

Characteristics of Red Spruce (*Picea rubens* Sarg.) Encroachment at Two Central Appalachian Heathland Study Areas

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ABSTRACT

During the late 19th and early 20th centuries, intensive land use nearly eliminated red spruce (Picea rubens Sarg.) throughout portions of West Virginia (WV). Red spruce has been slow to regenerate on mountaintop heathland barrens surrounding Canaan Valley, West Virginia (WV), and little is known about the nature of encroachment. Using field surveys, geospatial data, and statistical modelling, the objectives were to 1) characterize and compare red spruce encroachment at two upland heath study areas in West Virginia (Bear Rocks and Cabin Mountain), 2) characterize percent cover of major ground cover types associated with red spruce regeneration sites in order to elucidate biotic interactions, and 3) model the biophysical correlates of red spruce encroachment using geospatial data and statistical modelling. Red spruce count was similar at both study areas, but there were substantially more seedlings and saplings at Cabin Mountain. Modelling revealed a positive relationship between red spruce count and rock cover and a negative relationship between red spruce and stand distance.

KEYWORDS

Canaan Valley, Geospatial, Heath, Landscape Change, Picea Rubens, Red Spruce, Vegetation Expansion

INTRODUCTION AND BACKGROUND

Historical events may have profound and lingering effects on ecosystems (Foster, 2003). Canaan Valley, WV, and the surrounding Allegheny Highlands have a dramatic history of human land use that has left a lasting landscape legacy on its formerly extensive old growth red spruce (*Picea rubens* Sarg.) forests. Beginning with the establishment of pulp and paper mills in Davis, WV, and the arrival of the railroad in 1884, hundreds of thousands of acres of red spruce were eliminated through logging (Allard & Leonard, 1952). Removal of the extensive old-growth spruce forests altered the cool, moist microclimate and soil conditions necessary for red spruce growth and reproduction (Adams & Stephenson, 1989). Deep layers of moist humus dried out and eroded to bedrock in the wake of logging-associated fires (Allard & Leonard, 1952). When logging ceased by 1924, the formerly extensive red spruce forests had been nearly eliminated leaving a substantially altered ecosystem with an uncertain future (Allard & Leonard, 1952; Fortney & Rentch, 2003; Schimpf & Miller, 2016).

Subsequent to this intense anthropogenic disturbance, the former red spruce forests have been replaced by heath, grassland, and deciduous forest communities (Fortney & Rentch, 2003). Heath

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barrens and grassy balds present today in the southern and central Appalachian Mountains may have either anthropogenic or non-anthropogenic origins (Gimingham, 1972; Strausbaugh & Core, 1978; Specht, 1979). Some were purportedly maintained during the Pleistocene by mammalian herbivores (Weigl & Knowles, 1995). Others are the result of prehistoric and historic anthropogenic disturbances in the form of burning, agriculture, and timbering (DeViro, 1991; Rentch & Fortney, 1997; Wells, 1956). Although the present range of red spruce is expanding due to encroachment into these altered habitats (Allard & Leonard, 1952), modern spruce extent is still more restricted than historical distributions (Adams & Stephenson, 1989).

Myriad factors regulate tree encroachment in abiotically stressful, transitional ecosystems (e.g., alpine treelines, heathlands, bogs). Aspect and slope, for example, determine potential for a surface to receive solar radiation and regulate landscape interactions with regional climate and weather patterns (Barry, 2008). Aspect can thus influence the timing and spatial pattern of snowmelt, and in effect, exposure of seedlings to desiccating forces and frost damage (e.g., Frey, 1983; Miller & Halpern, 1998). Microtopography is also important in improving local site conditions that may increase seedling establishment and survival in exposed locations (Resler, 2006); fine-scale geomorphic features, such as boulders, hummock and hollow topography, and periglacial patterned-ground can provide leeward wind sheltering, shading, increase soil moisture retention, elevate roots from water inundation, and allow sediment to accumulate (e.g., Stine et al. 2011; Resler et al. 2005). These fine scale features exist within meso and macro topographic contexts that have further relevance to community growth and regeneration. Additionally, biotic characteristics such as groundcover and species associations can facilitate or impede regeneration. Research suggests that the vegetation stratum into which tree encroachment occurs can profoundly and differentially impact tree seedling germination and survival (e.g., George & Bazzazz, 2014) thereby affecting spatial pattern of regeneration, and ultimately recruitment.

Factors contributing to red spruce encroachment into heathlands are important to consider given the local extinction vulnerability of both red spruce ecosystems (given land use history) and heathland ecosystems (given spruce encroachment). The distribution of spruce is discontinuous throughout the central and southern Appalachians, restricted to areas characterized by the cool, moist environment conducive to red spruce growth and regeneration (Adams et al., 2010). Red spruce is restricted to the highest elevations, typically above ~ 900 m (3000 ft) in Allegheny Mountain region of the Appalachian Plateau (Adams et al., 2010), rendering red spruce stands ecological 'sky islands' under present environmental conditions, with limited migration capacity in light of climatic warming and current land uses. Globally, heathlands are characterized by ericoid shrubs and acidic, nutrient-poor soils (Gimingham, 1972; Fagúndez, 2013). Because these communities are represented by complex interspecific interactions and narrow specialist species, many are at risk from intensive land use, pollution, climate change, and tree encroachment (De Graaf et al., 2009; Fagúndez, 2013).

Here, the authors use geospatial technologies and primary data collected from field surveys to examine abiotic (i.e., terrain features and ground surface cover) and biotic (i.e., associated species and species cover) factors associated with red spruce regeneration and encroachment. The study focuses on two heathlands of the Central Appalachian highlands surrounding Canaan Valley, West Virginia. Our objectives were to: 1) characterize and compare red spruce encroachment at two upland heath study areas in West Virginia, 2) characterize percent cover of major ground cover types associated with red spruce regeneration sites in order to elucidate biotic interactions, and 3) model the biophysical correlates of red spruce encroachment using geospatial data and statistical modelling.

STUDY AREAS

The study focuses on red spruce encroachment into upland heathlands in the Allegheny Mountains of West Virginia (WV). Here, conditions are favorable to species that are less tolerant of the wider regional climatic regime (Dobroski, 2011). Although technically found at elevations below climatic

treeline (Leffler, 1981) treeless upland heathlands persist under abiotic conditions characterized by leached or infertile soil, abundant snowpack, and windward exposure to high winds that slow or preclude substantial conifer incursion, thereby delineating a “localized” treeline. Whittaker (1956) refers to this idea as a topographic climax—a climax community based upon a local variation rather than a blanket application of successional ideas.

