBH measurements for non-spruce trees <10 cm in diameter, so those values are not included in the graphs.

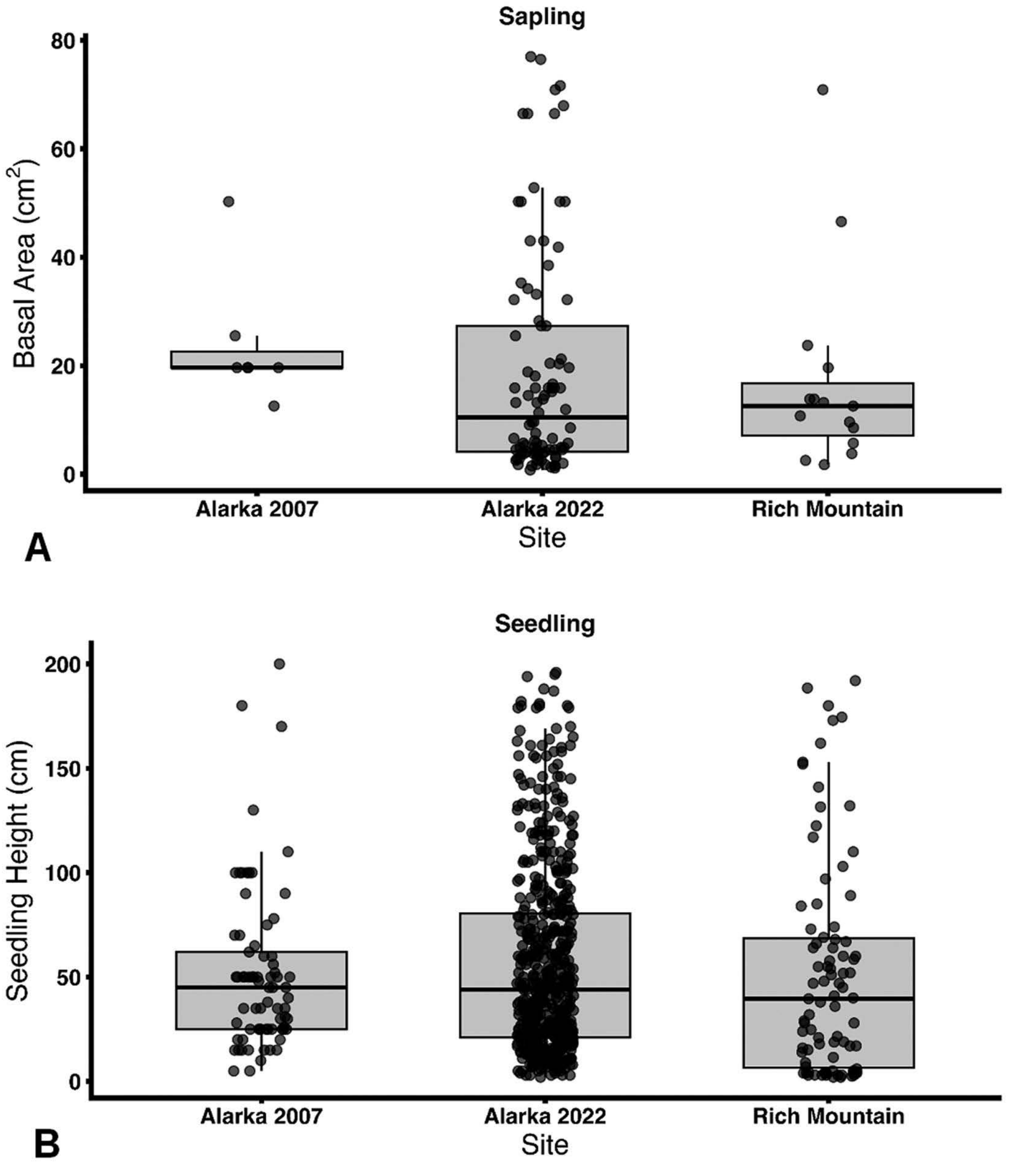

Figure 4. Comparison of **A.** red spruce sapling BA (cm^2) and **B.** red spruce seedling heights (cm) for Alarka Laurel 2007, Alarka Laurel 2022, and Rich Mountain 2023. Points represent individual observations; light gray represents single observations and black represents overlapping observations.

