ABSTRACT: Red spruce (Picea rubens) and red spruce-northern hardwood mixed stands once covered as much as 300,000 ha in the Central Appalachians, but now comprise no more than 21,000 ha. Recently, interest in restoration of this forest type has increased because red spruce forests provide habitat for a number of rare animal species. Our study reports the results of an understory red spruce release experiment in hardwood-dominated stands that have a small component of understory red spruce. In 2005, 188 target spruce were identified in sample plots at six locations in central West Virginia. We projected a vertical cylinder above the crown of all target spruces, and in 2007, we performed a release treatment whereby overtopping hardwoods were treated with herbicide using a stem injection technique. Release treatments removed 0–10% (Control), 11–50% (Low), 51–89% (Medium), and ≥90% (High) of the basal area of overtopping trees. We also took canopy photographs at the time of each remeasurement in 2007, 2010, and 2013, and compared basal removal treatments and resulting 2010 canopy openness and understory light values. The high treatment level provided significantly greater six-year dbh and height growth than the other treatment levels. Based on these results, we propose that a tree-centered release approach utilizing small canopy gaps that emulate the historical, gap-phase disturbance regime provides a good strategy for red spruce restoration in hardwood forests where overstory spruce are virtually absent, and where red spruce is largely relegated to the understory.

Index terms: canopy gaps, Central Appalachians, forest restoration, gap-phase disturbance, red spruce, regime

INTRODUCTION

Central Appalachian red spruce (Picea rubens Sarg.) and red spruce-northern hardwood mixed forests probably covered >300,000 ha in West Virginia and small portions of adjacent Maryland and Virginia prior to the turn of the 20th century (Hopkins 1891, 1899). Nationally recognized as an endangered ecosystem type (Noss et al. 1995), Central Appalachian red spruce provides the sole habitat for a number of rare and sensitive endemic or disjunct species (Steele and Powell 1999; Pauley 2008; Stephenson 2013). These include the Cheat Mountain salamander (Plethodon nettingi Green) and Virginia northern flying (VNF) squirrel (Glaucus sabrinus fuscus Miller), as well as the southernmost population of snowshoe hare (Lepus americanus Erxleben) in eastern North America. Additionally, this community provides the only large area of habitat for breeding birds of northern affinities in the mid-Atlantic, i.e., northern goshawks (Accipiter gentilis L.) and saw-whet owls (Aegolius acadicus Gmelin.). There is also increasing interest in these forests as a sink for soil organic carbon (Nauman and Connolly 2014).

Greatly reduced by exploitative logging, subsequent wildfires, soil loss, and overall site degradation a century ago, the acreage of forests dominated by red spruce varies but is believed to be no more than 21,000 ha (USDA Forest Service 2014), according to current estimates, although the total area of forest with some red spruce presence (i.e., individual trees to small patches), may still approximate its presettlement extent (Byers et al. 2013). This era of exploitative harvesting constituted an anthropogenic disturbance that had no natural analog, as large-scale fire events were extremely rare in this ecosystem (Thomas-Van Gundy et al. 2007). Harvesting and subsequent slash fires replaced a structurally complex, multi-cohort, irregular forest with a homogenous landscape of largely even-aged forests dominated by northern hardwood species such as red maple (Acer rubrum L.), sugar maple (Acer saccharum L.), black cherry (Prunus serotina Ehrh.), American beech (Fagus grandifolia Ehrh.), and yellow birch (Betula alleghaniensis Britt.), often of poor quality and limited commercial value (Korstian 1937; Minckler 1945; Clarkson 1964).

In the years since 20th century harvesting, this community type, though recognized for its biodiversity contribution to the local landscape, was rarely considered as an active management or ecological restoration objective, particularly on public land. Meaningful interest in ecological restoration of red spruce in the Central Appalachians began gaining attention when linked to improving habitat quality and extent for the then federally endangered VNF squirrel (Schuler et al. 2002). As a regulatory driver, the squirrel previously limited
management actions in the red spruce type on public land (i.e., Monongahela National Forest, Canaan Valley National Wildlife Refuge). In the 1990s, however, with the discovery of VNF squirrel populations on private and state lands with active, ongoing forest management programs, there was increasing interest in red spruce restoration and stand improvement to simultaneously benefit the squirrel and produce other forest outputs. Despite the squirrel’s delisting in 2013 (USFWS 2013), public perception persists that VNF squirrel presence, along with other environmental concerns, greatly limits commercial forestry operations. However, our work suggests the potential applicability of silvicultural practices, be they commercial or noncommercial, to improve red spruce stand structure and extent, in turn improving habitat for spruce-dependent species such as VNF squirrels. Furthermore, noncommercial approaches that emulate fine-scale natural disturbances common within the Central Appalachian red spruce ecosystem to release target trees to the overstory and increase intra-stand structure (e.g., snags, coarse woody debris) have begun, and can be performed with less expense and may have lower impact on wildlife than commercial approaches (Schuler et al. 2002).