We selected two publicly accessible upland heathland study areas in the Central Appalachian Mountains of WV (*Figure 1*). These are: Cabin Mountain (~1250 m a.s.l.) managed by the Canaan Valley National Wildlife Refuge (CVNWR), and Bear Rocks Preserve (1219 m a.s.l.), managed by The Nature Conservancy. Both study areas prominently feature Ericaceae, Rosaceae, and Lycopodiaceae families growing as dense, low-lying shrubs with sparse tree cover. Red spruce and balsam fir (*Abies balsamea* (L.) Mill) climax forests were more extensive, and at lower elevations (<500 m) toward the end of the Pleistocene (Allard & Leonard, 1952; Adams et al. 2010).

Whereas both sites are similar in elevation and latitude, significant differences in weather between the sites do occur, warranting a comparative approach. In the presence of cold-air damming (CAD) events, Bear Rocks often experiences much cooler and wetter conditions than those on Cabin Mountain. Easterly or northeasterly winds generated by the position of a synoptic scale anticyclone over New England or eastern Canada produce clouds and periods of light precipitation along with significant development of rime at Bear Rocks. Cabin Mountain often lies on the western edge of this cold-air damming effect, and the erosion of cold air under the influence of southerly or southwesterly winds can produce significantly warmer temperatures accompanied by clearing skies with little precipitation. Temperature differences of 7° C have been observed between these two sites when CAD conditions are present (unpublished data, Carroll, 2019). These CAD events, each lasting from one to four days, occur three to five times per month in the winter season (Bell & Bosart, 1988).

Climate conditions substantially truncate the growing season. The frost-free period in Randolph County, south of Cabin Mountain, is 90 days, with the possibility of frost occurring during any month of the year (Fortney & Rentch, 2003). Winds on the exposed plateau frequently gust in excess of 97 km per hour from the northwest, with 145 km per hour gusts recorded on Cabin Mountain (unpublished data, Carroll, 2019). These strong, directional winds result in flagging of red spruce. Average annual snowfall (2001 and 2019 winter seasons) was 440 cm at 1132 m between October and May (unpublished data, Leshner, 2019). Frost-shattered rock outcrops of likely periglacial origin (e.g., Clark & Ciolkosz, 1988) exist at both study areas (but are especially prominent at Cabin Mountain, *Figure 2*), and retain soil moisture and standing water (personal observation, White & Resler, 2018).

Although the land use history for the Canaan Valley and Allegheny Mountains is known generally, little is known about the specific land use history of each study area. Documents do indicate that steam-powered locomotives, which transported lumber for the Laurel Lumber Company (Lewis, 1998) resulted in fires on Cabin Mountain, and that the forested slopes of the Cabin Mountain study area were clearcut, and subsequent expansive soil loss resulted in bedrock exposure (Allard & Leonard, 1952).

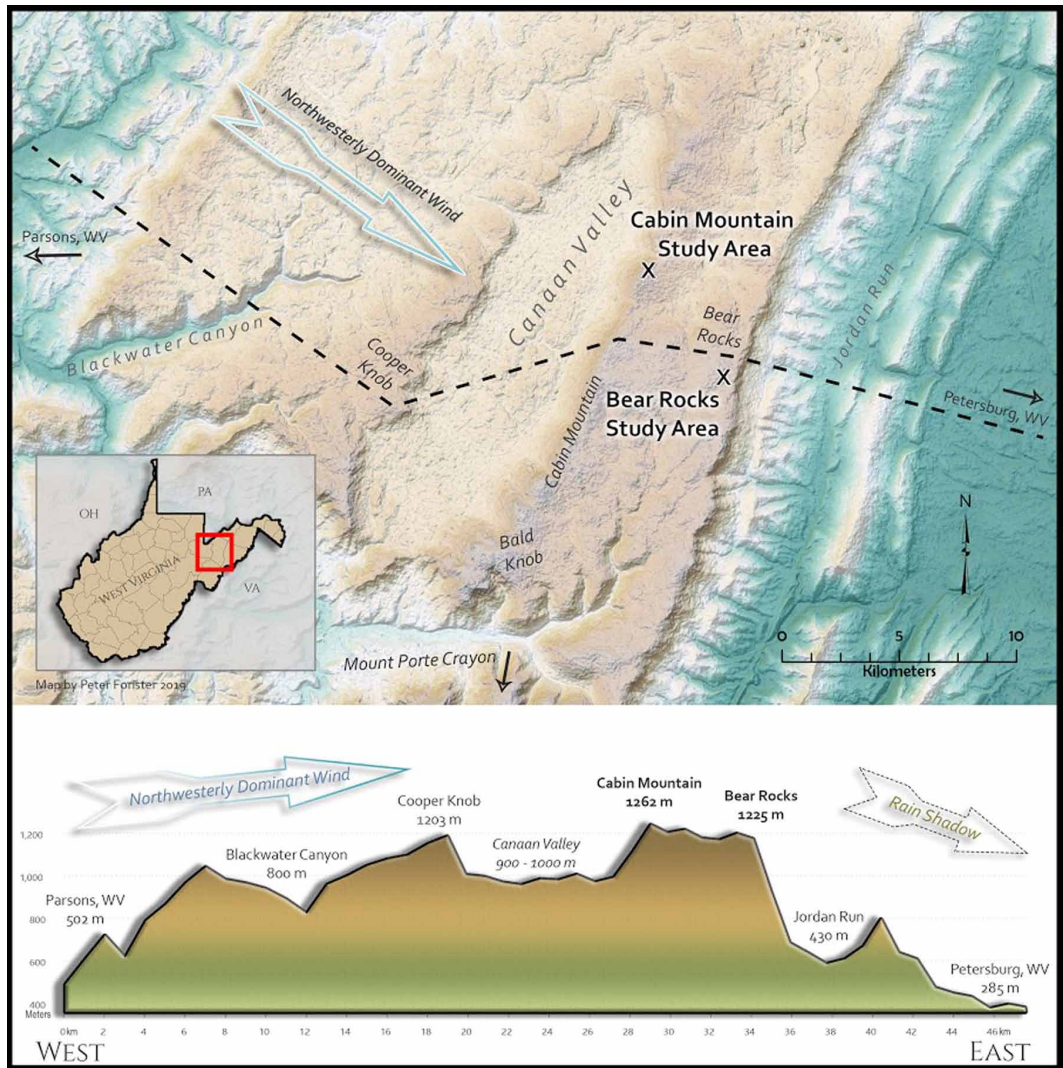
METHODS

Field Methods

Fieldwork occurred from June through September, 2018. Two sampling procedures were employed: vegetation quadrat sampling for meso-scale characterization of red spruce encroachment (seedlings, saplings, and mature trees), and fine-scale, paired plots for assessing plant and ground cover associated with spruce seedling regeneration sites.

