

Restoration of Red Spruce (*Picea rubens*) and Virginia Northern Flying Squirrel (*Glaucomys
sabrinus fuscus*) Habitat in West Virginia

Tanner Ray Humbert

Thesis submitted to the faculty of the Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

Master of Science

In

Forest Resources and Environmental Conservation

W. Mark Ford, Committee Co-Chair

David R. Carter, Committee Co-Chair

P. Corey Green

April 29th, 2025

Blacksburg, Virginia

Keywords: Forest restoration, Habitat Modeling, Red Spruce (*Picea rubens*), Single Tree,
Virginia Northern Flying Squirrel (*Glaucomys sabrinus fuscus*).

Copyright 2025, T.R. Humbert

Restoration of Red Spruce (*Picea rubens*) and Virginia Northern Flying Squirrel (*Glaucomys sabrinus fuscus*) Habitat in West Virginia

Tanner Ray Humbert

ABSTRACT

The Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*, VNFS) is a rare subspecies that relies on high-elevation red spruce (*Picea rubens*) forests in the central Appalachian Mountains of West Virginia and Virginia. Existing habitat suitability models emphasize the composition of the red spruce canopy but lack insights into the structural characteristics of the forest that are critical for VNFS occupancy. I examined VNFS habitat preference through previous survey presence data and a spatial raster concerning forest stand structure variables. My results indicate that VNFS presence is associated with mature forest conditions across all spruce composition classes. Meanwhile, a long-term silvicultural restoration study assessed red spruce's growth responses to four hardwood removal levels (0%, ~33%, ~67%, ~100%). By 2024, trees released demonstrated a significantly greater diameter at breast height (DBH) and height growth than the controls, with the high removal treatment exhibiting the strongest response. However, the growth differences between the treatments and the controls diminished over time, suggesting that these treatments may need multiple releases or a larger removal area. Integrating forest structural metrics with habitat models could enhance VNFS conservation and inform red spruce restoration efforts to improve forest resilience and long-term habitat viability.

Restoration of Red Spruce (*Picea rubens*) and Virginia Northern Flying Squirrel (*Glaucomys sabrinus fuscus*) Habitat in West Virginia

Tanner Ray Humbert

GENERAL AUDIENCE ABSTRACT

The Virginia northern flying squirrel (VNFS) is a rare species found in high-elevation red spruce forests of the Appalachian Mountains in West Virginia and Virginia. Models were created to predict VNFS habitat quality, focusing on tree cover and land shape rather than overall forest structure. Our analysis, utilizing past surveys and forest data, revealed that VNFS prefers older forests with taller trees and thicker trunks. A long-term study showed that red spruce trees grew taller in areas where neighboring hardwoods were removed. By 2024, these trees showed significantly greater growth at the plots where hardwoods were removed, fully surrounding the target red spruce. However, growth differences between managed and unmanaged areas diminished over time, suggesting that more extensive cutting around target red spruce may be needed to ensure spruce growth continues to accelerate. Insights from both studies can improve conservation strategies for VNFS specifically and support the restoration of red spruce forests for high-elevation wildlife generally in the future.

This thesis is dedicated to

Trisha M. Grindstaff (Mother),

Robin E. Necessary (Grandmother),

F. Thomas Necessary Jr. (Grandfather).

ACKNOWLEDGEMENTS

My research was funded by Grant Agreement No. G23AC00621-00/Research Work Order VA-211 from the U.S. Geological Survey Northeast Climate Adaptation Science Center to Virginia Tech. I also thank the Forest Resources and Environmental Conservation Department at Virginia Tech for supporting funding.

I graciously thank all who helped support this project. Specifically, my lab partner and co-field lead Abby W. McKellips of Virginia Tech Department of Forest Resources and Environmental Conservation, Matt Boarman of the U.S. Fish and Wildlife Service, Canaan Valley National Wildlife Refuge, Shane Jones, Jason Teets, and Kris Henning of the U.S. Forest Service, Monongahela National Forest, Steven Evans of the West Virginia Division of Forestry, Kumbrabow State Forest, Will Evans of The Nature Conservancy, West Virginia Office, and Virginia Tech, Forest Resources and Environmental Conservation for all logistical, planning, access and mapping help. Furthermore, I acknowledge my field technicians from the Virginia Tech Department of Forest Resources and Conservation: Christopher Harris, Henry Coddington, Benjamin Protzman, Dan Putnum, and Christen Beasley.

TABLE OF CONTENTS

ITEM	PAGE
LIST OF FIGURES	vii
LIST OF FIGURES con.	viii
LIST OF TABLES	ix
LIST OF TABLES con.	x
LIST OF TABLES con.	xi
CHAPTER ONE	I
Abstract.....	2
Introduction.....	2
Methods.....	4
Data collection.....	5
Data Analysis.....	5
Results.....	6
Discussion.....	7
Acknowledgments.....	8
References.....	19
CHAPTER TWO	22
Abstract.....	23
Introduction.....	23
Study Area.....	26
Field Methods.....	26
Data Analysis.....	27
Results.....	27
Discussion.....	28
Acknowledgments.....	30
References.....	43
Appendix A	46
Appendix B	49
References.....	53

LIST OF FIGURES

Chapter One

FIGURE	PAGE
Figure 1. Map of the study area in the central Appalachian Mountains of Maryland, West Virginia, and Virginia and the 2,172 records of various forms of Virginia northern flying squirrel (<i>Glaucomys sabrinus fuscus</i>) occurrence (2015 – 2022).....	10
Figure 2. Categorical map of the additive accumulations of the optimal Virginia northern flying squirrel (<i>Glaucomys sabrinus fuscus</i>) habitat in the (A) central Appalachian Mountains of Maryland, West Virginia, and Virginia with an inset of (B) Kumbrow State Forest, Huttonsville, West Virginia. *Basal area (BA) (m ² /ha), Quadratic Mean Diameter (QMD) (cm), Stand height (TH) (m), and red spruce canopy composition 10 – 100% (Spruce). (2015 – 2022).....	11
Figure 3. Map of the predicted probability of the Virginia Northern Flying Squirrel (<i>Glaucomys sabrinus fuscus</i> ; VNFS) in the (A) Central Appalachian Mountains of Maryland, West Virginia, and Virginia with an inset of (B) Kumbrow State Forest, Huttonsville, WV. (2015 – 2022)..	12
Figure 4. Fit plot of the generalized linear modeled probability and 95% confidence interval of Virginia northern flying squirrel (<i>Glaucomys sabrinus fuscus</i> ; VNFS) likelihood of presence in the Central Appalachian Mountains of Maryland, Virginia, and, West Virginia relative to stand height, quadratic mean diameter, and basal area colorized by the spruce canopy composition classifications (>50%, 10 – 50%, 0 – 10%, and 0%). (2015 – 2022).	14
Figure 5. The fit plot of the generalized linear modeled probability and 95% confidence interval of Virginia northern flying squirrel (<i>Glaucomys sabrinus fuscus</i> ; VNFS) likelihood of presence in the Central Appalachian Mountains of Virginia and West Virginia relative stand height binned by basal areas (BA) 15 m ² /ha, 30 m ² /ha, 45 m ² /ha, and 60 m ² /ha colorized by the Spruce canopy composition classifications (>50%, 10 – 50%, 0 – 10%, and 0%). (2015 – 2022).	15

Chapter Two

Figure 1. Map of study area and six study sites of single tree red spruce (<i>Picea rubens</i>) release across the Central Appalachian Mountains of West Virginia, June 2024. * Monongahela National Forest (MNF), Kumbrow State Forest (KSF), and Canaan Valley National Wildlife Refuge (CVNWR). (2005–2024).	31
Figure 2. Mean by year (\pm SE) of diameter at breast height cm (DBH) and total height m (Height) for three crop tree release treatments and a control group of red spruce (<i>Picea rubens</i>) at two study sites in Kumbrow State Forest, two sites at Monongahela National Forest, and two sites at Canaan Valley National Wildlife Refuge. * High (100 % basal area removal treatment). Medium (67% basal area removal treatment) and Low (33% basal area removal treatment). (2005–2024).	33

LIST OF FIGURES con.

