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Twenty-five Years of Succession in Isolated Montane Red Spruce Communities at Twelve Sites in the Central Appalachians

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ABSTRACT

Study plots (each 0.1 ha) were established and then sampled in 12 isolated red spruce communities in the Central Appalachians during the period of 1982 to 1985. These same plots were resampled >25 years later in June 2011 to assess the successional changes that had taken place. Collectively, the calculated importance value for red spruce (*Picea rubens*) decreased for the large tree (≥10 cm DBH [diameter at breast height]) stratum (-11.1) but increased for the small tree (≥2.5 cm but >10 cm DBH) stratum (+15.5). The relative density of red spruce increased in the sapling strata (+49.4%), but decreased for seedlings (-19.9%). Species richness of shrubs decreased from 12 species (2.2/site) to seven (1.8/site). Percent ground cover of rock and course woody debris were essentially unchanged (+1.2% and -0.3%, respectively), while percent ground cover of bryophytes and herbaceous plants decreased (-14.8% and -9.4%, respectively). Although red spruce decreased in the large tree stratum, the species experienced notable increases in the small tree and sapling strata. In many instances, small trees and saplings of red spruce have become well established in canopy gaps, often forming dense thickets, indicating the potential for red spruce-dominated communities to persist at these sites. These data suggest that these communities do not yet show any evidence of a negative response to global climate change, which has implications for forest management at higher elevations in the Central Appalachians.

Key words: Coniferous forests, forest stand dynamics, *Picea rubens*, remnant populations, subalpine, successional change.

INTRODUCTION

The isolated montane red spruce (*Picea rubens* Sarg.) communities of the Central and Southern Appalachian Mountains are relics of the Last Glacial Maximum and are among the most endangered forest types in the United States (Noss et al. 1995). Their present-day limited distribution is the result of long-term climate change and the accumulated effects of natural and often intense anthropogenic disturbance events (Korstain 1937, Shields 1962, Watts 1979). The sites where red spruce communities occur across the Central and Southern Appalachians function as refugia for an appreciable number of plant and animal species such as the Canadian bunchberry (*Cornus canadensis* L.), the Cheat Mountain Salamander (*Plethodon nettingi* Green) (Pauley 2008), and the Virginia Northern Flying Squirrel (*Glaucomys sabrinus fuscus* Miller) (Ford et al. 2004) and are typically characterized by some of the highest numbers of rare species per unit area for any sites in the eastern United States (Byers et al. 2010).

Widespread reports of reduced health and vigor (Mielke et al. 1986), high mortality rates (Siccama et al. 1982), and reduced radial growth trends (Adams et al. 1985) in red spruce prompted an intense research effort (especially in the northeastern United States) across red spruce communities from the 1980's through the 1990's. Climate change (McLaughlin et al. 1987), climatic variations (Johnson et al. 1988), natural stand dynamics (Eagar & Adams 1992), pollution (Geballe et al. 1990) as well as a host of other hypotheses were advanced during this period to explain the spruce decline phenomenon. A consensus was never reached, but a complex interplay of these and other factors likely accounted for the various local and regional decline episodes that were observed.

The Central Appalachian growth trend decline that occurred from the 1930's through 1990's appeared to have stabilized by the early 2000's (Schuler et al. 2002). More recent studies (Kosiba et al. 2018) have reported increased red spruce growth rates (across the northeast) which have been attributed to warmer temperatures (beyond the historical growing season) and, to a lesser extent, decreased rates of acid deposition. Ground-based surveys (Mayfield & Hicks 2010, Nowacki et al. 2010, Rollins et al. 2010) documented, for several sites across the region, abundant red spruce regeneration that has encroached surrounding hardwood communities. Projects (e.g., Schuler et al. 2002, Rentch et al. 2016) have tested the feasibility of various silvicultural manipulations to facilitate the perpetuation and expansion of the red spruce forest type with some success. However, results from environmental models have forecast the continued loss of suitable red spruce habitat, ultimately predicting a reduction in the extent of the red spruce forest type across the region (Iverson et al. 2008, Walter et al. 2017).

The primary objective of the study reported herein is to report the structural and compositional changes that occurred in plots established in 12 isolated red spruce communities in the Central Appalachians over the >25 year period between the 1980's and 2011. These plots were sampled originally to obtain baseline data on these red spruce communities in the 1980s and then were resampled in 2011 to assess the successional changes that had taken place over this period. A secondary objective was to relate patterns in the data obtained for the 2011 sampling period for the three physiographic provinces (Appalachian Plateau, Blue Ridge, and the Ridge and Valley) in which the spruce communities are located. A novel aspect of the research described herein was that two of the coauthors (HWA and SLS) carried out the sampling in both the 1980s and 2011.

MATERIALS AND METHODS

Tenth (0.1) hectare study plots were established and then sampled during the period between 1982 and 1985 in 12 isolated red spruce communities located across the Central Appalachians (Figure 1). These same plots were resampled in 2011 (Table 1). Compositional and structural quantitative data were collected for all major strata of vegetation, utilizing a series of nested subplots during both sampling periods. Diameter at breast height (DBH) and species identification were determined and recorded for living trees (stems ≥10 cm DBH) and small trees (<10 cm but ≥2.5 cm) in each 0.1 hectare plot. Four nested 5 x 5 m quadrats were placed at the 10, 20, 30, and 40 m marks along the central axis of each 0.1 ha plot and used to sample saplings (tree species <2.5 cm DBH but ≥1.0 m high) and shrubs (including vines). Saplings and shrubs were identified to species, counted, and recorded. Ten 1 x 1 m quadrats were placed at 5 m intervals along the central axis of each 0.1 ha plot and used to sample seedlings (tree species <1.0 m tall) and percent cover of bryophytes, course woody debris, herbaceous plants, and rocks. Seedlings were identified to species, tallied, and recorded. Percent cover was estimated using the Daubenmire cover class rating scale (Daubenmire 1968).