To characterize red spruce encroachment, 15, 15 m x 15 m quadrats were established at Bear Rocks, and 16 quadrats were placed at Cabin Mountain, for a total of 31 quadrats. Quadrat placement was determined prior to entering the field by generating random points with a threshold minimum distance of 30 m. The authors navigated to these coordinates (each of which became a plot centroid), in the field using a high-accuracy Trimble GeoXH GNSS. Sampling procedures in

Figure 1. Location of study areas and topographic profile



vegetation quadrats were adapted from Jennings et al. (2004) and Byers et al. (2010). The authors obtained a count of all red spruce present within each quadrat. For all trees with stems falling within the quadrat, we measured tree height (using triangulation from measures obtained using a transect tape and clinometer). Physiognomic characterization and percent estimations of herbaceous cover, subshrub cover (shrub vegetation up to 1 m in height), tall shrub cover (shrub vegetation up to 2 m in height), and tree cover (red spruce and other tree cover over 2 m in height) were based on field observations, and supplemented by inspection of field-obtained plot photographs. Within each plot, percent rock cover was estimated using visual estimations of real cover.

At Cabin Mountain, plant species richness and ground cover were recorded proximal to seedlings and saplings in order to elucidate biotic interactions. Thirty-two circular plots (45 cm radius) were centered around selected red spruce seedlings and saplings (defined as ≤ 1.37 m, randomly selected from vegetation quadrats) to document vegetated and non-vegetated cover associated with spruce regeneration. For comparison, these ‘regeneration’ plots (hereafter referred to as ‘tree plots’) were

Figure 2. Periglacial rock outcrops, interspersed with flagged red spruce, ferns, and heath vegetation at Cabin Mountain



paired with a ‘heath’ plot (hereafter referred to as ‘heath plots’) placed at a random compass direction 1 m away from the tree plot. To further assess spatial patterns in biotic and abiotic associations within each plot, the authors placed an additional 15 cm radius plot within the 45 cm radius tree plot (*Figure 3*). This procedure resulted in 32 paired tree-heath plots and 32 paired nested tree plots with concentric 45cm and 15cm sampling areas.

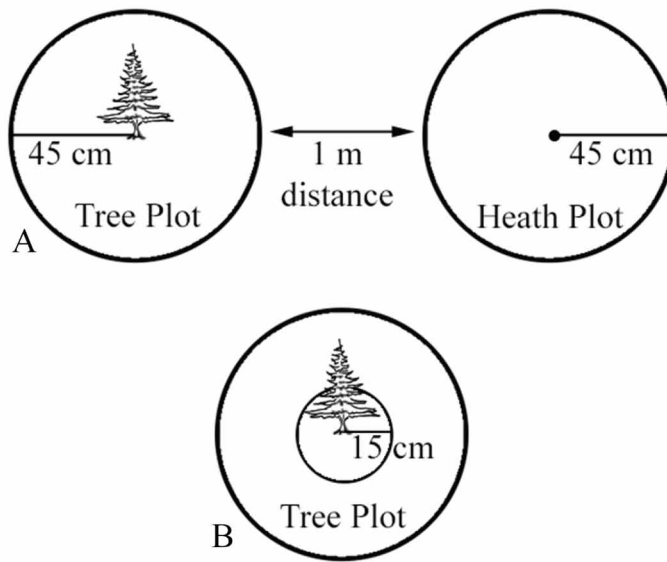
Within each paired tree-heath plot, each vascular plant species was identified and its real coverage (irrespective of overlap, e.g., Jennings et al., 2004) was recorded. Total % coverage of graminoids, mosses, and lichens were similarly observed. Finally, non-vegetated cover (e.g., litter and rock) was estimated. Moss, graminoid, and lichen were not identified to the species level.

Deriving Geospatial Variables

Field-derived variables can be corroborated with GIS-derived variables that serve as surrogates of environmental conditions (such as moisture and solar radiation) or biotic processes (such as dispersal, estimated, for example, by distance measures). In particular, digital elevation models (DEMs) have been effective for deriving ecologically relevant terrain variables in mountainous environments (e.g., Resler et al. 2014; Lambert et al. forthcoming).

A literature review informed the selection of variables potentially relevant to red spruce regeneration. A 1 m statewide mosaic digital elevation model (2018) from the West Virginia GIS Technical Center (WVGISTC) served as the data source for deriving terrain-related biophysical variables for subsequent inclusion in statistical analyses (*Table 1*). Since segments of the DEM had originally been collected at 3 m resolution and were resampled by WVGISTC as 1 m imagery for a statewide mosaic, the authors resampled to a 3 m horizontal resolution.

Figure 3. A) Paired tree-heath plot diagram representing a tree plot (left) and a heath plot (right) with one-meter distance separating each edge (not to scale). Heath plots were located in a random direction from the associated tree plot. B) Nested plot of 15 cm radius, centered on individual *P. rubens*. Each 15 cm radius plot was nested within the original 45 cm radius tree plots, and the assessment of each was conducted at the same time as the larger tree and heath plots. Since seedlings and saplings were more prevalent at Cabin Mountain, we restricted our paired plot sampling to this study area.



The authors used ArcMap 10.5's Zonal Statistics to derive values for *elevation*, *aspect*, *slope*, *curvature*, *flow accumulation*, and *insolation* for each vegetation quadrat. Though *elevation*, *aspect*, and *insolation* have been shown in other research to be useful in assessing vegetation communities (e.g., Coughland & Running, 1997; Dowbroski, 2011; Kambo & Danby, 2018; Wilkinson & Humphreys, 2005; Table 1), they were not included in the final model due to low variation in values across the study areas. *Distance to stand* referred to Euclidian distance from the plot centroid to the nearest visible red spruce stand in the basemap imagery.

Statistical Analyses

Multivariate correlation matrices assessed artificial correlation for all continuous numeric variables. Since raw percent cover vegetation types tended to be highly correlated with one another, these were combined into a categorical variable called Physiognomic Class, which contained three categories based on the dominant vegetation type of the quadrat. These categories included: Woodland (tree cover dominant), Shrubland (tall- and subshrub cover dominant), and Herbaceous (herbaceous cover dominant). The vegetation cover types were condensed to Physiognomic Class categories to reduce artificial correlation between the raw cover percentages (see section 4.2.3). Percent rock cover was included separately in its original form for each quadrat. Variables incorporated into the modelling ultimately included the response variable, *red spruce count per plot*, site as the random effect, *physiognomic class* and *rock cover* (field-derived predictor variables), and *slope*, *curvature*, *flow accumulation*, and *distance to stand* (GIS-derived predictors variables).