Table 2. Red spruce stand characteristics by year and site for saplings and seedlings (± SE).

	2007 Alarka Laurel	2022 Alarka Laurel	2023 Rich Mountain
Total no. plots (n)	39 (51 seedling plots)	128	69
Red spruce sapling density/ha	13.7 ± 5.6	72.1 ± 12.4	18.8 ± 5.9
Red spruce sapling basal area/ha	0.03 ± 0.01	0.14 ± 0.04	0.03 ± 0.01
No. and (%) of plots with red spruce saplings	6 (15.4%)	39 (30.5%)	10 (14.5%)
Red spruce seedling density/ha	143.1 ± 56.9	428.7 ± 66.3	126.1 ± 32.0
Red spruce seedling heights (cm)	51.8 ± 4.6	56.7 ± 1.9	52.0 ± 5.6
No. and (%) of plots with red spruce seedlings	17 (33.3%)	82 (64.1%)	25 (36.2%)

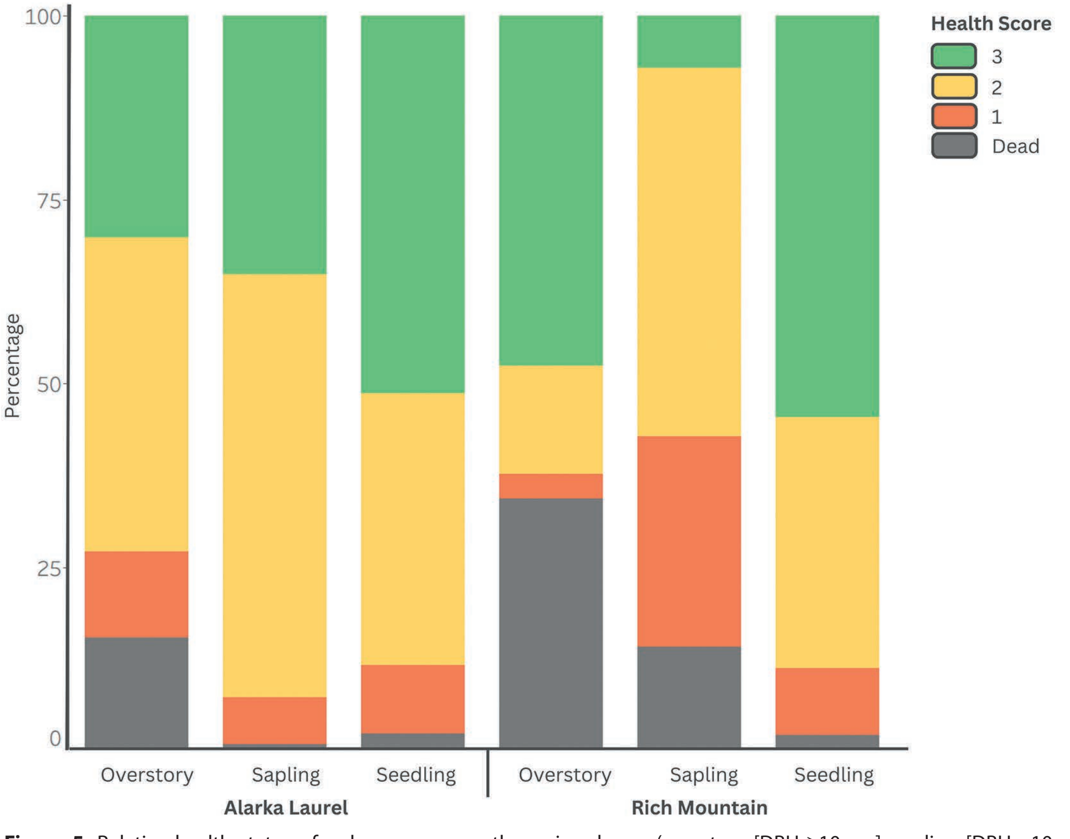

Figure 5. Relative health status of red spruce across three size classes (overstory [DBH ≥10 cm], sapling [DBH <10 cm], seedling [height only]) at Alarka Laurel (2022) and Rich Mountain (2023). Health scores: Dead, 1 (poor), 2 (fair), 3 (good). Data presented as percentage of red spruce individuals surveyed within each size class, excluding surveyed individuals with unknown health scores.