Chapter Two

FIGURE	PAGE
Figure 3. Absolute change of the mean by year (\pm SE) relative to 2005 of diameter at breast height cm (DBH) and total height m (Height) for three treatments and a control group of red spruce (<i>Picea rubens</i>) at two study sites in Kumbrabow State Forest, two sites at Monongahela National Forest, and two sites at Canaan Valley Nation Wildlife Refuge. * Heigh (100 % basal area removal treatment). Medium (67% basal area removal treatment) and Low (33% basal area removal treatment). (2005–2024).	34
Figure 4. Rate of difference of mean growth by year (\pm SE) relative to the previous measurement year of diameter at breast height cm (DBH) and total height m (Height) for three treatments and a control group of red spruce (<i>Picea rubens</i>) at two study sites in Kumbrabow State Forest, two sites at Monongahela National Forest, and two sites at Canaan Valley Nation Wildlife Refuge. * Heigh (100 % basal area removal treatment). Medium (67% basal area removal treatment) and Low (33% basal area removal treatment). (2005–2024).	35

Appendix

Figure A. Scatter plot and regression line of the relationship between Z-axis maximum values derived from LiDAR and ground measured heights at 66 dominant/co-dominant red spruce (<i>Picea rubens</i>) trees on the Monongahela National Forest in the Central Appalachian Mountains of West Virginia. * Coefficient of Determination (R^2). (June, 2024).....	47
Figure B. Scatter plot and regression line of the relationship between Treemap 2016 average dominant stand height raster cell values and ground measured heights at 66 dominant/co-dominant red spruce (<i>Picea rubens</i>) trees on the Monongahela National Forest in the Central Appalachian Mountains of West Virginia. * Coefficient of Determination (R^2). (June 2024). ...	48
Figure C. The fit plot of the generalized linear modeled probability and 95% confidence interval of Virginia northern flying squirrel (<i>Glaucomys sabrinus fuscus</i> ; VNFS) likelihood of presence in the Central Appalachian Mountains of Virginia and West Virginia relative canopy rugosity colorized by the spruce canopy composition classifications (>50%, 10 – 50%, 0 – 10%, and 0%). Model: VNFS~ Z-Max + Canopy Roughness Index + Spruce Class. (March 2025).	50
Figure D. The fit plot of the generalized linear modeled probability and 95% confidence interval of Virginia northern flying squirrel (<i>Glaucomys sabrinus fuscus</i> ; VNFS) likelihood of presence in the Central Appalachian Mountains of Virginia and West Virginia LiDAR-derived canopy height (z-axis maximum) colorized by the spruce canopy composition classifications (>50%, 10 – 50%, 0 – 10%, and 0%). * Model: VNFS~ Z-Max (Z – Axis Maximum (Tree height m)) + Canopy Roughness Index * Spruce Class. (March 2025).....	51

LIST OF TABLES

CHAPTER ONE

TABLE	PAGE
<p>Table 1. Generalized linear model selection of forest structure and composition variables predicting the likelihood of presence of Virginia northern flying squirrel (<i>Glaucomys sabrinus fuscus</i>; VNFS) in Central Appalachian Mountains of Maryland, Virginia, and West Virginia using nest-box (n = 279) and live-trapping captures (n = 279), den sites (n = 71), and foraging points from previous radio-telemetry studies (n = 1823). * Basal area (BA) (m²/ha), Quadratic Mean Diameter (QMD) (cm), Stand height (TH) (m), and Spruce canopy composition Classifications (>50%, 10 – 50%, 0 – 10%, and 0%), Akaike information criterion (AIC_c), difference of Akaike information criterion from lowest score (Δ AIC_c), Root Mean Square Error (RMSE), Coefficient of Determination (R²). * I(X²) notates a quadratic term. (2015 – 2022).</p>	16
<p>Table 2. The most supported generalized linear model (VNFS ~ Spruce + QMD + I(QMD²) + BA + I(BA²) + TH + I(TH²)) for predicting the likelihood of the presence of the Virginia Northern Flying Squirrel (<i>Glaucomys sabrinus fuscus</i>; VNFS) in the Central Appalachian Mountains of Maryland, Virginia, and West Virginia. *The Spruce canopy composition classifications (>50%, 10 – 50%, 0 – 10%, and 0%), Quadratic Mean Diameter (QMD) (cm), Basal Area (BA) (m²/ha), and Stand Height (TH) (m). *I(X²) notates a quadratic term. (2015 – 2022).</p>	19
<p>Table 3. The area and proportion of additive forest structure and composition categories that meet the optimum metrics outlined by the most supported generalized linear model for predicting the likelihood of presence of the Virginia Northern Flying Squirrel (<i>Glaucomys sabrinus fuscus</i>) in the Central Appalachian Mountains of Maryland, Virginia, and West Virginia. *Basal area (BA) (m²/ha), Quadratic Mean Diameter (QMD) (cm), Stand height (TH) (m), and Spruce canopy composition 10 – 100%. (2015 – 2022).</p>	18

CHAPTER TWO

<p>Table 1. Repeated measures analysis of variance of tree height and diameter at breast height by basal area removal treatment level and measurement year (2007–2024) regarding the pre-treatment measurement values (2005) of red spruce (<i>Picea rubens</i>) target trees in east-central West Virginia. * Tree Height (TH), Diameter at Breast Height (DBH), Degrees of Freedom (DF), Sum of Squares (Sum Sq), Mean Sum of Squares (Mean Sq), * The interaction of the treatment and measurement year (Treatment: Year). * Model: (Value (TH or DBH) ~ Baseline (measurement) + Treatment: Year + (1 Tree Number)). (2005–2024)..</p>	36
--	----

LIST OF TABLES con.