A Generalized Linear Mixed-Effect Model (GLMM), which accounts for potential violations of sampling interdependence (e.g., Hurlbert, 1984) was generated using the glmmTMB package in

Table 1. Geospatial-derived variables

Variable	Data Source	Resolution / Purpose	Justification
Elevation	Digital Elevation Model 1 m Statewide Mosaic (2018) - West Virginia GIS Technical Center	Mosaic resampled to 3 m horizontal resolution for processing at coarsest resolution	Elevation is a topographical element that impacts temperature and thus vegetation communities (e.g., Dobroski, 2011)
Aspect	Geospatial processing conducted on DEM (above) using ESRI's ArcMAP 10.5	Mosaic resampled to 3 m horizontal resolution for processing at coarsest resolution	Aspect governs insolation, snowmelt, wind exposure, and soil moisture (e.g., Kambo & Danby, 2018; Miller & Halpern, 1998; Rose & Malanson, 2012)
Slope	Geospatial processing conducted on DEM (above) using ESRI's ArcMAP 10.5	Mosaic resampled to 3 m horizontal resolution for processing at coarsest resolution	Slope can govern soil moisture dynamics (Kampf et al., 2015)
Curvature	Geospatial processing conducted on DEM (above) using ESRI's ArcMAP 10.5	Mosaic resampled to 3 m horizontal resolution for processing at coarsest resolution	Describes the complexity of a sloped surface, further impacting landscape-vegetation interaction (Wilkinson & Humphreys, 2005)
Flow Accumulation	Geospatial processing conducted on DEM (above) using ESRI's ArcMAP 10.5	Mosaic resampled to 3 m horizontal resolution for processing at coarsest resolution	Refers to moisture accumulation on a surface, impacts soil moisture, solifluction, and fluvial processes, all of which impact vegetation communities in arctic-alpine environments (le Roux & Luoto, 2014)
Insolation	Geospatial processing conducted on DEM (above) using ESRI's ArcMAP 10.5	Mosaic resampled to 3 m horizontal resolution for processing at coarsest resolution	Solar radiation is one of the critical factors influencing snowpack (Coughlan & Running, 1997), and snowpack is tied to seedling survival (Gerdol et al., 2013)
Distance to Stand	Measured using linear distance (m) from center of the plot to the nearest cluster of red spruce identifiable in aerial imagery	Nearest 5 m	Represents distance from seed source of the plot center (e.g., Dibble et al., 1999)

RStudio to assess correlates of red spruce count per quadrat. For GLMM analysis, vegetation quadrats were combined from both study areas to increase sample size. Multiple candidate models were assessed prior to determining the appropriate model fit for the dataset. For example, Poisson structures were tested, but found to be inappropriate due to variances within the data. AIC and BIC values were also compared among candidate models. All candidate models were run using the glmmTMB (Brooks et al., 2017) package's negative binomial (nbinom2 in the package) log link family structure without zero inflation. The authors used Mann-Whitney *U* tests to assess differences between study areas in red spruce height, count, and cover, as measured in the vegetation quadrats. To characterize ground cover associated with red spruce regeneration sites, Wilcoxon tests assessed differences in species and group coverage in matched paired plots (heath vs. tree plots, and 15 cm radius tree plots and 45 cm radius tree plots).

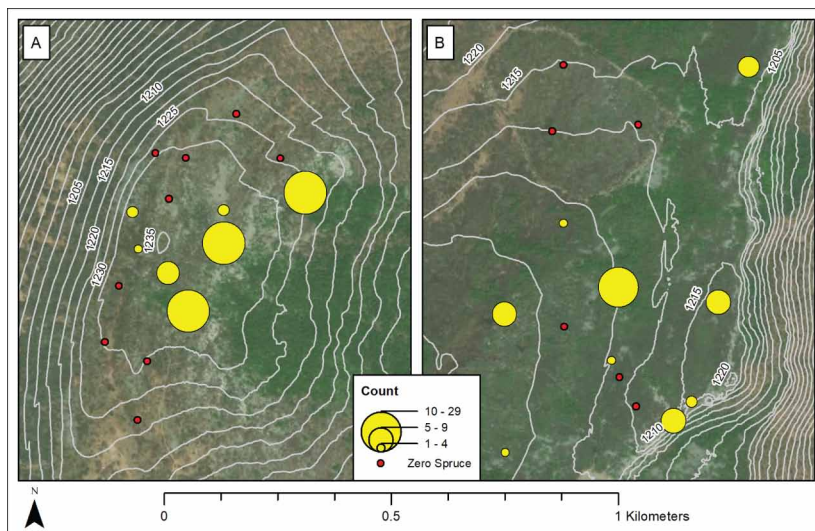
RESULTS

Red Spruce Characteristics and Differences Between Study Areas

Within the 15m x 15m vegetation quadrats, we measured 65 red spruce at Bear Rocks and 99 at Cabin Mountain, for a combined total of 164. Of those, 50 ($n = 22$ at Bear Rocks, $n = 28$ at Cabin Mountain) were taller than breast height (1.37 m) and 114 ($n = 43$ at Bear Rocks, $n = 71$ at Cabin Mountain) were shorter than breast height. The mean height of trees > 1.37 m at Bear Rocks was 5.48 m $\pm$ 2.98 compared to 3.58 m $\pm$ 2.20 at Cabin Mountain. The mean height of trees > 1.37 for the two study areas combined was 4.43 m $\pm$ 2.73. The mean height of trees ≤ 1.37 m at Bear Rocks was 66.79 cm $\pm$ 34.77 cm compared to 41.27 cm $\pm$ 29.41 cm at Cabin Mountain. The mean height of seedlings and saplings ≤ 1.37 m for the two study areas combined was 50.90 cm $\pm$ 33.76 cm. For all trees combined, median tree heights recorded at the Bear Rocks vegetation quadrats ($n = 65$) were significantly taller than trees at Cabin Mountain ($Z = 10.37$; $p < 0.01$, Mann Whitney U Test). At Cabin Mountain, more red spruce, particularly saplings and seedlings, were found to be spatially arranged along a gradient moving toward the dominant stand, apparent in Figure 4, which depicts the vegetation quadrat locations and associated red spruce counts.