overstory stem density increased. The decline in spruce basal area at Alarka Laurel, combined with the increase in spruce saplings and seedlings, which we observed were most abundant in gaps, suggests that the red spruce stand at Alarka Laurel is recruiting successfully and will likely recover from the decline of the overstory.

In both basins and for all years surveyed, red spruce was the dominant overstory tree species, both in basal area and density. In both basins, we observed several disturbances (e.g., fallen trees) resulting in small canopy gaps in the early successional stages. Gap dynamics play an important role in maintaining red spruce stands, with small gaps (<200 m^2) being the most common type of disturbance in spruce stands in the southern Appalachians (Busing 1985; White et al. 1985). Small canopy gaps (<40 m across, commonly caused by the death of a canopy tree), rather than large-scale disturbances (such as those caused by fire), benefit red spruce trees, likely because they allow light penetration but do not significantly alter other microclimate variables, such as soil moisture (Busing 1985).

Overstory red spruce BA, and density in Alarka Laurel and Rich Mountain, are similar to what is reported in comparable studies that surveyed overstory spruce ≥10 cm DBH. Korstian (1937) recorded from 82–340 overstory red spruce/ha in old growth stands in the mountains of western North Carolina, eastern Tennessee, and West Virginia, densities which are slightly higher than what we recorded at Alarka Laurel and Rich Mountain. However, BA was not reported, so it may be that these were smaller trees that resulted from some sort of disturbance event. In four West Virginia old growth spruce stands, overstory red spruce density ranged from 65–255 stems/ha and red spruce importance values ranged from 21.4–69.8 (Adams and Stephenson 1989), values that are comparable to Alarka Laurel and Rich Mountain. Overstory red spruce in a second growth spruce-hemlock forest in West Virginia that was cut in the 1920s had 159 stems/ha, a relative density of 12.2%, BA of 8.6 m2/ha, relative BA of 18.9%, and an importance value of 18.4 (Schuler et al. 2002). While overstory red spruce density was less, red spruce BA was slightly greater in Rich Mountain, and relative density, relative BA, and importance value were all higher in both Alarka Laurel and Rich Mountain.

Recruitment

Our surveys revealed an increase in red spruce saplings at Alarka Laurel, where sapling density increased over 5-fold from 2007 to 2022. The increased proportion and number of saplings and seedlings indicates that the population continues to recruit successfully; some of the seedlings we measured were especially small, with heights <4 cm. Overstory conifers, including spruce, are more drought-resilient than seedlings and saplings (Zang et al. 2012). Adverse effects to young spruce may occur in future drought conditions, thereby negatively impacting recruitment. However, bog basins are more resilient to drought, mitigating this impact on spruce seedlings and saplings (Clements et al. 2003).

Taken together, red spruce saplings and seedlings greatly outnumbered overstory spruce in both Alarka Laurel and Rich Mountain. A study in the Great Smoky Mountains (elevation 1,770–1,830 m) found that spruce under the age of 5 composed 70% of the stand population, few trees were over 20 years of age, and the oldest tree was 290 years old, indicating a relatively young stand given the species' maximum age of 359 years (Busing 1985). In four old growth stands in West Virginia, sapling density (measured as spruce ≥0.5 cm in height but ≤2.5 cm DBH), ranged from 100–430 stems/ha and spruce seedling density (measured as red spruce <0.5 m in height) ranged from 0–40,000 seedlings/ha, indicating that sapling and seedling density varies widely depending on the stand and recent disturbance events (Adams and Stephenson 1989). Red spruce rely on canopy dynamics to persist. Large seedling banks have only a few individuals that grow into saplings and then to the overstory, which is driven by disturbance and other abiotic factors (Mayfield and Hicks 2010).