Methods that utilize natural disturbance regimes as a guide to restoration plans have been proposed or used in other forested ecosystems in the United States (Covington et al. 1997; Landres et al. 1999; Stephenson 1999; Long 2009; Arseneault et al. 2011), and in spruce forests in Finland (Kuuluvainen et al. 2002). Canopy gap creation to release single or clusters of red spruce trees suppressed in the midstory and understory is one approach managers in the Central Appalachians are beginning to implement to improve the condition and extent of this forest type (e.g., see USDA Forest Service 2011). To determine the feasibility of this method, we quantified recruitment success of red spruce trees released by creating small canopy gaps in the overstory.

Herein, we present six-year diameter and height growth results following a series of release treatments in largely hardwood stands that have a small component of understory red spruce. In this experiment, we expect that height and dbh growth should increase along a gradient of removal of overtopping basal area ranging from no removal to 100%. This research has been part of a larger effort that has previously (a) described species, age, and diameter structures of these forests, (b) used forest vegetation modeling to simulate the effectiveness of stand-based silvicultural treatments to enhance long-term overstory recruitment of understory red spruce, and (c) described the canopy gap dynamics of current, second-growth forests whose species composition and structure are drastically different from their preharvest condition (see Schuler et al. 2002; Rentch et al. 2007; and Rentch et al. 2010).

METHODS

Study Area

Regionally, red spruce and red spruce-northern hardwood mixtures occur along high ridges and plateaus (>1000 m) in the Allegheny Mountain subsection of the Appalachian Plateau Physiographic Province (Fenneman 1939). Common overstory associates include eastern hemlock (Tsuga canadensis (L.) Carr.), red maple, sugar maple, black cherry, American beech, and yellow birch. Mountains are capped by Pennsylvanian sandstone and Devonian shale, and soils are frigid, well- and moderately well-drained spodosols (Jenkins 2002). Climate is continental, with frequent fog, high annual precipitation, and the possibility of freezing temperatures any month of the year. Average minimum and maximum temperatures are, respectively, -9.6 and -0.9 °C in January and 13.2 and 21.3 °C in July (NCDC 2014). Average annual precipitation is 156 cm yr⁻¹, including approximately 383 cm of snowfall. Red spruce site indices (base age 50 years) ranged from 12.8 m to 19.8 m, depending on elevation and soil type (Flegal 1999).

Our study area was characterized by large tracts of public forest land that contain over 66% of the existing and potential red spruce forest habitat in West Virginia (Beane et al. 2013). We selected two study stands in each of the following locations: Monongahela National Forest (MNF; MNF1 and MNF2) in Greenbrier and Pocahontas Counties; Kumbrabow State Forest (KSF; KSF1 and KSF2) in Randolph County; and Canaan Valley National Wildlife Refuge (CVNWR; CVNWR1 and CVNWR2) in Tucker County (Figure 1). Our study stand selection on the MNF was constrained by the need to avoid potential impacts to existing populations of VNF squirrel and the Cheat Mountain salamander, as well as to other planned silvicultural and land management activities (USDA Forest Service 2011). Selected stands on KSF and CVNWR were linked directly to ongoing VNF squirrel habitat research (e.g., Menzel et al. 2006; Ford et al. 2007). Study stand size was variable, ranging from 10 to 15 ha, due to the density of understory red spruce.

Tree age in the study areas varied by stand. The overstories of four study stands (CVNWR1, CVNWR2, KSF1, KSF2) comprised a single cohort originating after clearcut harvesting between 1890 and 1930. The remaining two stands (MNF1, MNF2) were also harvested during that period, but retained a few older residual trees with some dating as far back as 1840. Four of the study stands had two distinct understory cohorts of red spruce; one of initial harvest origin and another 20–60 years younger. The two remaining stands had more or less continuous establishment of understory red spruce (Rentch et al. 2007).