The number of red spruce trees per vegetation quadrat was highly variable, ranging from 1 to 29 trees per plot at Cabin Mountain and 1 to 25 trees per plot at Bear Rocks. Fifteen total quadrats had zero red spruce present (Table 2, $n = 9$ at Cabin Mountain and $n = 6$ at Bear Rocks). The authors found

Figure 4. Location of vegetation quadrats present at Cabin Mountain (A) and Bear Rocks (B) sites, with symbols proportional to red spruce count. Contour lines represent 5 m elevation. Plots at Cabin Mountain were along the ridge top in exposure to direct, north-westerly winds.

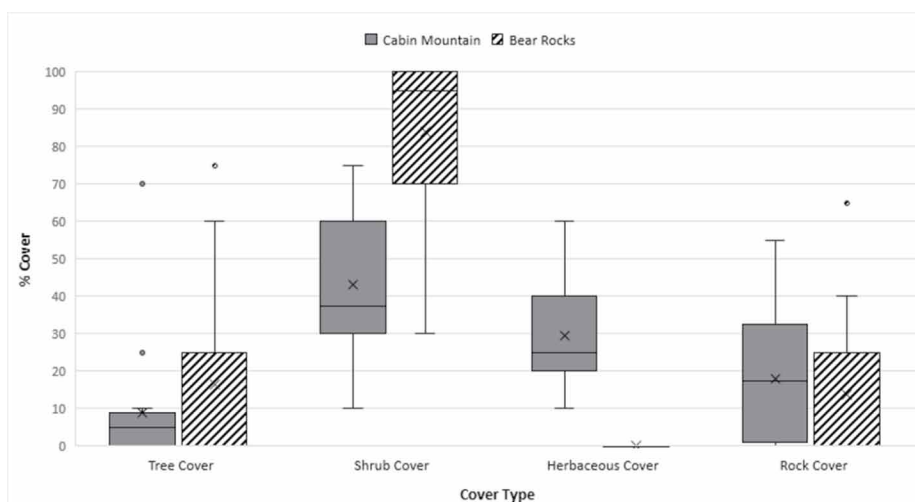


no significant differences in the median count of trees per vegetation quadrat (for all trees combined, trees ≤ 1.37 m, and trees > 1.37 m) at Bear Rocks and Cabin Mountain (All trees, $Z = 0.17$; $p = 0.68$, Trees ≤ 1.37 m, $Z = 0.09$; $p = 0.77$, and Trees > 1.37 m, $Z = 0.03$; $p = 0.86$).

Overall, vegetation quadrats without red spruce tended to have slightly higher coverage of subshrub and herbaceous vegetation (Table 2). Eleven of the 31 quadrats had $\geq 5\%$ tree cover, with a range of 0 to 75% tree cover across all quadrats. The median tree cover was 5% and mean tree cover

was 5.9% $\pm$ 6.1% in plots with red spruce. Across all vegetation quadrats, rock cover was more common in plots with red spruce (Table 2). Although range of rock cover is similar (55% in plots with no red spruce plots, and 65% in plots with red spruce), average rock cover in the plots without red spruce is 6% in comparison to 25% in plots with red spruce. Of 12 plots with < 5% (reported as 0%) exposed rock coverage, 10 were devoid of red spruce. Comparisons of cover type differences between the two study areas (Figure 5) revealed significantly higher median percent shrub cover at Bear Rocks than at Cabin Mountain ($Z = 14.70$; $p < 0.001$, Mann Whitney U Test) and significantly higher herbaceous cover at Cabin Mountain than at Bear Rocks ($Z = 2.25$; $p < 0.001$). No significant differences in rock cover ($Z = 1.0562$; $p = 0.30$) or tree cover ($Z = 0.06$; $p = 0.81$) were observed between the two study areas (Figure 5).

Figure 5. Percent cover of four ground cover types measured in vegetation plots. Significant differences ($p < 0.001$) were found in percent shrub and herbaceous cover between the two study areas.



Species and Ground Cover at Red Spruce Regeneration Sites

Sixteen vascular species were identified in the paired plot assessments at the Cabin Mountain study area, excluding red spruce. *Vaccinium angustifolium* was the most common vascular species, followed by *Osmunda cinnamomea*. These sixteen species represent seven families, the most common being Ericaceae, Rosaceae, and Lycopodiaceae. Mean cover varied widely and standard deviation from the mean was high for all species (Table 3).

For the tree-heath paired plots, only the graminoid coverage exhibited significant differences (Figure 6), with higher graminoid cover in the tree plots than the heath plots ($Z = 2.03$; $p < 0.05$, $n = 96$).

Among the nested tree-tree paired plots ($n = 96$), both rock cover ($Z = 1.08$; $p < 0.05$) and graminoid cover ($Z = 2.03$; $p < 0.05$) were significantly higher in the 45 cm radius plot than the 15 cm radius plot, suggesting less concentration of these cover types at the immediate base (15 cm radius) of the tree. Median *V. angustifolium* was significantly lower in the 15 cm plot than the 45 cm plot ($Z = 3.01$; $p < 0.01$), indicating lower coverage at the immediate base of the tree (within 15 cm from the stem) than at a further distance from the base (Figure 7).

Table 2. Red spruce characteristics for all quadrats, combined. Cover values (Rock, Subshrub, Herbaceous, Tall Shrub, and Tree Cover) are all measured in percent of area.

	Quadrats, no <i>P. rubens</i>	Quadrats, <i>P. rubens</i> present (min 1)	Max. <i>P. rubens</i> count*	Min. <i>P. rubens</i> count^
Number of Quadrats	15	16	2	4
Max, Min., Count	-	-	29	1
Range; Mean Count +/- SD	-	28; 10.25 +/- 10.61	-	-
Max, Min., no./ha-1	-	-	1288.89	44.44
Range; Mean no./ha-1 +/- SD)	-	1244.45; 455.56 +/- 471.56	-	-
Max., Min., Range Rock	55%, 0%, 55%	65%, 0%, 65%	35%, 20%, 15%	65%, 0%, 65%
Mean +/- SD Rock	6.4% +/- 14.44%	24.69% +/- 16.34%	27.5% +/- 7.5%	27.5% +/- 23.58%
Max., Min., Range Subshrub	100%, 20%, 80%	95%, 0%, 95%	35%, 25%, 10%	95%, 0%, 95%
Mean Subshrub +/- SD	64.2% +/- 28.25%	46.25% +/- 27.70%	30% +/- 5%	45% +/- 35.88%
Max., Min., Range Herbaceous	60%, 0%, 60%	40%, 0%, 40%	25%, 10%, 15%	15%, 0%, 15%
Mean Herbaceous +/- SD	23.4% +/- 22.10%	9.38% +/- 12.23%	17.5% +/- 7.5%	3.75% +/- 6.50%
Max., Min., Range Tall Shrub	25%, 0%, 25%	75%, 0%, 75%	10%, 0%, 10%	75%, 0%, 75%
Mean Tall Shrub +/- SD	4% +/- 7.84	13.13% +/- 23.94%	5% +/- 5%	20% +/- 36.74%
Max., Min., Range Tree Cover	70%, 0%, 70%	25%, 0%, 25%	25%, 5%, 20%	5%, 0%, 5%
Mean Tree Cover +/- SD	5.33% +/- 18.07%	5.94% +/- 6.12%	15% +/- 14.14%	3.75% +/- 2.5%

* Represents the two plots that had the maximum number of red spruce, 29 trees.