CHAPTER TWO

TABLE	PAGE
Table 2. Tukey’s Honest Significant Difference contrast of mean ± SE tree height and diameter at breast height by basal area removal treatment level and measurement year (2007–2024) regarding the pre-treatment measurement values (2005) of red spruce (<i>Picea rubens</i>) target trees in east-central West Virginia. * Tree Height (TH), Diameter at Breast Height (DBH)* The interaction of the treatment and measurement year (Treatment: Year). * Model: (Value (TH or DBH) ~ Baseline (measurement) + Treatment: Year + (1 Tree Number)). Values that do not share a letter vary significantly within years across treatments. (2005–2024).	37
Table 3. Repeated measures analysis of variance of cumulative tree height and diameter at breast height by basal area removal treatment level and measurement year (2007–2024) regarding the pre-treatment measurement values (2005) of red spruce (<i>Picea rubens</i>) target trees in east-central West Virginia. * Tree Height (TH), Diameter at Breast Height (DBH), Degrees of Freedom (DF), Sum of Squares (Sum Sq), Mean Sum of Squares (Mean Sq), * The interaction of the treatment and measurement year (Treatment: Year). * Model: (Absolute Value (TH or DBH) ~ Baseline (measurement) + Treatment: Year + (1 Tree Number)). (2005–2024).	40
Table 4. Tukey’s Honest Significant Difference contrast of mean ± SE cumulative tree height and diameter at breast height by basal area removal treatment level and measurement year (2007–2024) regarding the pre-treatment measurement values (2005) of red spruce (<i>Picea rubens</i>) target trees in east-central West Virginia. * Tree Height (TH), Diameter at Breast Height (DBH)* The interaction of the treatment and measurement year (Treatment: Year). * Model: (Absolute Value (TH or DBH) ~ Baseline (measurement) + Treatment: Year + (1 Tree Number)). Values that do not share a letter vary significantly within years across treatments. (2005–2024).	39
Table 5. Repeated measures analysis of variance of the rate of mean growth difference of tree height and diameter at breast height by basal area removal treatment level and measurement year (2007–2024) regarding the pre-treatment measurement values (2005) of red spruce (<i>Picea rubens</i>) target trees in east-central West Virginia. * Tree Height (TH), Diameter at Breast Height (DBH), Degrees of Freedom (DF), Sum of Squares (Sum Sq), Mean Sum of Squares (Mean Sq), * The interaction of the treatment and measurement year (Treatment: Year). * Model: (Growth rate (TH or DBH) ~ Baseline (measurement) + Treatment: Year + (1 Tree Number)). (2005–2024).	40

LIST OF TABLES con.

CHAPTER TWO

TABLE	PAGE
Table 6. Tukey’s Honest Significant Difference contrast of the growth rate tree height and diameter at breast height by measurement year (2007–2024) regarding the pre-treatment measurement values (2005) of red spruce (<i>Picea rubens</i>) target trees in east-central West Virginia. * Tree Height (TH), Diameter at Breast Height (DBH), Degrees of Freedom (DF), Standard Error (SE)* The interaction of the treatment and measurement year (Treatment: Year). * Model: (Growth Rate (TH or DBH) ~ Baseline (measurement) + Treatment: Year + (1 Tree Number)). (2005–2024).	43
Table 7. Tukey’s Honest Significant Difference contrast of the growth rate tree height and diameter at breast height by basal area removal treatment level regarding the pre-treatment measurement values (2005) of red spruce (<i>Picea rubens</i>) target trees in east-central West Virginia. * Tree Height (TH), Diameter at Breast Height (DBH), Degrees of Freedom (DF), Sum of Squares (Sum Sq), Mean Sum of Squares (Mean Sq), * The interaction of the treatment and measurement year (Treatment: Year). * Model: (Growth rate (TH or DBH) ~ Baseline (measurement) + Treatment: Year + (1 Tree Number)). (2005–2024).	42

Appendix

Table A. Analysis of variance of the generalized linear model of the Virginia Northern Flying Squirrel (<i>Glaucomys sabrinus fuscus</i>) likelihood of presence as predicted by LiDAR-derived canopy heights (Z-Max), basal area, canopy roughness, and spruce canopy composition class (>50%, 10 – 50%, 0 – 10%, and 0%). * Model: VNFS~ Z-Max + Canopy Roughness Index (Roughness) + Spruce Class. (March 2025).	52
---	----

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29

CHAPTER ONE

Stand Structure and Virginia Northern Flying Squirrel Presence

Tanner Humbert, Department of Forest Resources and Environmental Conservation; College of Natural Resources and Environment, Virginia Polytechnic Institute and State University, Blacksburg, VA 24060

Abby W. McKellips, Department of Forest Resources and Environmental Conservation; College of Natural Resources and Environment, Virginia Polytechnic Institute and State University, Blacksburg, VA 24060

David R. Carter, Department of Forestry; College of Agriculture and Natural Resources, Michigan State University, East Lansing, MI 48824

P. Corey Green, Department of Forest Resources and Environmental Conservation; College of Natural Resources and Environment, Virginia Polytechnic Institute and State University, Blacksburg, VA 24060

Jesse L. De La Cruz, Conservation Management Institute, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061

Alexander Silvis, West Virginia Division of Natural Resources, Elkins, WV 26241

W. Mark Ford, U.S. Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit, Blacksburg, VA 24060

30 *Abstract*

31 The Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*; VNFS) is a rare,
32 formerly endangered, Pleistocene-relict subspecies that occurs in high-elevation red spruce
33 (*Picea rubens*) forests of the central Appalachian Mountains of Virginia and West Virginia.
34 Owing to its cryptic nature and difficulty of capture, managers have relied on an evolving series
35 of predicted habitat suitability models that use elevation, landform index, and red spruce canopy
36 cover to assess potential occupancy on the landscape. However, extant models do not provide
37 insights into forest structure, i.e., stand height, basal area per hectare, trees per hectare, and tree
38 diameter, beyond the percent stand composition of red spruce. Such models are needed to inform
39 ongoing red spruce restoration efforts to promote high-elevation forest resiliency and long-term
40 VNFS habitat viability. We examined VNFS observations from nest-box surveys and radio-
41 telemetry data (natural dens and foraging points) relative to random pseudo-absence points with
42 spruce canopy composition class (0 = 0%, L= 0.1 – 10%, M= 10.1 – 50%, H= >50.1%) for the
43 most current VNFS predicted probability habitat model. The goal was to determine if the
44 relationship between squirrel presence and forest structural characteristics could be further
45 elucidated to guide where restoration efforts would be most beneficial. Using generalized linear
46 models in an *information-theoretic* approach, we found that within each spruce composition
47 class, VNFS presence was related positively to forest canopy height, basal area, quadratic mean
48 diameter, and trees per hectare, indicating that, within red spruce and mixed red spruce-northern
49 hardwood forests, VNFS are associated most with mature forest conditions. Our results could be
50 recombined with habitat suitability models to prioritize where, for example, red spruce forest
51 structural enhancement would facilitate shifting a given stand to a higher probability condition.
52

53 *Introduction*

54 Red spruce (*Picea rubens*) once occupied as much as 600,000 ha in the Central
55 Appalachians of West Virginia and portions of western Virginia and western Maryland (Rentch et
56 al. 2007a). Presently, only about 12,000 ha remain in the region, with the majority occurring in
57 West Virginia (Rentch et al. 2007a). At the turn of the 20th Century, red spruce was
58 exploitatively harvested, followed by extensive wildfire (Rentch et al. 2010). Many of these
59 areas experienced a compositional shift from a boreal-like, red spruce-dominated forest to
60 northern hardwood forests comprised of birch (*Betula spp.*), American beech (*Fagus*
61 *grandifolia*), red maple (*Acer rubra*), and sugar maple (*Acer saccharum*) (Rollins et al. 2010).
62 This shift reduced the remaining spruce to small, aggregated patches, though spruce is now
63 found widely in the midstory of the replacing northern hardwood cover types (Gray 2020).