Data Collection

In September–October 2005, we established sample plots (radius = 6.1 m) in each study stand centered on red spruce saplings/small trees (hereafter “target trees”) that were overtopped by hardwood trees and/or tall shrubs and, thus, candidates for overhead release. We selected target trees with a diameter at breast height (dbh) >2.54 cm and a live crown ratio >60%. We measured dbh and total height of each target tree. We projected a vertical cylinder above the crown of the target tree and then tallied and measured the dbh of all trees whose crowns fell within that space in an effort to quantify the degree of competition to the target tree. Mean number of sample plots per stand was 22 (SE, ± 7). In some
sample plots, we identified two or more target trees if all met our selection criteria and would be released by removal of the same overtopping hardwood trees. The mean number of red spruce target trees per stand was 30 (SE ±3).

We calculated the total basal area of all overtopping trees for each target tree and randomly assigned each a release treatment level: Control (0–10% removal of basal area of overtopping trees), Low (11–50%), Medium (51–89%), and High (≥90%). In July 2007, we applied release treatments in the field, using stem injection techniques with a 38% solution of Accord Concen-

trate™ (glyosphate, 53.8%) following established guidelines (Kochenderfer et al. 2012). We remeasured total height and dbh of all target trees during July 2007, June 2010, and July 2013.

We conducted canopy photography on clear to overcast days on the same day as tree measurement in 2007, 2010, and 2013. We took photographs using a Nikon E8400 digital camera with a fisheye lens attached (Nikon Model FC-E9). Analysis of hemispherical photographs required that photographs be oriented with the top center of the photograph towards magnetic north, which, along with determination of geographic position, allows for accurate determination of incident solar radiation across time and space. Initial camera locations were recorded and as much as possible, we replicated camera placement during subsequent re-measurements.

Data Analysis

We analyzed canopy photographs using the software WinSCANOPY (Regent Instruments, Quebec, Canada). Because the canopy imagery captured using a fish-eye lens greatly exceeded the extent of our treatments, we reduced the portion of the canopy analyzed by setting the sky grid to 400 pixels, which approximated a 38° mask. Photographs were analyzed for a variety of structural and light environment characteristics. In this study, we report percent canopy openness (i.e., the fraction of open sky unobstructed by vegetation) in the canopy above the lens in a three dimensional space, and Direct Site Factor (hereafter termed percent understory light), the relative amount of incident direct radiation penetrating below the canopy during the growing season (WinSCANOPY 2008). The 2007 series of canopy photographs were taken at the time of treatment, so this represented baseline conditions.

We analyzed tree height and dbh percent growth for years 2007–2013 based on the percent of overtopping basal area removed. We also examined changes in understory and overstory light levels associated with different basal area removal treatments. All growth analysis was done using mixed linear models with repeated measures and preplanned orthogonal contrasts (PROC MIXED, SAS 2013). Initial 2007 dbh and height values were used as covariates in our models.

RESULTS

The 2007 mean diameter at breast height and height of the 177 target trees in six study locations were 8.6 (0.20) cm (mean (SE)) and 6.0 (0.12) m, respectively. Target trees had a pretreatment mean canopy openness value of 17.4 (0.6)%, and a mean understory light of 18.9 (0.9)%. There were no significant differences in 2007 mean
values for height, dbh, canopy openness, or understory light by treatment level. Total plot basal area averaged 33.3 (1.1) m²/ha, and the average overtopping basal area was 17.9 (1.2) m²/ha. On average, each target red spruce was overtopped by 3.4 (0.12) trees.

Mean values of actual overtopping basal area removed were 1%, 35%, 65%, and 100%, for Control, Low, Medium, and High treatments, respectively. By 2013, six-year total dbh and height growth ranged from 2.0 to 2.8 cm for dbh growth, and 1.2 to 1.8 m for height growth (Figure 2 A-B). Across all treatment levels, the percent increase in dbh exceeded the change in height growth (Table 1). Both the High and Low basal area removal treatments showed significantly greater percent height and dbh growth than the control (Table 1). The amount of percent height and dbh growth during the first three years (2007–2010) and the last three years (2010–2013) was very comparable for all treatments (Figure 2 A-B). Both height and dbh growth consistently were greatest following the High level of treatment. At lower levels of treatment, responses varied by time and were not proportional to degree of release.