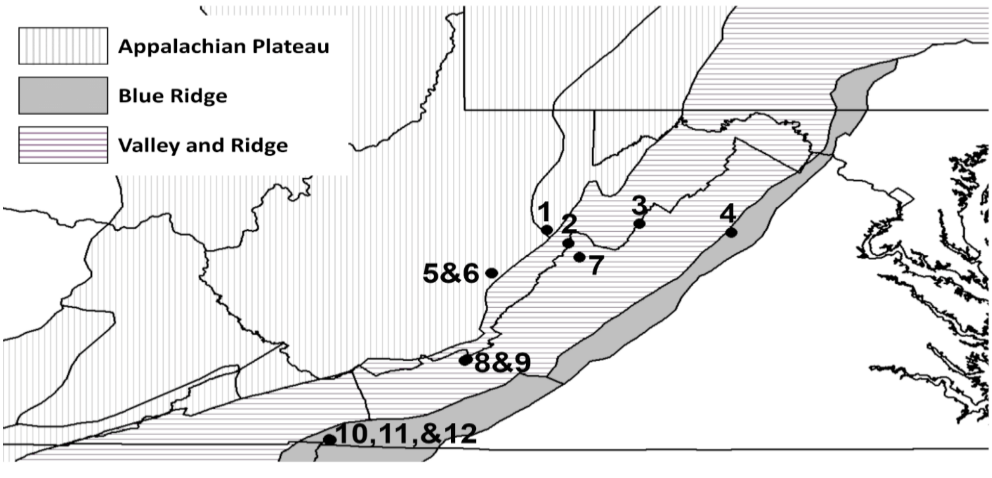

Figure 1. Sampling sites: 1. Blister Run, 2. Tamarack, 3. Spitzer, 4. Limberlost, 5. Frosty Gap 34, 6. Frosty Gap 35, 7. Sounding Knob, 8. Little Spruce Bog, 9. War Spur, 10. Whitetop I, 11. Whitetop II, 12. Whitetop III

Table 1. Site characteristics, locations, and sampling dates for the isolated red spruce communities considered in the present study.

Site Name	1st Sample	Last Sample	Latitude	Longitude	Elevation (m)	Exposure (°)	Slope (%)	Physiographic Province
Blister Run	4/9/1983	6/8/2011	38.6014	-79.8537	1,120	335	5	Appalachian Plateau
Frosty Gap 34	6/6/1985	6/8/2011	38.1991	-80.2996	1,311	140	2	Appalachian Plateau
Frosty Gap 35	7/6/1985	6/8/2011	38.1974	-80.2975	1,313	160	20	Appalachian Plateau
Limberlost	5/15/1982	6/10/2011	38.5762	-78.3766	990	100	5	Blue Ridge
Whitetop I	7/6/1983	6/6/2011	36.6398	-81.6048	1,680	20	25	Blue Ridge
Whitetop II	7/6/1983	6/6/2011	36.6364	-81.6030	1,641	145	13	Blue Ridge
Whitetop III	7/6/1983	6/6/2011	36.6384	-81.5919	1,486	287	10	Blue Ridge
Little Spruce Bog	7/10/1982	6/7/2011	37.3776	-80.5151	1,150	25	3	Ridge and Valley
Sounding Knob	5/2/1982	6/15/2011	38.3475	-79.5933	1,312	320	10	Ridge and Valley
Spitzer	5/15/1982	6/10/2011	38.6574	-79.1173	1,101	130	5	Ridge and Valley
Tamarack	4/23/1983	6/9/2011	38.4766	-79.6851	1,176	240	25	Ridge and Valley
War Spur	7/9/1982	6/7/2011	37.3921	-80.4948	1,073	90	15	Ridge and Valley

RESULTS

Large Tree Stratum. In 2011, the large tree stratum was characterized by 5.7 species/site (s = 2.4) with the highest number of species (10) recorded for Little Spruce Bog. The lowest number of species (3) was recorded at Blister Run, Frosty Gap 34, and Whitetop I. The mean basal area was 40.05 m^2/ha (s = 11.2) and ranged from 16.48 m^2/ha at Limberlost to 56.06 m^2/ha at Whitetop II. Tree density ranged from 970 trees/ha at Whitetop I to 260 trees/ha at Limberlost, with an overall mean of 549 (s = 198) trees/ha. The mean proportion of basal area and mean proportion of stems per site represented by red spruce was 55.0% (s = 28.0) and 48.8% (s = 28.1), respectively. Whitetop I was characterized by the greatest proportion of red spruce relative basal area (91.8%) and the greatest proportion of red spruce relative density (93.8%). Red spruce accounted for 11.0% of the total basal area at Limberlost and 7.7% of the total trees at War Spur, with these representing the lowest values for these variables across all sampled sites. The mean importance value index for red spruce was 51.9 (s = 27.3) and ranged from 92.8 at Whitetop I to 11.3 at Limberlost (Table 2).

The Ridge and Valley physiographic province was characterized by the highest mean number of species in the large tree stratum, with 7.4 (s = 2.1) species per site, whereas the corresponding values for the Appalachian Plateau and the Blue Ridge were similar, with 4.3 (s = 2.3) and 4.5 (s = 1.7) species per site, respectively. The Blue Ridge had the highest total number of trees with 648 trees/ha (s = 306) and the Ridge and Valley was characterized by the greatest basal area at 42.89 m^2/ha (s = 8.1). Red spruce had its highest mean value for relative density, at 63.8% (s = 37.7) and highest mean importance value, with 61.0 (s = 36.3) in the Blue Ridge physiographic province. Red spruce relative basal area, at 49.2 m^2/ha (s = 30.0), and importance value, at 42.6 (s = 26.0), were lowest across the Ridge and Valley (Table 2).

Between the earlier sampling period and 2011, red spruce basal area in the large tree stratum decreased at eight sites with a mean change of -5.54 m^2/ha (s = 9.37) across all sites. The mean change in red spruce density was -178 (s = 147) trees per hectare, with all twelve sites experiencing a loss of red spruce trees. The proportion of basal area and trees attributed to red spruce decreased at most sites, resulting in overall decreases of -10.9% (s = 15.3) and -11.4% (s = 15.2), respectively. The mean change in the importance value for red spruce was -11.1 (s = 14.4), with only three sites—Blister Run (18.3), Limberlost (1.6) and Tamarack (1.3)—experiencing increases in the large tree stratum (Table 3).

The decrease in red spruce basal area was highest for the Blue Ridge and Appalachian Plateau physiographic provinces, decreasing by 7.97 m^2/ha (s = 9.1) and 7.48 (s = 9.3) respectively. The most pronounced loss of 277 (s = 222.3) red spruce stems per hectare occurred for the sites located in the Appalachian Plateau. The greatest percentage decreases of red spruce basal area (relative basal area), stems per hectare (relative density), and calculated importance values we documented for the Appalachian Plateau and Ridge and Valley physiographic provinces (Table 3).