64 The Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*; VNFS) is a subspecies of the
65 northern flying squirrel found in the high-elevation regions of the Central Appalachian
66 Mountains in western Virginia and West Virginia (Wells-Gosling and Heaney 1984). Most of the
67 squirrel's distribution occurs in isolated patches across the summits of its highest mountains on
68 the Monongahela and George Washington national forests, Canaan Valley National Wildlife
69 Refuge, Kumbrabow State Forest, and surrounding private lands (Ford et al. 2022). The VNFS is
70 a red spruce obligate that favors canopy spruce for suitable denning (tree/snag cavities or dreys)
71 and foraging habitat (Menzel, 2003). Ford et al. (2004, 2022) observed that VNFS select forest
72 stands within this landscape with > 30% canopy cover of red spruce, sheltered or convex
73 landscapes, and elevations over 800 m. Within their selected habitat, den trees tend to have the

74 following attributes: a mean den tree height of 9m, DBH of 34 cm, and an average overstory
75 height of 13 m (Menzel et al., 2004).

76 Various studies note that the VNFS has the largest individual reported home ranges compared to
77 other subspecies of northern flying squirrels (Menzel et al., 2006). In the southern Appalachians,
78 where exploitative logging and wildfires were less widespread and habitat quality is higher than
79 in the central Appalachians, the Carolina northern flying squirrel (*Glaucomys sabrinus coloratus*;
80 CNFS) has an average 95% adaptive kernel home range of 6.50 ± 2.19 ha and 12.6 ± 0.9 ha for
81 males and females, respectively (Ford et al., 2014). In contrast, Menzel et al., (2006) reported
82 that VNFS had an average home range of 54.2 ± 18.4 ha and 15.3 ± 7.1 ha for males and
83 females, respectively. This distinctive difference is attributed to the implicit lower connectivity
84 and quality of the available forest habitat in West Virginia (Menzel et al., 2006; Ford et al., 2007,
85 2014; Diggins and Ford 2017). Notably, some of the squirrels radio-tracked by Menzel et al.
86 (2006) were in low-elevation and suboptimal habitats (Ford et al., 2007). Subsequent work in the
87 central Appalachians by Diggins and Ford (2017) found that in higher quality habitats, VNFS
88 does exhibit home ranges more similar to those observed for CNFS and that this quality habitat
89 was directly linked to red spruce or other boreal conifer, i.e., Norway spruce (*Picea abies*) cover.

90 In 1985, the U.S. Fish and Wildlife Service listed the VNFS as endangered (Federal Register §
91 50 FR 26999-27002). This was due to habitat loss and fragmentation. In 2004, the squirrel was
92 labeled as vulnerable by the International Union for the Conservation of Nature (IUCN) (Menzel
93 et al., 2006). The contemporary rarity of the VNFS was closely correlated with the decrease in
94 red spruce forest acreage in the Central Appalachian and declining forest growth and health from
95 industrial-based atmospheric deposition of S and N in the 1940s-80s (Ford and Diggins 2022).
96 However, following years of monitoring leading to the determination of population stability and
97 regional persistence, along with the recognition that red spruce natural and assisted recovery was
98 feasible, in 2013, the VNFS was delisted (Federal Register § 78 FR 14022 2013). Nonetheless,
99 VNFS remains a sensitive species as red spruce forests continue to be vulnerable to habitat
100 degradation from climate change impacts or direct habitat conversion (Yetter et al. 2021, Ford et
101 al., 2022). Recognizing that the presence of VNFS is linked to mature red spruce composition, it
102 is considered a sentinel species for assessing spruce forest integrity and serves as a natural
103 “barometer” for the success of spruce restoration (Ford et al., 2022; Smith, 2012).

104 Due to the rare and cryptic nature of the VNFS, traditional live-trapping and monitoring methods
105 are difficult (Ford et al., 2022). Ultrasonic acoustic monitoring is effective and efficient for
106 determining VNFS occupancy; however, it has high post-processing costs and is still being
107 refined for use by managers (Diggins et al., 2020). For the past two decades, managers have
108 relied on predictive habitat modeling to delineate potentially occupied habitats and the quality
109 thereof for VNFS as a surrogate tool. Qualitative and quantitative modeling for habitat selection
110 has been a reliable method for landscape- and local-scale analyses to explain ecological
111 processes and biological predictions for various floral and fauna species (Dale et al., 2002;
112 Northrup et al., 2022). Odom et al. (2001), using elevation and landform indices, performed a 1st
113 to 2nd order examination of VNFS distribution that had relatively high precision for identifying
114 unoccupied range but was equivocal on the occupied range. Using 3rd order findings from Ford et
115 al. (2004) and Menzel et al. (2006), it was determined that VNFS presence was associated with
116 forest stands with > 30% red spruce composition. Menzel et al. (2006) observed that range-wide
117 VNFS presence was linked to increasing red spruce composition and elevation. However,
118 response data were primarily limited to historic nest-box data with considerable sampling bias

119 (Ford et al., 2010). Radio-telemetry data from Diggins and Ford (2017) provided additional
120 VNFS natural den and foraging observations that Ford et al. (2022) used in conjunction with
121 historic nest-box data and better landform and forest cover class inputs (Byers et al., 2010), to
122 create a more robust landscape-level predictive habitat model for VNFS. Ford et al. (2022) noted
123 that this model gave more detail on squirrel distribution probability relative to elevation,
124 landform, and across red spruce composition classes. However, this work still did not incorporate
125 forest stand-level structure measures found to be biologically important by Diggins and Ford
126 (2017) for VNFS and Ford et al. (2014) for the similar CNFS in the southern Appalachians.
127 These metrics, i.e., forest height, stand basal area, stand density, and tree diameter, could help
128 assess the need for red spruce restoration or stand enhancement (Rentch et al. 2016).
129 Additionally, they provide goals and endpoints for restoration efforts by forest managers.

130 Forest stand structure is foundational to understanding wildlife habitat (Hayes et al., 1981).
131 Vertical and horizontal structure in vegetative communities determines the shelter, cover, nest
132 selection, and forage available to the faunal inhabitants of a forest system (Nudds, 1977). In
133 forest management, stand structure is commonly quantified by DBH, height, basal area (BA),
134 and stand density (Ali, 2019). Ford et al. (2014) found that CNFS selected red spruce stands with
135 canopy heights > 20 m. Furthermore, the VNFS has been found to select den trees significantly
136 associated with features such as greater average stand DBH, stand height, individual height, and
137 red spruce composition, although it is highly variable (Menzel, 2003). Relative to the VNFS in
138 the Central Appalachians or CNFS in the Southern Appalachians, only one study explored the
139 relationship between volume and VNFS habitat structure. However, it was found to be
140 insignificant (Menzel, 2003). Despite BA having little significance on den tree selection, many
141 studies discuss the importance of VNFS and CNFS using cover to provide protection from the
142 elements (Curtis, 1970; Diggins and Ford, 2017; Ford et al., 2014a, 2022; Menzel, 2003). The
143 VNFS, as a forest-dwelling cavity nester, preferentially selects habitat based on overstory stand
144 height, average DBH, and midstory tree cover (Menzel, 2003). Understanding the relationship
145 between these variables and VNFS presence is essential to provide forest managers with
146 modeling tools and specific habitat guidelines for efficient and practical habitat
147 management/restoration in the red spruce ecosystem.