**Change in Light Levels**

Removal of overtopping basal area increased understory light to a greater extent than percent canopy openness. The mean level of canopy openness in 2010 for the High release treatment was 28%, with very little difference between Medium, Low, and Control treatments (Figure 3A). For understory light, the maximum values were 42 and 41% in the High and Medium release treatments, respectively, and there was a better distribution of values corresponding to release treatment levels (Figure 3B). At the most recent remeasurement in 2013, six years after treatment, percent openness and understory light still exceeded pretreatment values for all treatments.

**DISCUSSION**

Our results suggest that full overhead release (High treatments) yielded significantly greater dbh and height growth of understory red spruce than the control. The lack of a stronger response from Medium and Low release treatments may, in part, be attributed to the low correlation between basal area removal and increases in light levels. For example, whereas the High release treatment removed 100% of overtopping basal area, the resulting canopy openness light level in 2010 was only 28%, respectively, much less than expected, and much less than the optimal 50% light levels recommended by Seymour (1995), Moore et al. (2007), and Dumais and Prevost (2014). The weak relationship between basal area removal and light increases, may, in part, be due to the extent of the canopy analyzed in hemispheric photographs. Although we restricted our canopy analysis to what approximated our treatment zone (trees overtopping target red spruce), the irregular shape and size of the competing trees required a larger view of overhead conditions than that influenced by our treatments. A true full release of an understory tree of the size and stature reported here from all overhead shading would require an opening that exceeds the size of a typical gap in this forest type (i.e.,
The low correspondence between percent basal area removal and increase in light may also be the result of our release protocols. We only considered for removal those trees that fell within a vertical cylinder projected above the perimeter of the crowns of target red spruce. Given the large height disparity between the hardwood overstory and the red spruce understory, a more reasonable removal prescription would have girdled trees that lay within 3–4 m of this cylinder. Assuming an average spruce crown diameter of 2 m, this additional 3–4 m would typically yield a canopy gap of approximately 50–80 m², which conforms to mean canopy gap size in these forests (Rentre et al. 2010). We considered a 45 degree cone projected from the terminal of the target tree, as recommended by Smith et al. (1997), but this technique is operationally difficult for managers in practice. Moreover, in cases where the respective heights of target trees and the hardwood overstory are widely disparate, this method yields too large a canopy gap. Finally, increases in light after treatment were undoubtedly reduced somewhat by the presence of residual stems and woody crowns of dying and dead trees.

Despite the modest increases in light levels produced by overtopping tree removal, there was little evidence of any delay in growth response, similar to the quick growth response of plantation grown red spruce after release observed by Hornbeck and Kochenderfer (1998). Moreover, there was also a persistence of the response. A comparison of height and dbh growth for years 2007–2010 and 2010–2013 showed approximately equal growth increases for both time periods. However, given the estimated canopy closure rates for the High treatment (10 to 20 years for canopy openness and understory light, respectively), it is unlikely that the canopy gaps we created would remain open for a sufficiently long period of time to permit canopy ascension of these smaller-sized red spruce after one release event.

In natural stands, canopy gaps created by windthrow are the ecological basis of most red spruce regeneration and eventual canopy ascension (Dumais and Prevost 2007). In West Virginia, Rentch et al. (2010) found that canopy gaps averaged 53.4 m² in size in largely northern hardwood stands with a small red spruce understory component. Red spruce’s autoecology and ecophysiology are well-suited to respond to such small gaps. Red spruce is adapted to heavy shade, reaching up to 82% of maximum net photosynthetic rate at light levels similar to sunflecks (Alexander et al. 1995). Light interception in the understory is also enhanced by red spruce’s capacity to modify its crown architecture, favoring lateral growth over height growth (Dumais and Prevost 2007). These adaptations result in a high rate of survival of red spruce seedlings and long-term persistence of red spruce in the understory. Indeed, the wide range of ages of understory red spruce (20–70 years) in our study attests to this adaptation (Rentch et al. 2007).

Conversely, large canopy openings with sudden increases in light may stress shade tolerant species such as red spruce, increasing the risk of photo-inhibition and photo-damage (Alexander et al. 1995; Dumais and Prevost 2007). Exposure of understory red spruce to full sunlight also may introduce temperature stress and affect water relations (Alexander et al. 1995). Together, these factors may delay the onset of, or reduce shoot growth, for up to several years.