Table 2. Large tree stratum data for 2011 sorted by physiographic province and then by red spruce importance value. The standard deviation (s) follows each mean in parenthesis. Note: AP = Appalachian Plateau, BR = Blue Ridge, and RV = Ridge and Valley.

	All species			**Red Spruce**			
Site Name	**Species Richness**	**Basal Area m^2/ha**	**Trees/ha**	**Relative Basal Area**	**Relative Density**	**Importance Value**	**Physiographic Province**
Frosty Gap 34	3	38.31	670	83.7	71.6	77.7	AP
Frosty Gap 35	7	36.06	360	58.2	36.1	47.2	AP
Blister Run	3	28.44	440	39.0	43.2	41.1	AP
Whitetop I	3	40.36	970	91.8	93.8	92.8	BR
Whitetop II	4	56.06	790	76.4	88.6	82.5	BR
Whitetop III	7	50.51	570	53.7	61.4	57.6	BR
Limberlost	4	16.48	260	11.0	11.5	11.3	BR
Tamarack	7	54.40	540	77.7	57.4	67.5	RV
Sounding Knob	5	48.43	600	77.3	51.7	64.5	RV
Spitzer	9	37.61	590	55.2	45.8	50.5	RV
Little Spruce Bog	10	37.67	410	19.5	17.1	18.3	RV
War Spur	6	36.31	390	16.5	7.7	12.1	RV
Mean AP	4.3 (2.3)	34.27 (5.1)	490 (161)	60.3 (22)	50.3 (19)	55.3 (20)	
Mean BR	4.5 (1.7)	40.85 (17.5)	648 (306)	58.2 (35)	63.8 (38)	61.0 (36)	
Mean RV	7.4 (2.1)	42.89 (8.1)	506 (100)	49.2 (30)	35.9 (22)	42.6 (26)	
Pooled Mean	5.7 (2.4)	40.05 (11.2)	549 (198)	55.0 (28)	48.8 (28)	51.9 (27)	

Table 3. Change in red spruce for the large tree stratum (1980's to 2011) sorted by physiographic province and then by red spruce importance value. The standard deviation (s) follows each mean in parenthesis. Note: AP = Appalachian Plateau, BR = Blue Ridge, and RV = Ridge and Valley.

Site Name	**Basal Area m^2/ha**	**Trees/ha**	**Relative Basal Area**	**Relative Density**	**Importanc e Value**	**Physiographi c Province**
Frosty Gap 35	-15.94	-410	-34.0	-39.9	-37.0	AP
Frosty Gap 34	-8.94	-400	-14.1	-23.0	-18.5	AP
Blister Run	2.44	-20	14.8	21.8	18.3	AP

Whitetop III	-19.22	-340	-29.8	-11.2	-20.5	BR
Whitetop II	0.49	-280	-9.9	-6.5	-8.2	BR
Whitetop I	-11.27	-40	-2.0	-2.1	-2.1	BR
Limberlost	-1.89	-40	2.3	0.9	1.6	BR
War Spur	-16.44	-50	-28.4	-12.8	-20.6	RV
Spitzer	-4.34	-230	-15.2	-21.8	-18.5	RV
Sounding Knob	1.36	-100	-15.1	-20.3	-17.7	RV
Little Spruce Bog	-5.74	-150	-8.2	-15.3	-11.7	RV
Tamarack	13.01	-80	9.0	-6.5	1.3	RV
Mean AP	-7.48 (9.3)	-277 (222)	-11.1 (25)	-13.7 (32)	-12.4 (28)	
Mean BR	-7.97 (9.1)	-175 (158)	-9.9 (14)	-4.7 (5)	-7.3 (10)	
Mean RV	-2.43 (10.8)	-122 (70)	-11.6 (14)	-15.3 (6)	-13.5 (9)	
Pooled Mean	-5.54 (9.4)	-178 (147)	-10.9 (15)	-11.4 (15)	-11.1 (14)	

Across all sites 18 species were recorded from the large tree stratum during the earlier sampling period in the 1980s and that number increased to 22 for the 2011 sampling. American witchhazel (*Hamamelis virginiana* L.) was recorded in the 1980s but not in 2011. Mountain maple (*Acer spicatum* Lam.), mountain holly (*Ilex montana* Torr. & A. Gray ex A. Gray), tuliptree (*Liriodendron tulipifera* L.), mountain magnolia (*Magnolia fraseri* Walter), and white oak (*Quercus alba* L.) were recorded in 2011 but not in the 1980s.

Small Tree Stratum. In 2011, the small tree stratum was characterized by 5.3 (*s* = 1.5) species per site and ranged from three (Blister Run and Whitetop I) to seven (Frosty Gap 35) species across the sites. The overall mean basal area was 1.63 m^2/ha (*s* = 0.86) with the highest value recorded at Whitetop II (3.23 m^2/ha) and the lowest at War Spur (0.71 m^2/ha). Tree density ranged from 220 stems/ha at Little Spruce Bog to 1630 stems/ha at Whitetop III, with an overall mean of 872 stems/ha (*s* = 506). Collectively, the proportion of basal area attributed to red spruce was 46.4% (s = 35.4) and ranged from zero percent (Little Spruce Bog and War Spur) to 97.7% (Blister Run). The percentage of stems attributed to red spruce ranged from zero percent (Little Spruce Bog and War Spur) to 93.7% (Blister Run), with an overall mean of 49.7% (s = 39.2) across the sampled sites (Table 4).

Species richness in the small tree stratum was similar across the three physiographic provinces, with the highest value 5.6 (*s* = 0.9) species per site recorded for the Ridge and Valley. The Blue Ridge province was characterized by the highest basal area at 2.22 m^2/ha (*s* = 1.0) while the greatest density 1,227 (*s* = 379) stems/ha was recorded for the Appalachian Plateau. Red spruce accounted for the highest proportion of basal area (relative basal area) and stems per hectare (relative density) for the Appalachian Plateau. Red spruce relative basal area varied from 71.1% (*s* = 23.3) in the Appalachian Plateau to 25.2% (*s* = 29.3) in the Ridge and Valley. Likewise, red spruce relative density varied from 78.7% (*s* = 15.1) in the Appalachian Plateau to 30.9% (*s* = 36.7) in the Ridge and Valley (Table 4).