^ Represents all plots that had the minimum number of red spruce. In this case, there were four plots with only one red spruce present.

Biophysical Correlates of Red Spruce Count for Combined Study Areas

The GLMM analysis revealed a positive relationship between rock cover and red spruce count per vegetation quadrat, indicating that the higher the percent rock cover per quadrat, the higher the number of red spruce per quadrat. Further, the model revealed a negative association between stand distance and red spruce count per vegetation quadrat, at a minimum of 95% confidence (*Table 4*), indicating that the red spruce count per plot decreased with distance to the continuous red spruce stand.

DISCUSSION

Here the authors used geospatial technologies, primary field-collected data, and statistical analysis to characterize red spruce regeneration and encroachment into two upland heathland study areas. Overall characteristics of red spruce seedlings, saplings, and mature trees were assessed using vegetation quadrats placed randomly at two study areas. Additionally, to elucidate biotic interactions, fine-scale paired plots were used to examine ground cover characteristics associated with red spruce seedling regeneration sites. Finally, biophysical correlates of red spruce encroachment (count per quadrat) were assessed for both study areas combined using GLMM.

Table 3. Vascular species identified in paired plots (Strausbaugh & Core, 1978; Weakley et al. 2012) with descriptive statistics for 45cm radius paired plot values, heath (H) and tree (T). All values were rounded to nearest 5% for cover estimate.

Species	No. Plots (45cm H)	No. Plots (45cm T)	No. Plots (15cm T)	Max Cover (H)	Mean +/- SD(H)	Max Cover(T)	Mean +/- SD(T)
<i>Vaccinium angustifolium</i> Ait.	26	29	20	85	35 +/- 20	70	25 +/- 15
<i>Vaccinium corymbosum</i> L.	2	2		95	25 +/- 40	20	5 +/- 10
<i>Kalmia latifolia</i> L.	3	2		80	30 +/- 30	10	5 +/- 5
<i>Menziesia pilosa</i> (Michx.) Juss.	0	1		-	-	10	-
<i>Sorbus Americana</i> (Marsh.)	0	1		-	-	5	-
<i>Rubus hispidus</i> L.	9	9	6	30	15 +/- 10	35	15 +/- 10
<i>Amelanchier laevis</i> (Wiegand)	1	4	1	5	-	10	5 +/- 0
<i>Photinia melanocarpa</i> (Michx.) Robertson & Phipps	0	1		-	-	5	-
<i>Diphasiastrum digitatum</i> (Dillenius ex A. Braun) Holub	1	0		5	-	-	-
<i>Dendrolycopodium</i> <i>obscurum</i> (L.) A. Haines	9	11	8	30	10 +/- 5	25	10 +/- 5
<i>Lycopodium clavatum</i> L.	2	1		15	10 +/- 5	5	-
<i>Pteridium aquilinum</i> (L.) Kuhn	6	4	1	30	20 +/- 10	25	15 +/- 5
<i>Dennstaedtia punctilobula</i> (Michx.) T. Moore	4	3	2	20	10 +/- 5	15	5 +/- 5
<i>Osmundastrum</i> <i>cinnamomeum</i> (L.) C. Presl	9	11	4	40	30 +/- 20	80	25 +/- 20
<i>Acer rubrum</i> Linnaeus	1	1	1	5	-	5	-
<i>Oclemena acuminata</i> (Michx) Greene	1	2	1	5	-	10	10 +/- 5

Red Spruce Characteristics and Differences Between Study Areas

Overall, red spruce trees were present in approximately half (15/31) of the total vegetation quadrats, indicating that red spruce regeneration and encroachment into heath is occurring at the two study areas, despite historical, intensive land use. The majority of spruce trees were found at the Cabin Mountain study area (99/164), but there were no significant differences found between red spruce count per quadrat between the two study areas. Although the number of trees > 1.37 m were comparable between Cabin Mountain and Bear Rocks ($n = 28$ and $n = 22$, respectively), there were substantially more seedlings and saplings (≤ 1.37 m) at Cabin Mountain ($n = 71$) than at Bear Rocks ($n = 43$). Furthermore, trees were significantly taller at Bear Rocks than at Cabin Mountain. Tree ring dating

Figure 6. Percent cover of six major cover types measured in heath-tree paired plots (45 cm). Significant differences in graminoid cover ($p < 0.05$) were found between paired tree and heath plots.