148 The goal of our study was to explore the relationships between VNFS presence and forest
149 structure in high-elevation red spruce forest habitats. We then use relationships to modify the
150 current VNFS resource selection model provided by Ford et al. (2022) by incorporating stand
151 structure predictors. Based on the previous work (Menzel et al., 2006; Ford et al., 2007; Diggins
152 and Ford, 2017; Ford et al., 2022), we hypothesized that although percent red spruce
153 composition, elevation, and shelter landforms will still be the overarching drivers of VNFS
154 presence, habitat suitability will increase for stands that display older-aged characteristics such as
155 taller trees, larger diameters, and higher stocking density that are more indicative of pre-harvest
156 and pre-fire conditions that occurred in the Central Appalachians (Schuler et al., 2002).

157 *Methods*

158 Our study was conducted in the Allegheny Highlands of the Central Appalachian
159 Mountains, primarily within or adjacent to the Monongahela National Forest in eastern West
160 Virginia (Figure 1). This mountainous region is characterized by high elevations (600-1,482 m),
161 steep slopes, broad valleys, and often planar, plateau-like ridges (Ford et al., 2022). Owing to the
162 relatively high elevations and montane boreal conditions, the climate is relatively cool, with

163 average annual summer highs (2000 – 2024) of 23.56° C and lows of 17.56° C, and average
164 annual winter highs (2000 – 2024) of 7.72° C and winter lows of -6.61° C (NOAA, 2025). For
165 the majority of the region from the Allegheny Front west, annual precipitation is high (\geq
166 110.59cm), much of which falls as rain from May – July (NOAA, 2025). Soils are often rocky
167 and shallow, sandy and silt loams, and highly acidic due to the sandstone and shale parent
168 materials (Rollins et al., 2010). Prior to harvesting and fire, red spruce dominated at the highest
169 elevations, sheltered ravines and side slopes, and riparian areas at mid-elevations. Minor
170 associates include eastern hemlock (*Tsuga canadensis*), yellow birch, and American beech with
171 an understory mostly comprised of ericaceous shrubs such as great rhododendron
172 (*Rhododendron maximum*) or mountain cranberry (*Vaccinium vitis-idaea*) (Byers et al., 2010).
173 At lower elevations, the dominant forest composition shifts to a northern hardwood association.
174 Common species include; American beech, yellow birch, red and sugar maple, black cherry
175 (*Prunus serotina*), and Fraser magnolia (*Magnolia fraseri* Walt.), with some red spruce, and
176 American beech brush in the mid- and understory (Schuler et al., 2002, Byers et al., 2010,
177 Thomas-Van Gundy and Morin, 2021).
178

179 *Data collection*

180 To update the Ford et al. (2022) VNFS resource selection model to incorporate forest
181 stand structural metrics, we reassembled their VNFS presence points from contemporary nest-
182 box, natural den, and foraging locations data (2,172 records) along with randomly placed
183 pseudo-absence (1,635 records) points. Pseudo-absence points (Pearce and Boyce 2006) were
184 required for comparison because true absence points for VNFS were unknown (Ford et al.,
185 2022). To assign presence and pseudo-absence points a red spruce cover class value, we acquired
186 spatial data provided by Byers et al. (2010) which delineated red spruce composition classes as:
187 (None 0) = 0%, Low (1) = 0.1 – 10%, Medium (2) = 10.1 – 50%, and High (3) = >50.1%.
188 Lastly, we overlaid the U.S. Forest Service raster product Treemap 2016, which provided
189 structure metrics such as trees per hectare (TPH), basal area (BA), stand average dominant tree
190 height (TH), and quadratic mean diameter (QMD) (Riley et al., 2021). QMD is calculated as:

$$191 QMD = \sqrt{\left(\frac{BA}{TPH} * 0.00007854\right)} \text{ (Curtis and Marshall, 2000).}$$

192 *Data Analysis*

193 We conducted our structurally-based resource selection analyses (Boyce et al., 2002)
194 using R version 4.3, and R Studio version 5.24 (RStudio, 2024). To determine the relationship
195 between VNFS presence and forest structural variables, we compared VNFS use points
196 versus pseudo-absences using an orthogonal polynomial generalized linear model (GLM)
197 with a binomial error distribution with the *dplyr*, *pROC*, *car*, and *parallel* libraries. We
198 tested six GLMs that contained various combinations of stand height, basal area, DBH, and
199 trees per hectare (Table 1). Models were compared with the *Akaike information criterion*
200 (AIC_c) and the *delta Akaike information criterion* (ΔAIC_c) to select the best-approximating
201 model that was the most parsimonious and contained covariates of significance (Bozdogan,
202 1987). The root mean square error (RMSE) was calculated for each model to assess the overall
203 accuracy of the modeled predictions compared to the original value (Hodson, 2022). We used
204 the coefficient of determination (R^2) to measure the variability of VNFS presence explained
205 by the variability of the included independent structure covariates in the model (Anderson-

Formatted: Font: Not Italic

Formatted: Font: Italic

206 Sprecher, 1994). Lastly, each model's area under the curve (AUC) was calculated to assess
207 model accuracy (Cook, 2007).

208 Following model selection to create a new spatial distribution map of predicted habitat
209 quality for VNFS, we utilized the single-variable structure optimums produced from the
210 modeling efforts to make a categorical raster (De La Cruz et al., 2023). This provided the
211 spatial accumulation of these structure optimums. We accomplished this using the spruce
212 class vector developed by (Byers et al., 2010) and packages *terra*, *dplyr*, and *raster* in R
213 studio (Figure 2). Once the categorical map was created, we derived area estimates per
214 colorized combination of optimums. Likewise, to develop a spatial distribution map of
215 VNFS likelihood of presence, we use the top resource selection model to create a spatial
216 likelihood raster (Ford et al., 2022) for VNFS presence using *terra*.

217 *Results*

218 Of our models examined, the “Quadratic BA + TH + QMD” model (the winning model)
219 was the top-approximating model with high predictive support, although the “Quadratic global
220 model” was within four Δ AIC and had empirical support (Table 1). All forest structural covariates
221 included in the top model were significant contributors to predicting VNFS presence. However,
222 the red spruce condition class was still the larger driver of model performance and accuracy
223 (Table 2). Spruce canopy composition under the “winning model” was significant to VNFS
224 presence at every class except for the medium spruce class. Additionally, high red spruce
225 canopy composition had a high and positive effect on VNFS compared to other classes (Table
226 2). Furthermore, VNFS's presence increased across all spruce classes as expected from
227 previous work (Menzel model, Ford et al., 2022). The TH had a negative parameter estimate
228 (Table 2) with VNFS predictions rising 10m and remaining level through 20m and then
229 departing at TH beyond 25m across all spruce classes (Figure 4). Similarly, VNFS
230 predictions with the QMD approach 99% VNFS presence probability at 10 – 30 cm
231 diameters and drop after 35cm (Figure 4). Also, similar to height, the reported diameter
232 estimate is negatively related to VNFS presence (Table 2). The likelihood of squirrel
233 presence volume presented a positive relationship to VNFS presence (Table 2) while having
234 an increase in VNFS probability across all spruce classes with basal areas ≥ 30 m²/ha
235 (Figure 4). The VNFS probability of presence peaks with the combination of stand height at
236 15 – 20 m, QMD at 10 – 30 cm, and a basal area greater than 30 m²/ha across all spruce
237 classes (Figure 4). Finally, the VNFS probability of presence increased with BA, whereby
238 the selection for height remained the same across all spruce classes and basal areas (Figure
239 5). The resource selection function (RSF) developed in this study performs equivocally to
240 those produced in other studies. The AUC of the winning model was 0.92, whereas the AUC
241 of the model from Ford et al. (2022) was also 0.92. Moreover, the R² (0.50) value for the
242 model presented in Menzel (2003) is comparable to this model.