The overall mean values for red spruce basal area, density, relative basal area, relative density, and IV increased in the small tree stratum between the earlier sampling period and 2011. Red spruce basal area increased by 0.38 m^2/ha (*s = 0.92*) and red spruce density increased by 327 (*s = 501*) trees per hectare. The proportion of basal area and stems per hectare attributed to red spruce increased by 12.5% (*s = 40.7*) and 18.5% (*s = 43.0*) respectively. The overall mean change in red spruce importance value (IV) was 15.5 (s = 41.4) and was highly variable ranging from a decrease of -76.6 at Whitetop III to an increase of 73.2 at Blister Run (Table 5).

With respect to calculated values for various red spruce parameters, the Appalachian Plateau was characterized by the largest increases (basal area, density, relative basal area, relative density, and IV) between the two sampling periods, whereas the Blue Ridge experienced the smallest increases (basal area and density) and even decreases (relative basal area, relative density, and IV).

Across all sites 21 species were recorded from the small tree stratum during the earlier sampling period and this number decreased to 19 species in 2011. Sugar maple (*Acer saccharum* Marshall), hawthorne (*Crataegus* sp.), chestnut oak (*Quercus montana* Willd.), and northern red oak (*Quercus rubra* L.) were recorded in the 1980s but not in 2011. Alternate-leaf dogwood (*Cornus alternifolia* L. f.) and eastern white pine (*Pinus strobus* L.) were recorded in 2011, but not during the earlier sampling period.

Sapling Stratum. In 2011, the sapling strata was characterized by 4 (*s* = 1.9) species per site, ranging from seven species at Whitetop III to one species at Whitetop II (Table 6). Stems per hectare ranged from 9,200 at Frosty Gap 34 to 100 at both Little Spruce Bog and War Spur, with an overall mean of 2,054 (*s = 2,386*) stems per hectare across all sites. The relative density of red spruce stems ranged from 100% at Whitetop II to zero percent at War Spur, with a pooled mean value of 75% (*s* = 31.7).

Table 4. Small tree stratum data for 2011 sorted by physiographic province and then by red spruce importance value. The standard deviation (*s*) follows each mean in parenthesis. Note: AP = Appalachian Plateau, BR = Blue Ridge, and RV = Ridge and Valley.

	All Species			Red Spruce			
Site Name	**Species Richness**	**Basal Area m^2/ha**	**Trees/ha**	**Relative Basal Area**	**Relative Density**	**Importance Value**	**Physiographic Province**
Blister Run	3	1.33	790	97.7	93.7	95.7	AP
Frosty Gap 34	5	1.51	1,470	61.0	79.0	70.0	AP
Frosty Gap 35	7	2.69	1,420	54.6	63.4	59.0	AP
Whitetop II	4	3.23	1,370	91.2	92.7	91.9	BR
Whitetop I	3	2.55	930	87.7	92.5	90.1	BR
Whitetop III	8	2.32	1,630	22.2	9.2	15.7	BR
Limberlost	5	0.77	460	16.4	10.9	13.6	BR
Sounding Knob	6	1.25	930	68.7	79.6	74.1	RV
Spitzer	6	0.79	300	39.7	60.0	49.9	RV
Tamarack	6	1.56	660	17.6	15.2	16.4	RV
Little Spruce Bog[1]	6	0.82	220	0	0	0	RV
War Spur[2]	4	0.71	280	0	0	0	RV
Mean AP	5 (2)	1.84 (0.7)	1,227 (379)	71.1 (23)	78.7 (15)	74.9 (19)	
Mean BR	5 (2)	2.21 (1.0)	1,098 (514)	54.4 (41)	51.3 (48)	52.8 (44)	
Mean RV	6 (1)	1.02 (0.4)	478 (306)	25.2 (29)	30.9 (37)	28.1 (33)	
Pooled Mean	5 (2)	1.63 (0.9)	872 (506)	46.4 (35)	49.7 (39)	48.0 (37)	

[1]Red spruce was present as a small tree at Little Spruce Bog in 1982, but absent from that stratum in 2011. [2]Red spruce was absent as a small tree at War Spur during both sampling periods.

Table 5. Change in red spruce for the small tree stratum (1980's to 2011) sorted by physiographic province and then by red spruce importance value. The standard deviation (*s*) follows each mean in parenthesis. Note: AP = Appalachian Plateau, BR = Blue Ridge, and RV = Ridge and Valley.

Site Name	**Basal Area m^2/ha**	**Trees/ha**	**Relative Basal Area**	**Relative Density**	**Importance Value**	**Physiographic Province**
Blister Run	0.82	540	77.9	68.4	73.2	AP
Frosty Gap 34	0.81	1,120	40.2	65.6	52.9	AP
Frosty Gap 35	1.36	880	42.8	53.4	48.1	AP
Whitetop III	-0.09	-50	-74.7	-77.8	-76.2	BR
Limberlost	0.01	20	9.9	6.0	8.0	BR
Whitetop I	-1.52	-460	-5.8	-1.1	-3.5	BR
Whitetop II	2.20	980	-3.7	7.4	1.8	BR
Sounding Knob	0.85	730	67.9	77.7	72.8	RV
Tamarack	0.21	70	9.6	2.7	6.1	RV
Spitzer	-0.03	100	-13.0	21.9	4.4	RV
Little Spruce Bog	-0.02	-10	-1.4	-1.8	-1.6	RV
*War Spur	0.00	0	0.0	0.0	0.0	RV
Mean AP	1.00 (0.3)	847 (291)	53.6 (21)	62.4 (8)	58.0 (13)	
Mean BR	0.15 (1.5)	123 (610)	-18.6 (38)	-16.4 (41)	-17.5 (30)	
Mean RV	0.20 (0.4)	178 (312)	12.6 (32)	20.1 (34)	16.4 (32)	
Pooled Mean	0.38 (0.9)	327 (501)	12.5 (41)	18.5 (43)	15.5 (41)	

Species richness ranged from five (*s* = 2.1) species per site in the Appalachian Plateau to three (*s* = 0.8) species per site in the Ridge and Valley. The Appalachian Plateau was characterized by the highest sapling density with 4,390 (*s* = 4,177) stems per hectare, whereas the Ridge and Valley had the lowest number with 938 (*s* = 998) stems per hectare. Red spruce relative density was highest in the Appalachian Plateau where saplings of this species accounted for 86% (*s* = 16.4) of the stems. The Ridge and Valley had the lowest proportion of stems attributed to this species with 71% (*s* = 40.2).