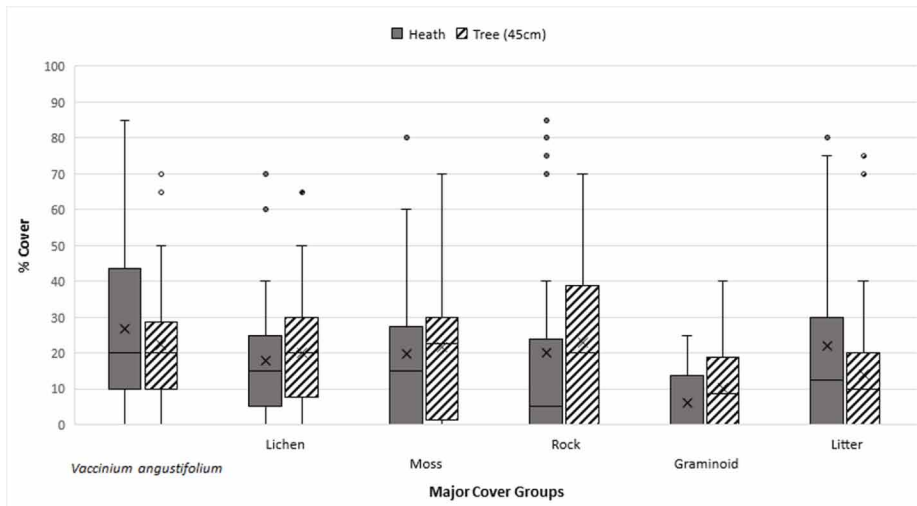
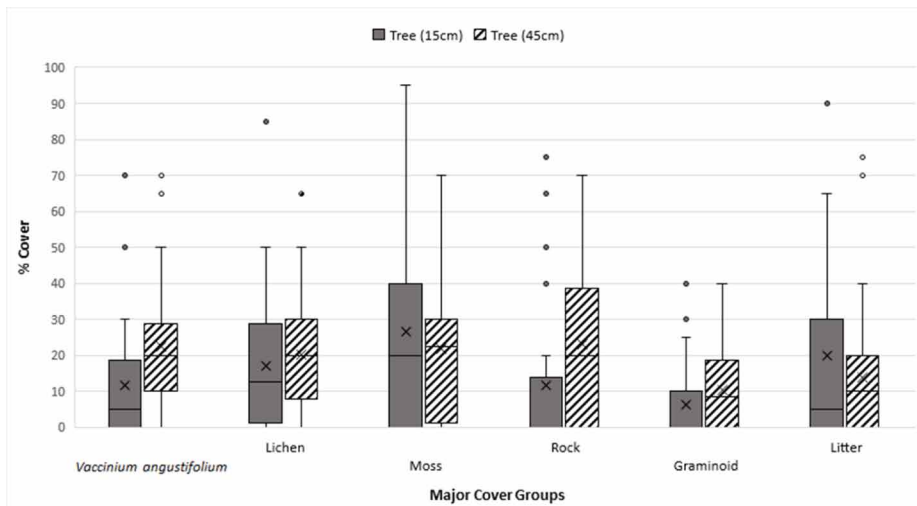


Figure 7. Percent cover of six major cover types measured in 15 cm and 45 cm nested tree plots. Rock cover, graminoid cover and *V. angustifolium* cover were significantly lower in the 15cm plots than the 45 cm plots.



would be needed to confirm tree ages and to explore whether the shorter tree heights at Cabin Mountain indicate more recent regeneration or slower growth rates.

Overall shorter trees at Cabin Mountain compared to Bear Rocks could be explained by differences in geography between the two areas, land use histories, or a combination of both. Differences in land use intensity and timing may have played an important role. If Cabin Mountain is indeed experiencing more recent regeneration than observed at Bear Rocks, a more intense land use legacy at Cabin Mountain that has resulted in longer recover times may be part of the explanation. Unfortunately, the authors were not able to obtain a detailed land use history of the Bear Rocks study area, and therefore explanations surrounding land use remain speculative. Further studies are needed to uncover site-specific land use histories to determine their role in explaining observed encroachment patterns.

Table 4. Biophysical correlates of red spruce count, as determined by GLMM analysis using glmmTMB. Shrubland and Woodland are categories of Physiognomic Class. The third category, Herbaceous, was automatically included as part of the intercept, and values of Shrubland and Woodland were generated relative to Herbaceous cover.

Variable	Estimate	Std. Error	z Value	Pr(> z)
(Intercept)	2.333651	0.995237	2.345	0.01904
Shrubland*	0.235273	0.847447	0.278	0.78130
Woodland*	1.376370	1.246687	1.104	0.26958
Rock	0.061011	0.022405	2.723	0.00647
Slope	-0.268753	0.160527	-1.674	0.09409
Stand Distance	-0.033316	0.007564	-4.404	1.06e-05
Flow Acc.	-0.001992	0.001774	-1.122	0.26172
Curvature	-0.362009	0.374246	-0.967	0.33339

AIC = 132.6, BIC = 147.0. * Categories of Physiognomic Class. The third category, Herbaceous, was automatically included as part of the intercept, and values of Shrubland and Woodland were generated relative to Herbaceous cover.

Ecologically significant differences in weather patterns could also explain differences between the two study areas. The western and eastern geographic locations of Cabin Mountain and Bear Rocks, respectively on the elevated plateau (*Figure 4*) results in exposure of each study area to differing weather conditions that likely have substantial ecological relevance. Despite Cabin Mountain's exposure to high topographically-channeled winds, cooler conditions coupled with significant rime ice development associated with cold air damming events at Bear Rocks may cause foliage damage and mortality (e.g., Foster, 1988 for balsam fir forests). Specifically, a comparative study to examine wind speed and direction at each study site would therefore be relevant to understand the role of wind-stress and rime ice on red spruce seedlings. Furthermore, since red spruce seeds are wind-dispersed (Burns & Honkala, 1990), more research is needed to determine the role of wind in seed dispersal.

Finally, cover type characteristics may present a barrier to successful seed germination. Specifically, the higher shrub cover observed at Bear Rocks likely forms dense mats that act as a barrier to seed germination, resulting in seed and seedling desiccation. Several studies have reported that leaf and twig litter can act as a barrier to seedling germination (e.g., Burns & Honkala, 1990; Moore, 1917; Westveld, 1926, 1930, as cited in Baldwin, 1934).

Ground Cover Characterization of Red Spruce Regeneration Sites, and Potential Biotic Interactions

Species associations and ground cover characteristics are useful for elucidating biotic interactions such as competition or facilitation. Furthermore, microsite conditions at the locations where seeds land are crucial for successful establishment. Red spruce establishment may be limited by shrubs through competition and barrier effects (Griscom et al., 2011). Although competition and facilitation were not explicitly tested in this study, the authors described heath species and compared ground coverage in paired 45 cm tree-heath plots to expound potential relationships. As determined by a Wilcoxon test, significantly more graminoid cover was found in tree plots than heath plots (*Figure 6*) suggesting that graminoid cover (as opposed to shrub cover) may benefit red spruce establishment. Furthermore, significantly higher herbaceous cover was found at Cabin Mountain compared to Bear Rocks, where there were substantially more seedlings and saplings. In an experimental study of conifer seedling survival in different cover types (Germino et al., 2002) survival of emergent conifer seedlings was highest (90%) within grasscover at alpine treelines where seedlings were shaded from sunlight, and lowest in openings within grass (19%). Exposure to high sunlight may exacerbate low-temperature and water stress in young conifer seedlings, inhibiting their establishment.