243 Following model selection, our spatial analyses revealed that the specific optimums
244 generated by the model accounted for the variation in structure under low, medium, and high
245 red spruce canopy compositions. The specific optimums used to produce the map were TH \geq
246 20, Spruce 10-100%, QMD ≥ 5 cm, and BA ≥ 30 . The study area containing structure and
247 composition that met all the optimums for VNFS habitat was 1238 ha or 9.5% of the total

248 area (Table 3, Figure 2). The region was 84.9% area-deficient in red spruce composition, and
249 42.4% of the total area lacked the appropriate basal area (Table 3, Figure 2). Finally, the
250 areas of the categorical map that meet all optimums align with areas of high probability on
251 the VNFS likelihood map (Figure 2, Figure 3). However, there is some deviation between
252 areas of ~ 50% and areas of low red spruce composition.

253 *Discussion*

254 The results of our study demonstrate that the presence and habitat suitability for
255 VNFS are linked primarily to red spruce cover, but forest stand structure metrics are
256 significant predictors of habitat suitability and, presumably, occupancy. Similar to the CNFS
257 subspecies, our results confirm that VNFS habitat suitability increases with red spruce
258 forests with mature characteristics. However, in contrast to CNFS work from the southern
259 Appalachians, our model indicates a decline in flying squirrel presence with tree heights
260 over 25 m (Ford et al., 2014a; Moores et al., 2007). We believe this is an artifact of sampling
261 bias introduced in utilizing pseudo-absent points. The limited data points we had to
262 represent VNFS presence captured a smaller range of tree heights than the pseudo-absence
263 points. Invariably, the pseudo-absence points captured areas of mature or highly productive
264 northern and Allegheny hardwood stands with taller tree heights than might be found on
265 extant spruce stands. Secondly, false negatives likely were produced by a pseudo-absent
266 point that fell in a red spruce stand with an average height taller than 25 m. Lastly, past land
267 use in the central Appalachians eliminated tall spruce stands from harvesting that may not have
268 had residuals or regeneration reach comparable height yet. The rarity of these conditions may
269 create an illusion of avoidance as the VNFS would have larger access to the connected
270 stands of <25 m tall red spruce. It is also possible that these late succession spruce stands
271 are separated by hardwood forests that are acting as a barrier to movement or colonization
272 (Weigl, 1978). Similarly, our QMD optimums match earlier VNFS studies that relate the
273 squirrel's nest selection to stands with an overstory mean DBH of ~ 15cm (Menzel, 2003).
274 Furthermore, the "bell curve-like" selection for stand diameter could be an effect that could
275 be attributed to the same biases as TH. Despite the model's probable bias, the similarity of
276 both statistics and spatial distribution of probability to the previous models would indicate
277 our structural model has the utility to inform management. Although earlier models
278 outperform this study's best model, older models lack explorations of structural variables,
279 making comparison difficult. Unlike prior research, we utilized a classified spatial vector
280 product rather than field-derived data or digital elevation models to assess VNFS presence
281 and pseudo-absence records. This choice also may have introduced bias due to potentially
282 lower resolution and accuracy. However, datasets such as Treemap 2016 retain exploratory
283 value to inform management and support further research efforts (Riley et al., 2021). Future
284 efforts could focus on gathering additional field-derived plot-level structure data to improve
285 this model.

286 Little data exists on stand volume characteristics for conditions selected by VNFS. Menzel
287 (2003) and Ford et al. (2004) observed average overstory basal areas of about 34.5 m²/ha
288 surrounding natural VNFS den trees or snags. Although this is less than direct evidence
289 about VNFS presence relationships to stand volume, it does align with our findings that

290 stand with a high probability of VNFS occupancy occurring in conditions of $\geq 30\text{m}^2/\text{ha}$.
291 Moreover, squirrel probability increases with basal area in all spruce canopy classes, even
292 the class that does not have a spruce component. This suggests that even compositionally
293 poor stands could potentially support VNFS if the structure is optimal – though whether that
294 would be a ‘sink’ habitat is unknown. Finally, the selection ranges for each variable
295 validates that the VNFS prefers mature red spruce stands with heterogeneity in horizontal
296 and vertical structures.

297 The spatial distribution of VNFS likelihood and optimal structure combinations does not
298 deviate from the distributions in the earlier work of Ford et al. (2022). The trends of
299 presence probability for all three products are similar and contained in the exact locations,
300 underscoring the most significant driver of VNFS occupancy, which is red spruce cover. The
301 current model does not identify new habitat areas but provides a finer-scale resolution
302 habitat map. This resolution allows managers to see that VNFS’s probability of presence can
303 be highly variable at the local landscape scale, even in areas of high spruce cover. In part,
304 this is due to the higher fidelity of habitat delineation that comes from moving from Ford et
305 al. (2022)’s 2nd order examination versus our more fine-scale 3rd order analysis (Johnson,
306 1980). This visualizes the benefits of modeling higher orders of habitat selection that, in
307 turn, can be more useful for informing management. For example, in Kumbrabow State
308 Forest (KSF), a range of forest compositions and stand structures exist that show much more
309 variability in predicted VNFS habitat suitability or occurrence than previously assumed
310 (Figure 2, Figure 3). Managers could use our findings to better target finer-scale areas
311 restoration efforts in a more efficient manner. Another use of our spatial output would be the
312 ability to locate areas that contain the appropriate composition of red spruce but not the
313 suitable structure.