Between the earlier sampling period and 2011, the density of red spruce saplings increased at 11 of the 12 sites, ranging from an increase of 9,160 stems per hectare at Frosty Gap 34 to 90 stems per hectare at Little Spruce Bog. Red spruce was absent in the sapling strata at the War Spur site, having decreased from 10 stems per hectare in the earlier sampling. The mean change in red spruce sapling density across all sites was an increase of 1,527 (*s* = 2,482) stems per hectare. The mean change in the relative density of red spruce saplings was 49% (s = 35.9) across all sites. Red spruce relative density increased at 11 sites, with increases ranging from 99.6% at Frosty Gap 34 to 8.4% at Whitetop I. War Spur was the only site that experienced a decrease (-5.3%) in red spruce sapling relative density.

The Appalachian Plateau experienced the greatest increase in red spruce sapling density (3,917 stems/ha, *s* = 4,545), whereas the Blue Ridge had the lowest increase (668 stems/ha, *s* = 333). Red spruce sapling relative density increased across all three physiographic provinces, with the greatest increase of 74% (s = 23.1) recorded for the Appalachian Plateau and the lowest increase of 22% (s = 20) for the Blue Ridge (Table 6).

Across all sites 18 species were recorded from the sapling stratum during the earlier sampling period and this decreased to 16 species in 2011. Sugar maple (*Acer saccharum* Marshall), American hazelnut (*Corylus americana* Walter), eastern white pine (*Pinus strobus* L.), and black cherry (*Prunus serotina* Ehrh.) were recorded during the 1980's but were absent in 2011. Alternate leaf dogwood (*Cornus alternifolia* L. f.) and pin cherry (*Prunus pensylvanica* L. f.) were recorded in 2011 but were absent in the 1980's.

Seedling Stratum. The seedling stratum in 2011 was characterized by a mean of five (*s* = 2.1) species per site, ranging from a single species at Whitetop I to seven species at both Frosty Gap 35 and Tamarack. The mean number of seedlings per hectare ranged from 116,000 at Frosty Gap 35 to 19,000 at Limberlost, with a mean number of 53,417 (*s* = 33,974) for all sites pooled. The mean relative density of red spruce seedlings was 31% (*s* = 38.4) and ranged from 100% at Whitetop I to zero percent at Spitzer (Table 7).

Table 6. Sapling stratum data for 2011 and the change in red spruce from the earlier sampling period to 2011 sorted by physiographic province and then by red spruce relative density for 2011. The standard deviation (*s*) follows each mean in parenthesis. Note: AP = Appalachian Plateau, BR = Blue Ridge, and RV = Ridge and Valley.

	All species			**Change in Red Spruce**		
Site Name	**Species Richness**	**Trees/ha**	**Red Spruce Relative Density**	**Trees/ha**	**Relative Density**	**Physiographic Province**
Frosty Gap 34	3	9,200	99.6	9160	99.6	AP
Blister Run	6	1,670	91.0	1,110	69.8	AP
Frosty Gap 35	7	2,300	67.8	1,480	54.0	AP
Whitetop II	1	1,800	100.0	780	9.7	BR
Whitetop I	4	2,020	97.5	580	8.4	BR
Whitetop III	7	1,940	64.9	1,050	51.0	BR
Limberlost	4	1,030	26.2	260	17.9	BR
Sounding Knob	4	2,190	94.1	2,060	94.1	RV
Spitzer	3	470	93.6	380	39.1	RV
Little Spruce Bog	2	100	90.0	90	90.0	RV
Tamarack	3	1,830	76.5	1,380	64.7	RV
War Spur	2	100	0.0	-10	-5.3	RV
Mean AP	5 (2)	4,390 (4,177)	86.1 (16)	3,917 (4,545)	74.5 (23)	
Mean BR	4 (2)	1,698 (454)	72.2 (35)	668 (333)	21.8 (20)	
Mean RV	3 (1)	938 (998)	70.8 (40)	780 (903)	56.5 (41)	
Pooled Mean	4 (2)	2,054 (2,386)	75.1 (32)	1,527 (2,482)	49.4 (36)	

Table 7. Seedling stratum data for 2011 and the change in red spruce from the earlier sampling period to 2011 sorted by physiographic province and then by red spruce relative density for 2011. The standard deviation (*s*) follows each mean in parenthesis. Note: AP = Appalachian Plateau, BR = Blue Ridge, and RV = Ridge and Valley.

	All Species			**Change in Red Spruce**		
Site Name	**Species Richness**	**Trees/ha**	**Red Spruce Relative Density**	**Trees/ha**	**Relative Density**	**Physiographic Province**
Frosty Gap 34	2	47,000	97.9	9500	-1.9	AP
Frosty Gap 35	7	116,000	18.1	-69,400	-78.2	AP
Blister Run	6	68,000	8.8	-2,000	-2.4	AP
Whitetop I	1	28,000	100.0	-99,000	0.0	BR
Whitetop II	3	26,000	80.8	-210,000	-17.9	BR
Limberlost	4	19,000	21.1	3,900	17.8	BR
Whitetop III	6	21,000	19.0	-2,000	-31.0	BR
Tamarack	7	53,000	9.4	1,100	-18.4	RV
Sounding Knob	6	30,000	6.7	1,150	-87.8	RV
Little Spruce Bog	6	110,000	2.7	2,500	1.0	RV
War Spur	3	39,000	2.6	800	-3.5	RV
Spitzer	3	84,000	0.0	-1,000	-16.5	RV
Mean AP	5 (3)	77,000 (35,369)	41.6 (49)	-20,633 (42,623)	-27.5 (44)	
Mean BR	4 (2)	23,500 (4,203)	55.2 (41)	-76,775 (100,596)	-7.8 (21)	
Mean RV	5 (2)	63,200 (33,222)	4.3 (4)	910 (1,253)	-25.0 (36)	
Pooled Mean	5 (2)	53,417 (33,974)	30.6 (38)	-3,0371 (65,901)	-19.9 (32)	

The Appalachian Plateau was characterized by the highest mean number of seedlings per hectare (77,000, *s* = 35,369) and the Blue Ridge with the lowest (23,500, *s* = 4,203). The highest relative density of red spruce seedlings was recorded for the Blue Ridge (55%, *s* = 41.4), with the lowest proportion being four percent (s = 3.7), which was recorded for the Ridge and Valley.