Observations from nested tree plots at Cabin Mountain revealed no red spruce seedlings present directly under or within dense *Vaccinium* vegetation. *Vaccinium* coverage within a 45 cm radius of the tree is significantly concentrated beyond the first 15 cm from the stem, potentially indicating a competitive association, at least at early life stages of red spruce. Thick mats of *Vaccinium* likely act as a barrier to successful red spruce seed germination, resulting in seed desiccation during the one-year duration they are viable (Burns & Honkala, 1990). It is also possible that deer-browse, which was apparent in the study areas, alters ground cover characteristics, thereby affecting biotic interactions between seedlings and ground cover (Griscom et al., 2011). Finally, although moss cover was not statistically associated with red spruce regeneration, the authors observed multiple red spruce seedlings emerging within mounds of damp moss. Future studies should assess the potential role of moss as a facilitating moisture source.

Figure 8. a) A red spruce grows between two boulders at Cabin Mountain, and b) Red spruce growing directly from shallow soil bed amidst rocks on Cabin Mountain. Note standing water in foreground.



Biophysical Correlates of Red Spruce Count for Combined Study Areas

Biophysical models revealed a positive relationship between rock cover and red spruce count. This finding was supported by observations from the vegetation quadrats. Across all quadrats, rock cover was more common in vegetation quadrats with red spruce (Table 2). Average rock cover in the plots without red spruce is 6% in comparison to 25% in plots with red spruce. Of the 12 quadrats with < 5% exposed rock coverage (reported as 0%), 10 were devoid of red spruce. Rock cover likely enhances seed germination and seedling. Cabin Mountain vegetation quadrats where red spruce was present ($n = 7$) featured a mean of 27.14% $\pm$ 9.95% rock cover, as opposed to 10.67% $\pm$ 17.37% rock cover in the Cabin Mountain plots that had no red spruce ($n = 9$). At Bear Rocks, the plots with no red spruce present each also had no rock cover, compared to a mean of 22.78% $\pm$ 19.74% in plots with red spruce present ($n = 9$).

The authors suggest rock cover provides a micro-environment conducive to red spruce seed germination and seedling establishment. The association between ‘nurse’ rocks and encroachment has been documented in other abiotically stressful environments (e.g., Pérez, 2009; Resler et al., 2005; Resler, 2006). Should a seed land in the lee of a rock, or fall between cracks among rocks, it is probable that rock cover provides increased moisture availability for plants beneath boulders or in blocky soil (e.g., Pérez, 1991; 2009), temperature regulation (e.g., Greenwood et al., 2015 for treelines), slope stabilization (Pérez, 2017), and mediate the effects of fire (Coop & Schoettle, 2009). For example, fire events have been found to expose rock cover by burning away organic matter and litter (Stine & Butler, 2015), and rock features that help to retain soil moisture can support regeneration where desiccated, post-fire soils cannot. At Bear Rocks and Cabin Mountain, rocky outcrops are areas

with minimal duff and litter buildup, and comparatively high soil moisture (personal observation, White & Resler, 2018) that can be conducive to seed germination. Ironically, it appears as if rocky outcrops exposed due to historical land use events provide a facilitative element for subsequent red spruce establishment.

Modelling also revealed a negative relationship between distance to stand and tree count. Red spruce count decreased with increasing distance from seed source. Research has shown that distance to mature, seed-producing trees is relevant to establishment, and thus to the spatial patterns of red spruce encroachment into heath (e.g., Cavallin & Vasseur, 2009; Dibble et al., 1999; Feoli, 2010). Red spruce seeds are wind-dispersed (Burns & Honkala, 1990), and the typical wind speed, consistency, and direction at each study area would therefore be relevant to understanding the distribution of spruce seeds beyond the stand and into the heath. Across all vegetation quadrats, the median distance from stand at plots with no red spruce present was 95m (mean 120 +/- 66, *Table 2*), and to plots with red spruce the median distance was 27.5 (mean 40 +/- 40, *Table 2*). These numbers roughly correspond with research that has identified an approximate dispersal range of roughly 100 m from the parent tree for red spruce, with successful dispersal to greater distances being unlikely (e.g., Dumais & Prévost, 2007; Hughes & Betchel, 1997; Walter et al., 2017).

Data availability and suitability limited the inclusion of variables in the model presented in this study. Provided the data were available at relevant spatial and temporal resolutions, wind direction, wind speed, and snow cover data would likely inform the understanding of spatial encroachment patterns of red spruce. Research into land use history of each site, and the assignment of categorical variables based on land use type, duration, and time since abandonment, could illuminate the relationship between land use legacy and subsequent regeneration. In the future, the inclusion of soil moisture maps would be informative, however at present, such data exist at too coarse a spatial resolution to be valuable for the questions addressed here. Additionally, more sample plots, across a wider area of heath, could help establish how regeneration patterns and communities interact with micro- and meso-topographic conditions. It remains important, albeit challenging, to supplement and validate geospatial-derived information with in-situ field data collection in data-sparse areas.

CONCLUSION

Little is understood about the specific factors contributing to spruce expansion in upland heathlands. To our knowledge, this is the first study to provide baseline information on both biotic and abiotic factors contributing to red spruce encroachment in upland heathlands in the Central Appalachians. The results described here suggest red spruce do regenerate in heathlands, but further research must be conducted to determine the rate of stand encroachment into heathland.

The objectives of this study were threefold. To meet them, the researchers conducted field surveys on regenerating red spruce and surrounding ground cover of two heathland communities. Rock cover, such as the abundance of frost-shattered rock and periglacial deposits that are common in both study sites, was shown to be strongly associated with the regeneration of red spruce, potentially due to sheltering effects or moisture retention. The linear distance of vegetation quadrats from reproducing stands of red spruce was shown to be negatively correlated to the presence of red spruce at heathland sites, suggesting that there is a zone of ideal viability that demarcates the expanding edge of a red spruce stand. Together, these two elements provide baseline information about factors contributing to the spatial patterns of red spruce encroachment into heathlands. More research will be necessary to adequately inform best management practices, particularly studies involving in-situ field collection and sampling of these communities over a longer time scale.

Whether the coming decades will witness a community shift from heathland to red spruce, the persistence of the heath, or a developing stable state of spruce-dotted heathland bordering spruce forest will depend largely on land management practices and the long-term viability of either community in the face of climate change. More frequent disturbance events associated with the

Anthropocene (Asselin et al., 2006; Loudemilk et al, 2012) – particularly fire, increased drought, and insect infestations such as the balsam woolly adelgid – in conjunction with chronic pressures of climate change, could prevent a full return to the former climax community, allowing heath to persist. Ultimately, isolated populations of red spruce that remain on mountaintops such as on Cabin Mountain could be replaced with a novel, more disturbance-tolerant community that favors heath vegetation (Bargmann et al., 2014). Moving forward, the scale of time over which the ecosystem responds will determine whether or not the red spruce and balsam fir forests of the pre-logging period will return.

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