Health

In Alarka Laurel and Rich Mountain, the majority of spruce trees in all three size categories appeared visually healthy. The observed southern pine beetle infestations on overstory spruce at Alarka Laurel may partially explain their lower mean visual health scores, in contrast to seedlings and saplings. Between the 2007 and 2022 surveys at Alarka Laurel, the percentage of trees showing pine beetle damage declined. While this may reflect a genuine reduction in infestation pressure, two important caveats apply: southern pine beetle populations fluctuate naturally over time, and our assessments did not include pitch tube collection from the cambium layer, limiting their completeness as a measure of active infestation (Clarke and Nowak 2009; Collins et al. 2010; An and Gan 2022).

The noted absence of eastern spruce gall adelgid (*Adelges abietis* L.) in the 2007 study suggests this pest was not evident in Alarka Laurel at that time, though pests of this genus are rarely harmful and may stunt growth only in extreme cases (Friend and Wilford 1933). The 2007 survey did not record red spruce health numerically, however, so little temporal quantitative comparison can be made for Alarka Laurel to track health impacts of pests. Future studies in the Alarka Laurel basin could survey red spruce health with our visual scale to monitor population health over time and assess whether pest presence correlates with impacts on growth or recruitment.

Management Implications and Future Studies

Gap-phase dynamics, which were evident at both study sites, are recognized as a key driver of red spruce stand regeneration and maintenance (Rentch et al. 2010). Rentch et al. (2016) provided experimental evidence for this in a West Virginia red spruce stand, where small canopy gaps were created above suppressed spruce (>2.54 cm DBH) previously overtopped by hardwoods. After six years, trees in plots where >90% of overtopping hardwood basal area had been removed exhibited significantly greater radial and height growth relative to controls, underscoring red spruce sensitivity to canopy competition. Strategic and modest management of the evergreen shrub understory, combined with selective thinning of hardwoods, particularly red maple, may similarly benefit suppressed red spruce at our study sites. Red maple expanded dramatically across the eastern United States over recent decades and was the second most abundant tree species at Alarka Laurel, with basal area increasing considerably between 2007 and 2022 (Abrams 1998; Fei and Steiner 2009). Targeted removal of red maple could facilitate the release of suppressed spruce seedlings while retaining more ecologically desirable species such as oaks, an approach supported by the suppression-release dynamics observed at both Alarka Laurel and Rich Mountain.

Continued monitoring of these southernmost red spruce stands, including periodic re-surveys of our transects, is warranted, given the potential impacts these stands are likely to encounter over the coming decades. Monitoring temperature and precipitation within these basins promotes understanding of how these stands have remained resilient to climatic factors. Long-term monitoring of pest activity, particularly southern pine beetle outbreaks, should be incorporated into ongoing management efforts, given the potential for episodic infestations to substantially limit the growth and condition of overstory red spruce in these basins. Because spruce sapling and seedling growth is often limited by light availability (Busing 1985), measurements of the shrub layer, including gaps, should be prioritized, as these data can help forecast future recruitment and help inform management decisions. To that end, if managers decide to thin evergreen shrubs or overstory hardwood species to aid red spruce release into the overstory, we recommend monitoring to assess whether these treatments are successful in the recruitment of red spruce seedlings and growth of red spruce saplings.

CONCLUSION

The Alarka Laurel and Rich Mountain red spruce stands appeared stable and healthy. Each of the stands exhibited overstory, sapling, and seedling proportions comparable to other red spruce stands, with abundant seedlings at both sites and an overall healthy overstory spruce population. While the climate at these sites was likely relatively stable in the recent past and provided refugia for these stranded red spruce, further intensification of climate change could have detrimental effects if temperature increases reach the basins. Future monitoring of these disjunct stands is warranted, given their rarity, vulnerability to climatic change, and their efficacy as indicator species.

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