Table 1. Pairwise comparisons of (A) mean percent height change (%HGC) and (B) mean percent dbh change (%DGC) of red spruce target trees in east-central West Virginia, 2007–2013, by basal area removal treatment level.

| Treatment 1 | %HGC (SE) | Treatment 2 | %HGC (SE) | DF | t value | P   |
|-------------|-----------|-------------|-----------|----|---------|-----|
| Control     | 22.5 (2.1)| High        | 28.6 (1.9)| 175| 3.39    | 0.009|
| Control     | 22.5 (2.1)| Medium      | 24.3 (2.3)| 175| 1.35    | 0.178|
| Control     | 22.5 (2.1)| Low         | 25.5 (3.2)| 175| 2.16    | 0.032|
| Medium      | 24.3 (2.3)| High        | 28.6 (1.9)| 175| 1.67    | 0.097|
| Low         | 25.5 (3.2)| High        | 28.6 (1.9)| 175| 1.05    | 0.296|
| Low         | 25.5 (3.2)| Medium      | 24.3 (2.3)| 175| -0.65   | 0.514|

| Treatment 1 | %DGC (SE) | Treatment 2 | %DGC (SE) | DF | t value | P   |
|-------------|-----------|-------------|-----------|----|---------|-----|
| Control     | 26.3 (2.6)| High        | 29.6 (2.7)| 177| 2.64    | <0.001|
| Control     | 26.3 (2.6)| Medium      | 28.5 (3.8)| 177| 1.93    | 0.056|
| Control     | 26.3 (2.6)| Low         | 29.7 (4.2)| 177| 2.32    | 0.021|
| Medium      | 28.5 (3.8)| High        | 29.6 (2.7)| 177| 0.43    | 0.671|
| Low         | 29.7 (4.2)| High        | 29.6 (2.7)| 177| 0.19    | 0.849|
| Low         | 29.7 (4.2)| Medium      | 28.5 (3.8)| 177| 0.24    | 0.813|
Moreover, larger gaps would undoubtedly encourage more hardwood competition that may ultimately delay spruce ascension into the main canopy. The maximum degree of release that would most benefit red spruce growth without increasing individual tree stress and hardwood competition is unclear. However, generally, low- to medium-sized canopy openings provide the best combination of light and shelter, minimizing physiological stress and maximizing the speed of acclimation to higher light levels and higher temperatures. In more northern subboreal forests, Moore et al. (2007) found red spruce saplings reached 80% of maximum height growth in 50% open sky and Seymour (1995) recommended 50% of full sunlight for good height growth.

In terms of gap size, Dumais and Prevost (2014), working in Quebec, found red spruce advance regeneration responded best in intermediate-sized gaps (100–300 m²) created by group selection harvest, as opposed to small (<100 m²) gaps created by single tree selection or large gaps (>700 m²) created by clearcuts. Smaller openings also convey competitive advantages to species such as red spruce that have abundant advanced regeneration present in the understory and recruit continuously, as opposed to gap obligate species such as yellow birch and red maple that generally become established after a canopy disturbance (Duchesne and Prevost 2013).

In the Central Appalachians, there is some evidence that red spruce is recovering from past exploitative practices even without active intervention. For example, Fortney and Rentch (2003) and Madron (2013) compared aerial photography of two regions of West Virginia and found that forest cover of red spruce increased over a period of approximately 40 years. Rollins et al. (2010) found increased densities of red spruce trees, saplings, and seedlings between 1992 and 2005, along with either declining or steady hardwood densities, across three hardwood-red spruce ecotones at three locations in West Virginia. Mayfield and Hicks (2010) observed similar results on Gaudineer Knob (near study stands KSF1 and KSF2 on the Monongahela National Forest). Finally, Rentch et al. (2010) studied canopy gaps along ten 500-m transects in the general area of the current study. Although American beech, yellow birch, and red maple were the most common gap makers, red spruce was projected to be the gap filler in nearly 40% of the gaps.

Thus, whereas others have raised concerns related to red spruce and anticipated effects of climate change (Iverson et al. 2008; Beane 2010), current stand and landscape level dynamics seem to indicate that red spruce is regenerating, increasing in abundance, and occupying a greater share of the landscape in the Central Appalachians, albeit slowly (Morin and Widmann 2010; Nowacki et al. 2010). Moreover, others have reported improved growth rates of red spruce in the northern Appalachians (Kosiba et al. 2013). Therefore, taking advantage of opportunities for red spruce restoration and achieving greater resilience in the face of anticipated climate changes seems to be a viable strategy for now. Improvements in air quality and moderation of extreme winter temperatures also may be enhancing spruce growth and lessening winter injury, thereby aiding in the process (Kosiba et al. 2013).