Between the earlier sampling period and 2011, the density of red spruce seedlings had decreased -30,371 (*s* = 65,901) per hectare, with Whitetop II experiencing the greatest decrease of -210,000 seedlings per hectare. Recorded values of red spruce seedlings increased at five of the 12 sites, with Frosty Gap 34 experiencing the greatest increase of 9,500 seedlings per hectare. The overall change in seedling relative density was a decrease of -20% (*s* = 32.0) across all sites pooled. Limberlost experienced the greatest increase in seedling relative density (17.8%) and Sounding Knob experience the greatest decrease (87.8%).

The Blue Ridge was characterized by the greatest decrease in red spruce seedling density (-76,775 stems per hectare, *s* = 100,569) and the Ridge and Valley was the only physiographic province that experienced an increase (910 seedlings per hectare, *s* = 1,253). The relative density of seedlings decreased for all three physiographic provinces. The Appalachian Plateau and Ridge and Valley experienced similar decreases of -27% (*s* = 43.9) and -25% (*s* = 36.0), respectively. The change recorded for the Blue Ridge was appreciably smaller (-8%, *s* = 21.2).

Across all sites 17 species were recorded from the seedling stratum during the earlier sampling period and this decreased to 13 for the 2011 sampling. Green ash (*Fraxinus pennsylvanica* Marshall), cucumber tree (*Magnolia acuminata* (L.) L.), black gum (*Nyssa sylvatica* Marshall), eastern white pine (*Pinus strobus* L.), pin cherry (*Prunus pensylvanica* L. f.), and sassafras (*Sassafras albidum* (Nutt.) Nees) were present in the earlier sampling but absent in 2011. American beech (*Fagus grandifolia* Ehrh.) and northern red oak (*Quercus rubra* L.) were present in 2011 but absent in the earlier sampling.

Shrub Stratum. The shrub stratum in 2011 was characterized by 1.8 (*s = 1.1*) species per site and ranged from four species at Limberlost to no species at Whitetop II (Table 8). Mean, pooled, and stems per hectare values were 13,244 (s = 22,459) with Frosty Gap 34 highest (81,000) and Whitetop II the lowest (0).

Species richness per site in 2011 ranged from two in the Blue Ridge to 1.6 in the Ridge and Valley. The Appalachian Plateau had the highest recorded density of stems for the shrub stratum (35,267 stems per hectare, *s* = 40,487) and the Blue Ridge had the lowest density of stems (5,250, *s* = 8,179).

Across all sites 12 species were recorded from the shrub stratum during the earlier sampling and this number decreased to seven for the 2011 sampling. Alternate leaf dogwood (*Cornus alternifolia* L. f.), minniebush (*Menziesia pilosa* (Michx. ex Lam.) Juss. ex Pers.), Appalachian gooseberry (*Ribes rotundifolium* Michx.), deerberry (*Vaccinium stamineum* L.), and hobblebush (*Viburnum lantanoides* Michx.) were present in the earlier samples but absent in 2011. The 2011 sampling period did not yield any additional species for the shrub stratum.

Ground Cover Classes. The mean percentage of herbaceous cover across all sites in 2011 was 36.6% (*s* = 39.8) and ranged from almost 100% at Limberlost to zero percent at War Spur (Table 9). The percentage of cover attributed to rock ranged from 6.8% at Limberlost to zero percent at Blister Run, Frosty Gap 34, Frosty Gap 35, Spitzer, and Whitetop III, with an overall pooled mean value of 3.2% (*s* = 4.9). The mean cover of course woody debris was 14.5% (*s* = 7.2) and ranged from 28.8% at Blister Run to 6.8% at Whitetop II. Whitetop I was characterized by the largest value of cover attributed to bryophytes (52.3%) and War Spur with the lowest (6.3%). The overall pooled mean for bryophyte cover was 28.0% (s = 16.8).

In 2011, the Blue Ridge was characterized by the largest cover values for the herbaceous stratum and bryophytes (77% *s* = 39.9 and 35.6% *s*=19.0) and the Ridge and Valley by the lowest values (7.3% *s* = 7.7 and 20.1% *s* =17.2). Ground cover attributed to rock was greatest for the Ridge and Valley (5.7% *s* = 6.5) and lowest for the Appalachian Plateau (0% *s* = 0.0). The Appalachian Plateau had the highest cover value for course woody debris (20.2% *s* = 8.3) and the Blue Ridge had the lowest cover value (8.8% *s* = 5.9).

The changes in ground cover classes from the earlier sampling and the 2011 sampling were greatest for bryophyte cover, which decreased by -14.8% *s* = 22.4 for all sites pooled and ranged from an increase of 19.5% at Spitzer to a decrease of 55% at Frosty Gap 35. Rock and course woody debris cover remained virtually constant (1.2% *s* = 5.6 and -0.3% *s* = 8.9). Mean change in the value for the ground cover class was -9.4 (*s* = 27.8).

Bryophyte cover decreased across all three physiographic provinces, ranging from -32.8% (*s* = 25.8) in the Appalachian Plateau to -1.8% (*s* = 17) in the Ridge and Valley. Herbaceous cover increased in the Appalachian Plateau and Ridge and Valley but decreased in the Blue Ridge (-38.7% *s* = 21.5). Cover values for rock and coarse woody debris remained relatively unchanged across the three physiographic provinces.

Table 8. Shrub stratum data for 2011 and the change in species richness and density since the earliler sampling period sorted by physiographic province and then stems/ha in 2011. The standard deviation (*s*) follows each mean in parenthesis. Note: AP = Appalachian Plateau, BR = Blue Ridge, and RV = Ridge and Valley.