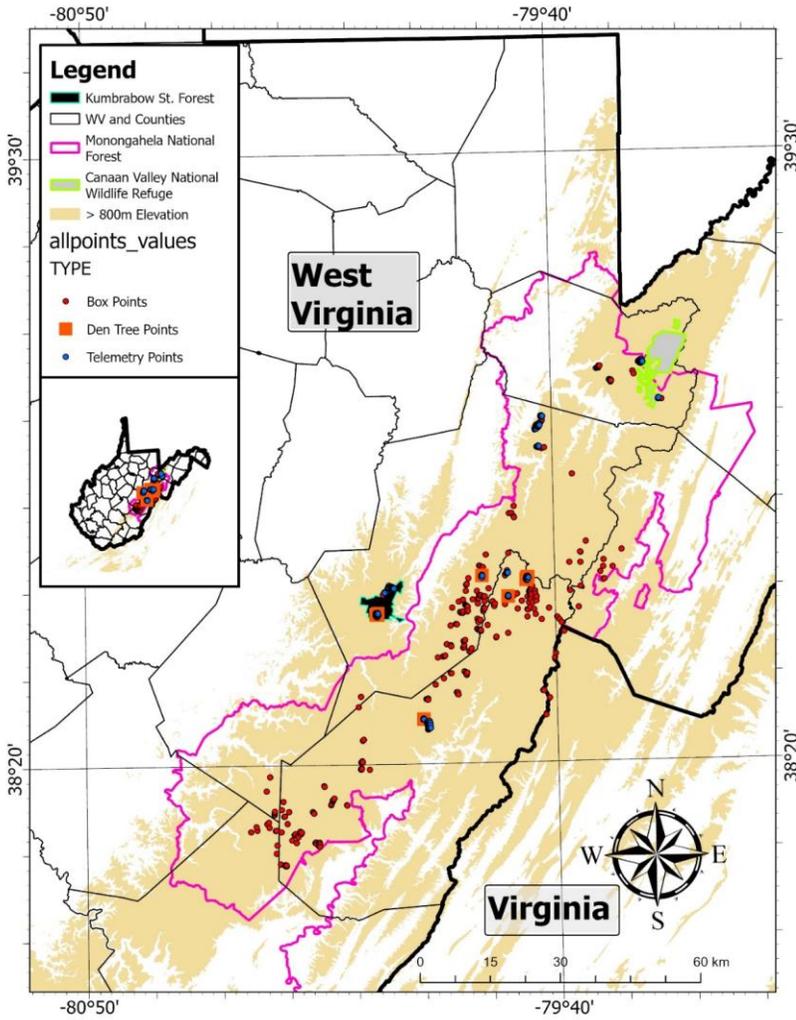
314 Though our work provides insight into VNFS selection, it does not assess what red spruce
315 forest structure was optimal for VNFS habitat before the exploitative logging and wildfires
316 at the turn of the 20th century. A complete understanding of previous pre-European
317 conditions in this landscape is not currently possible. The present-day range of VNFS can
318 only be used to describe its present structural requirements. However, continued acoustic
319 and telemetry monitoring can continue to add to our understanding of what habitat the
320 squirrel prefers as the current stands of red spruce mature and develop late successional
321 characteristics. Telemetry and monitoring studies of CNFS in the unharvested and unburned
322 areas in the southern Appalachians, such as the Great Smoky Mountains National Park in
323 North Carolina and Tennessee, might provide suitable pre-European condition analogs to
324 facilitate a better understanding of VNFS habitat for the central Appalachians.

325 *Acknowledgment*

326 This research was funded by Grant G23AC00621-00 Research Work Order 211 from the
327 U.S. Geological Survey Northeast Climate Adaptation Science Center and the Cooperative
328 Research Unit Program to Virginia Tech. We graciously thank all who helped support this
329 project. Specifically, Matt Boarman of the U.S. Fish and Wildlife Service, Canaan Valley
330 National Wildlife Refuge, Shane Jones, Jason Teets, and Kris Henning of the U.S. Forest
331 Service, Monongahela National Forest, Steven Evans of the West Virginia Division of
332 Forestry, Kumbrabow State Forest, Will Evans of The Nature Conservancy, West Virginia

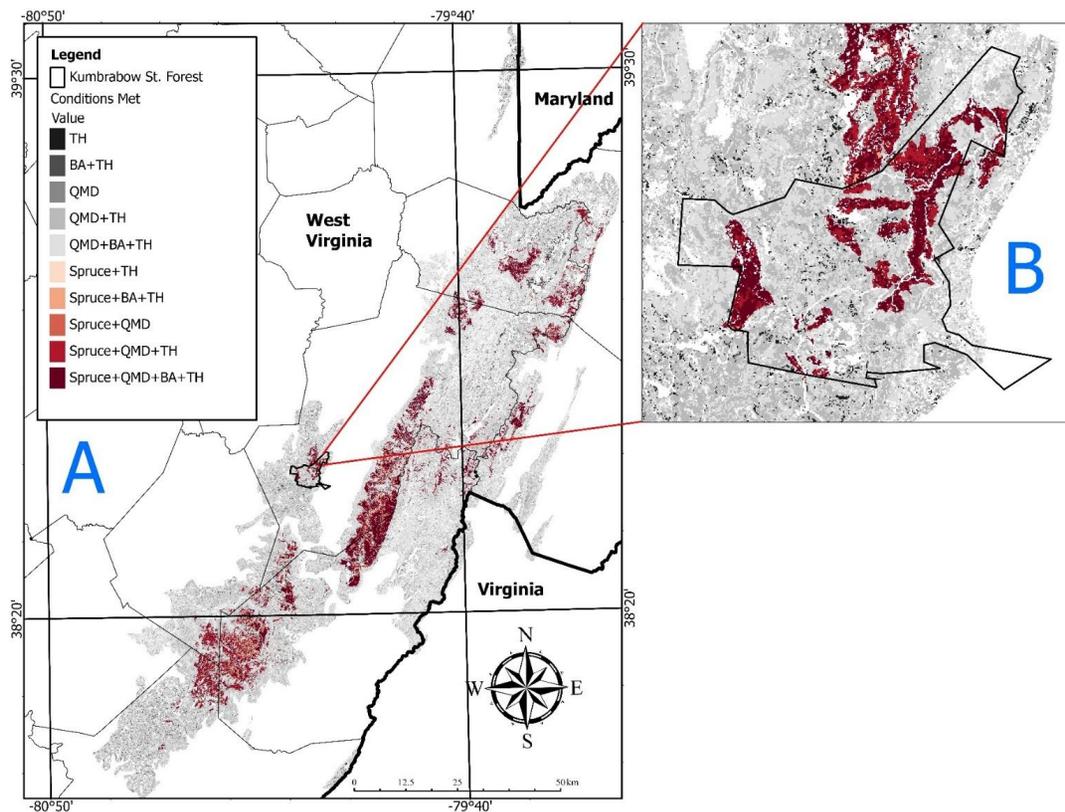
333 Office, and Virginia Tech, Forest Resources and Environmental Conservation for all
334 logistical, planning, access and mapping help.

335



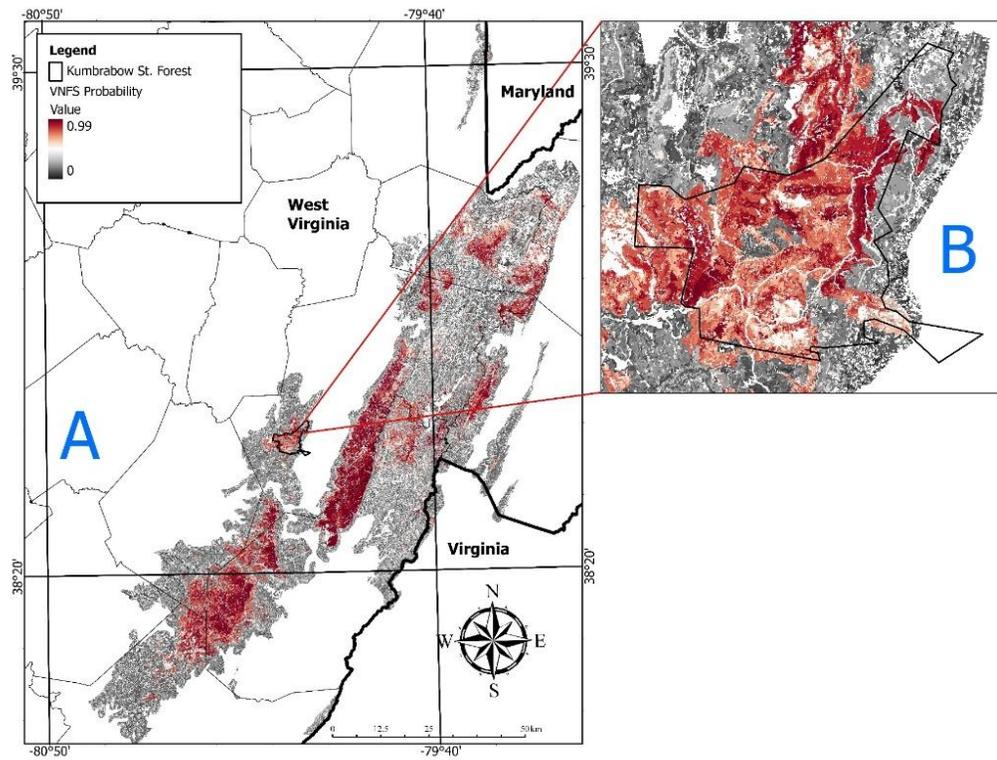
337
 338 Figure 1. Map of the study area in the central Appalachian Mountains of Maryland, West
 339 Virginia, and Virginia and the 2,172 records of various forms of Virginia northern flying
 340 squirrel (*Glaucomys sabrinus fuscus*) occurrence (2015 – 2022).