The changes reported in the Central Appalachian red spruce forest are occurring...
in an environment characterized by overwhelmingly even-aged stands, the residue of wholesale harvesting during 1880–1920. Current canopy gap formation rates suggest that natural restoration processes should continue, though at a slow pace. As stands mature, crown sizes of hardwood overstory trees increase, as do canopy gap sizes, resulting in gaps that remain open for a longer time period. This suggests that the likelihood that understory red spruce can eventually capture gaps before they close from above will likewise increase. Nevertheless, forest management objectives in the region, particularly those focused on increasing suitable habitat for the area’s threatened and endangered species, may warrant that more active silvicultural treatments are needed to accelerate the rate of red spruce restoration.

MANAGEMENT IMPLICATIONS

Any silvicultural prescription to increase the rate of red spruce restoration must take into account the current state of the resource. A common scenario is (a) a canopy dominated by hardwood trees species, (b) absent or widely scattered mature, seed-bearing red spruce trees, and (c) a widely scattered, suppressed component of understory red spruce, many as old as the overstory. Accordingly, a tree-centered release approach using canopy gap creation, whereby understory red spruce are selected for release, would be most productive. This technique focuses the impacts of density reductions of overtopping hardwood trees on those individual red spruce understory trees that are the target of current restoration efforts, and less on the stand as a whole. Managers could experiment with a variety of opening sizes, depending on which competitors of red spruce were present, the status of the red spruce understory, and the physical characteristics of the site.

In view of the weak correlation in this experiment between percent basal area removed and increases in available light, a larger canopy opening may be appropriate. We recommend that release prescriptions should target trees for removal that fall within 3–4 m of the perimeter of the crown of the target tree, although this size may have to be adjusted depending on the relative growth attributes in second-growth stands, and tree quality. Our approach would be sensitive to spatial limitations imposed by existing or potential habitat for the red spruce-dependent VNF squirrel, Cheat Mountain salamander, and other biotic components of these high-elevation communities. Depending on the specific method of release—harvesting, girdling, or herbicide application to competing trees—other structural characteristics of irregular stands such as standing snags, coarse woody debris, and a vertically differentiated canopy could be enhanced (Kuuluvainen et al. 2002; Raymond et al. 2009). As an additional bonus, revenue from harvest of commercial tree species could be used to offset costs of noncommercial operations. The use of commercial harvesting to release understory red spruce would require directional felling and equipment movement that would avoid any damage to the understory spruce. Such practices are being implemented on high-elevation forests managed by the West Virginia Division of Forestry with initial success at protecting understory red spruce trees from operational activities (Barbara Breshock, Assistant State Forester, Forest Management and Stewardship, West Virginia, pers. comm).

Implementation of our tree-centered approach should be one part of a diverse restoration strategy that also includes underplanting red spruce on historical habitat where it is now absent (Hornbeck and Kochenderfer 1998), increasing old-growth attributes in second-growth stands, and protecting older stands that are legacies of the original forest. Strategic releases and planting to reduce fragmentation of isolated patches of red spruce currently are identified as priority management actions on the Monongahela National Forest (see Management Prescription 4.1, Monongahela National Forest Land and Resource Management Plan; USDA Forest Service 2011). We also think this approach could be used to mitigate eastern hemlock loss in riparian areas at mid- to high-elevations to help protect existing coldwater fisheries resources in the region.

We propose these steps at the same time that we recognize additional ecological concerns that may complicate or compromise future restoration efforts. Airborne pollution, acid deposition, and ozone all have historically been implicated in red spruce decline (Adams et al. 1985) and impairment of overall ecosystem function (Boggs et al. 2005; Petty and Thorne 2005). Currently, however, climate change is considered the primary threat to the long-term integrity of red spruce forests in the region (Beane et al. 2013). Red spruce in this region are particularly vulnerable to climate change due to their restricted topographic location on the highest mountaintops, low elevation barriers to migration, and narrow climatic tolerances (Byers et al. 2010). Tree distribution simulations by both Iverson et al. (2008) and Beane (2010) predict significant losses of suitable red spruce habitat under several warming scenarios, particularly on marginal areas near the elevational or latitudinal limits of its distribution. Restoration of red spruce, particularly in those areas identified as once being occupied by red spruce, or areas now modeled as having highly suitable habitat, will provide red spruce and other biotic components the greatest capacity to adapt to climate change while maintaining diversity and ecosystem function.

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