	2011 Sampling Period				**Change Since 1st Sample**		
Site Name	**Species Richness**	**Stems/ha**	**Dominant Shrub**	**Dominant Relative Density**	**Species Richness**	**Stems/ha**	**Physiographic Province**
Frosty Gap 34	1	81,000	*Vaccinium erythrocarpum* Michx.	100	-1	56,400	AP
Blister Run	2	20,800	*Rhododendron maximum* L.	84.1	-1	16,500	AP
Frosty Gap 35	2	4,000	*Viburnum lantanoides* Michx.	85	1	-3,800	AP
Limberlost	4	17,300	*Lindera benzoin* (L.) Blume	91.3	2	15,300	BR
Whitetop III	3	3,400	*Viburnum lantanoides* Michx.	50	-1	-8,400	BR
Whitetop I	1	300	*Viburnum lantanoides* Michx.	100	0	-1,400	BR
Whitetop II	0	0	No shrubs present	0	-1	-7,100	BR
Spitzer	1	13,000	*Kalmia latifolia* L.	100	-1	50	RV
Little Spruce	3	9,300	*Rhododendron maximum* L.	87.1	0	3,600	RV

Bog							
War Spur	1	8,700	*Rhododendron maximum* L.	100	-3	-6,700	RV
Tamarack	2	900	*Smilax* L.	88.9	1	600	RV
Sounding Knob	1	200	*Kalmia latifolia* L.	100	-1	-350	RV
Mean AP	2 (1)	35,267 (40,487)			0 (1)	23,033 (30,627)	
Mean BR	2 (2)	5,250 (8,179)			0 (1)	-400 (10,899)	
Mean RV	2 (1)	6,420 (5,611)			-1 (1)	-560 (3,767)	
Pooled Mean	2 (1)	13,242 (22,459)			0 (1)	5,392 (17,924)	

Table 9. Ground cover class data for 2011 and the change since the earlier sampling period sorted by physiographic province and then bryophyte cover in 2011. The standard deviation (*s*) follows each mean in parenthesis. Note: AP = Appalachian Plateau, BR = Blue Ridge, and RV = Ridge and Valley.

	2011 Sampling Period				**Change Since 1st Sample**				
Site	**Herb**	**Rock**	**Wood**	**Bryophyte**	**Herb**	**Rock**	**Wood**	**Bryophyte**	**Province**
Frosty Gap 34	3.3	0.0	12.3	44.3	-18.0	UNK	UNK	-39.0	AP
Blister Run	33.8	0.0	28.8	25.5	9.8	-1.0	17.8	-4.5	AP
Frosty Gap 35	57.5	0.0	19.5	23.5	40.3	UNK	UNK	-55.0	AP
Whitetop I	74.0	0.5	1.3	52.3	-37.0	-2.5	-10.8	-29.8	BR
Whitetop II	21.8	2.5	6.8	50.5	-41.3	-4.5	-7.3	-0.5	BR
Limberlost	108.5	6.8	14.0	26.0	-64.5	6.8	2.0	-39.0	BR
Whitetop III	104.0	0.0	13.0	13.5	-12.0	0.0	-4.0	-0.5	BR
Spitzer	3.3	0.0	13.3	49.5	2.3	0.0	1.3	19.5	RV
Little Spruce Bog	2.0	8.5	18.3	20.5	2.0	4.5	-6.8	-14.5	RV
Tamarack	14.3	0.3	21.8	12.0	-3.8	0.3	-3.3	-23.0	RV
Sounding Knob	17.0	4.3	16.8	12.0	10.0	-4.8	8.8	6.0	RV
War Spur	0.0	15.5	8.8	6.3	0.0	13.5	UNK	3.3	RV
Mean AP	31.5 (27)	0.0	20.2 (8)	31.1 (11)	10.7 (29)	-1.0	17.8	-32.8 (26)	
Mean BR	77.1 (40)	2.4 (3)	8.8 (6)	35.6 (19)	-38.7 (22)	-0.1 (5)	-5.0 (5)	-17.4 (20)	
Mean RV	7.3 (8)	5.7 (6)	15.8 (5)	20.1 (17)	2.1 (5)	2.7 (7)	0.0	-1.8 (17)	
Pooled Mean	36.6 (40)	3.2 (5)	14.5 (7)	28.0 (17)	-9.4 (28)	1.2 (6)	-0.3 (9)	-14.8 (22)	
Number of Sites	12	12	12	12	12	10	9	12	

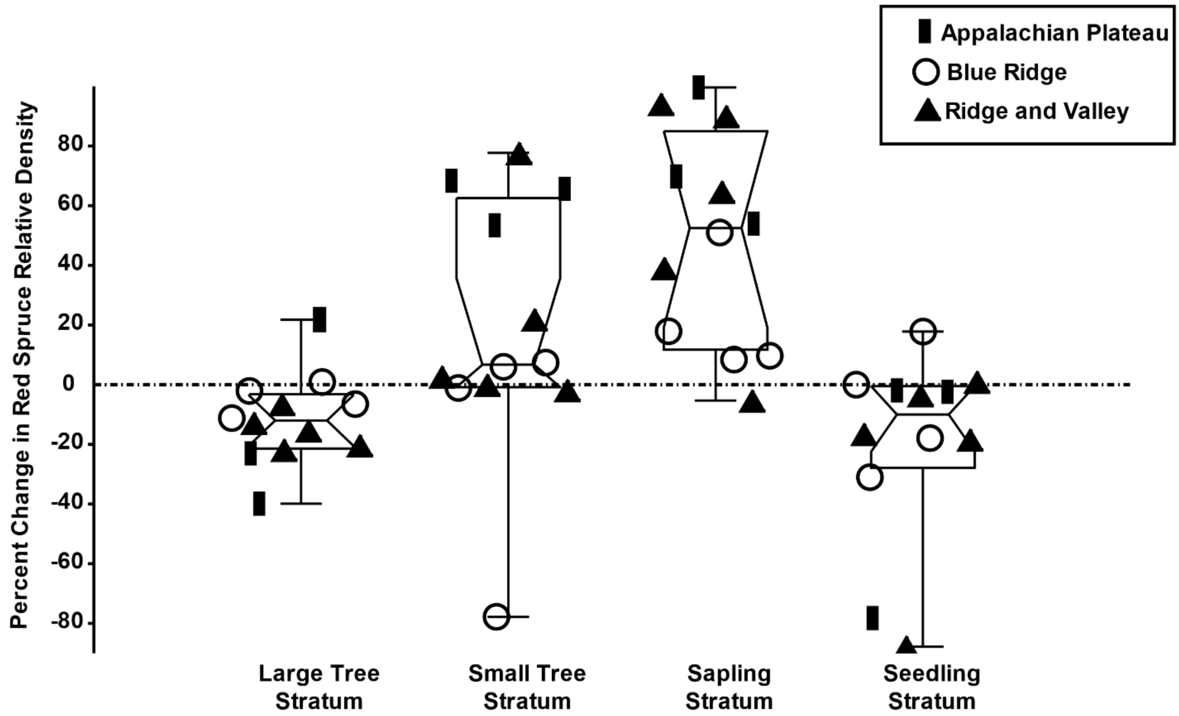

Figure 2. The percent change in red spruce relative density from the earlier sample to 2011 by strata for all sampled locations.

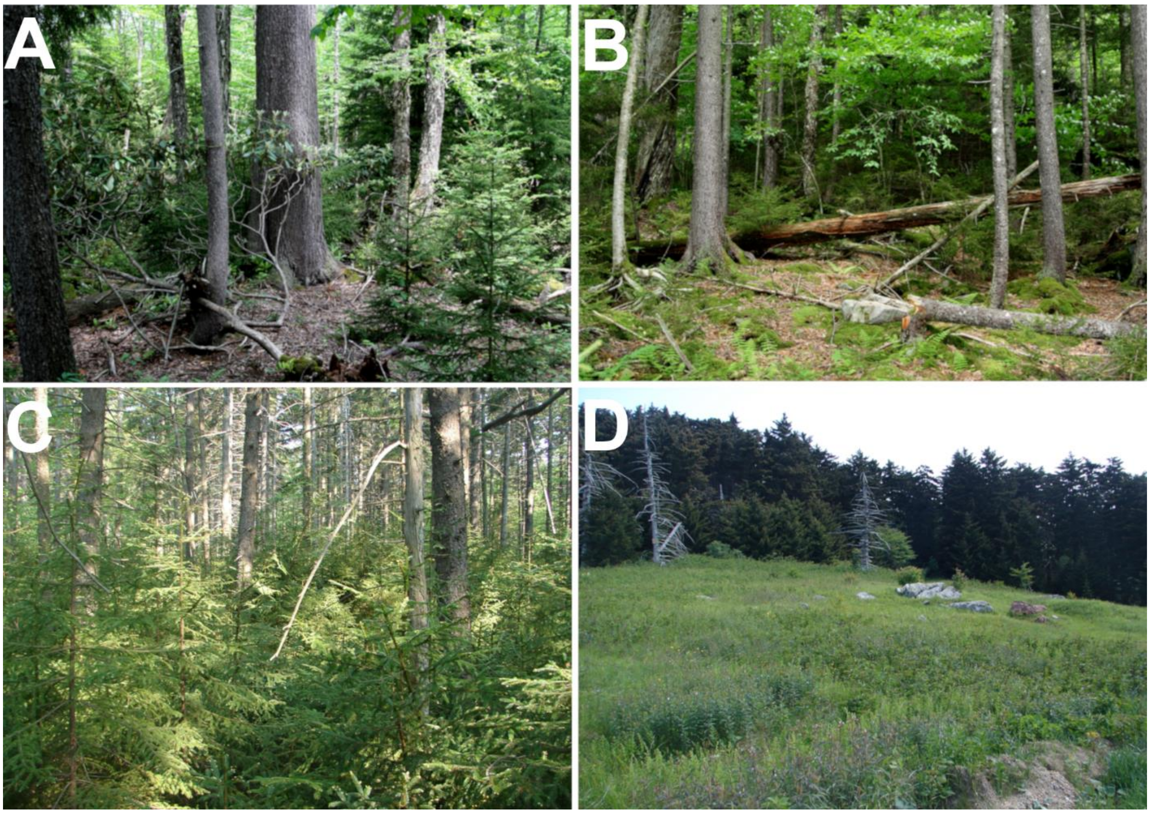

Figure 3. Variable expressions of the red spruce forest type across the central Appalachians. A. Mixed diameter class with red spruce saplings. B. Smaller diameter classes with abundant ground cover and established spruce seedlings. C. Dense thicket of red spruce saplings in the understory. D. Profile view of a mountain top island of spruce.

DISCUSSION

Studies of short-term successional dynamics in montane spruce dominated communities across the Central Appalachians are few despite the interest in conserving this forest type (Adams & Stephenson 2010). The study reported herein documented the successional changes that have occurred across the major strata of vegetation over a period of >25 years across twelve isolated red spruce communities in this region of the eastern United States. We are unaware of any other studies that provide the level of detailed data on the structure and composition of red spruce sites as what is presented herein. The data obtained during the earlier sampling represent a unique baseline snapshot of the structure and composition of red spruce communities during the 1980s, and the sampling carried out in 2011 clearly document the successional changes that have occurred over a quarter of a century.

The overall picture that emerges from the data presented herein is (a) continued reduction in large overstory spruce trees followed by vigorous recruitment from the sapling and small tree strata (Figure 2) and (b) the changes that have occurred among individual sites is highly variable across the landscape and not correlated with physiographic province (Figure 3). The loss of overstory spruce trees appears to have opened ecological space which has been captured largely by red spruce. In 2011 it was not uncommon to encounter virtually impenetrable thickets consisting of young spruce trees (small trees and saplings). While the overall picture is vigorous recruitment of red spruce, examination of the values for standard deviation associated with the means calculated for various parameters in this study indicate a high degree of variability among individual sites and among the three physiographic provinces.

It seems that site-specific parameters may exert a substantial influence over the red spruce dynamics that have occurred across the central and southern Appalachians. Studies that focus on documenting and understanding site-specific parameters may be useful in informing red spruce conservation and restoration efforts moving forward. Are there easily identified and quantified site parameters that can be used to predict the likelihood of red spruce persisting at a location? If so, these indicators could be used to developing more effective planting efforts and silvicultural treatments such as overstory release.

Currently, there is a prime opportunity to establish study sites in these spruce thickets and document the stand dynamics that occur. Will spruce persist or will something else overtake it as the stands move through the stem-exclusion stage? Are there abiotic or biotic parameters that could emerge as predictor of spruce success? If so at what level – small tree, sapling, ground cover? In addition to observational studies, it would be useful to strategically manipulate various site parameters to add experimental understanding to the magnitude of influence these parameters produce.

Several forest growth models predict the continued reduction in the coverage of the spruce forest type. As time progresses it will be important to monitor what occurs across the landscape using remote sensing data in conjunction with ground-truthing surveys to add detail and understanding to the dynamics that are occurring across the landscape. Collectively, the data can help identify parameters that can be used to strengthen the predictive ability of a particular model and ultimately aid forest managers in developing effective management plans. For example, it is widely cited that that red spruce grows best under cool and moist environmental conditions, and that it is common to have substantial bryophyte cover present. The overall trend across sites in the present study was a decrease in total bryophyte cover. However, the increases noted for red spruce small trees and saplings were not correlated with this parameter in our data.

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