341



342

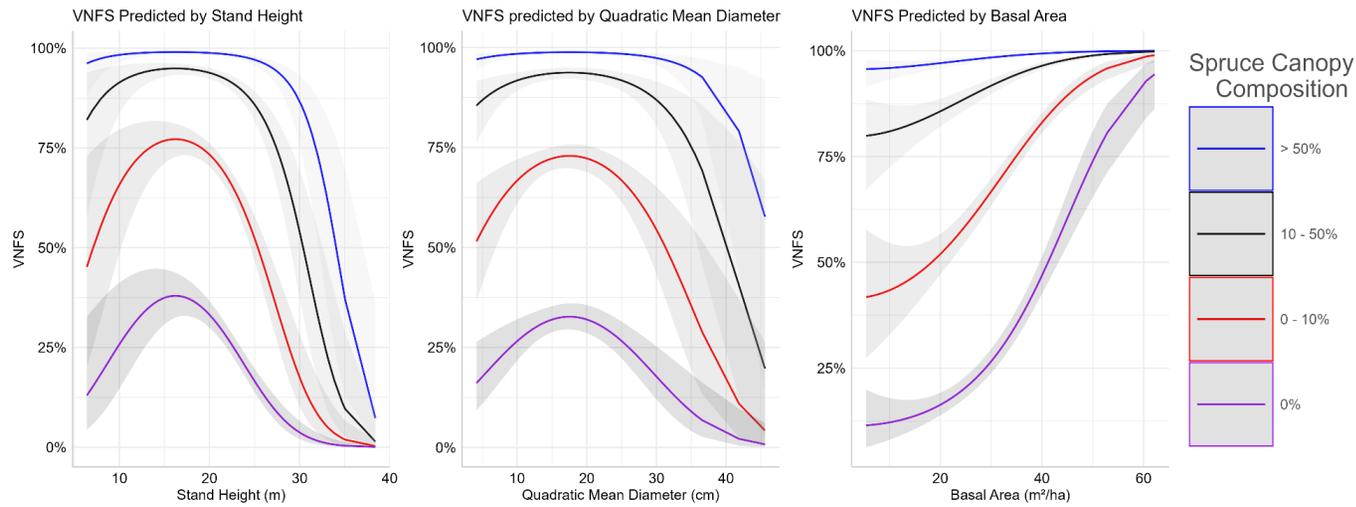
343 Figure 2. Categorical map of the additive accumulations of the optimal Virginia northern flying squirrel (*Glaucomys sabrinus*
 344 *fuscus*) habitat in the (A) central Appalachian Mountains of Maryland, West Virginia, and Virginia with an inset of (B)
 345 Kumbrabow State Forest, Huttonsville, West Virginia. *Basal area (BA) (m²/ha), Quadratic Mean Diameter (QMD) (cm), Stand
 346 height (TH) (m), and red spruce canopy composition 10 – 100% (Spruce). (2015 – 2022).



348 Figure 3. Map of the predicted probability of the Virginia Northern Flying Squirrel (*Glaucomys sabrinus fuscus*; VNFS) in the (A)
349 Central Appalachian Mountains of Maryland, West Virginia, and Virginia with an inset of (B) Kumbrabow State Forest, Huttonsville,
350 WV. (2015 – 2022).

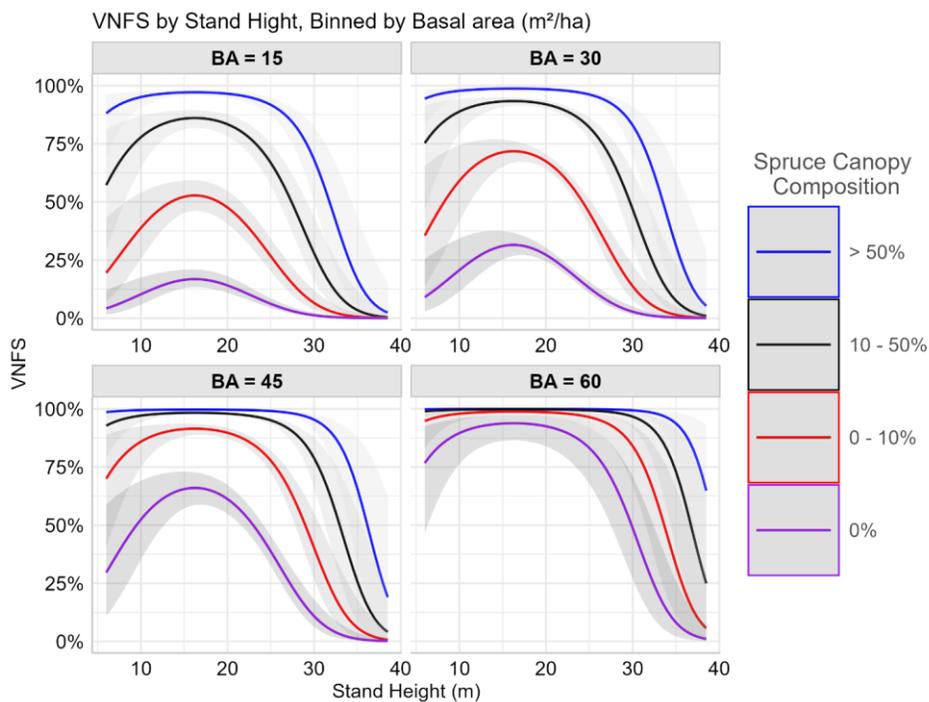
351

352



353

354 Figure 4. Fit plot of the generalized linear modeled probability and 95% confidence interval of Virginia northern flying squirrel
 355 (*Glaucomys sabrinus fuscus*; VNFS) likelihood of presence in the Central Appalachian Mountains of Maryland, Virginia, and, West
 356 Virginia relative to stand height, quadratic mean diameter, and basal area ~~colorized~~ by the spruce canopy composition classifications
 357 (>50%, 10 – 50%, 0 – 10%, and 0%). (2015 – 2022).



358
 359 Figure 5. The fit plot of the generalized linear modeled probability and 95% confidence interval
 360 of Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*; VNFS) likelihood of presence in
 361 the Central Appalachian Mountains of Virginia and West Virginia relative stand height binned by
 362 basal areas (BA) 15 m²/ha, 30 m²/ha, 45 m²/ha, and 60 m²/ha by the Spruce canopy composition
 363 classifications (>50%, 10 – 50%, 0 – 10%, and 0%). (2015 – 2022).

364

365 Table 1. Generalized linear model selection of forest structure and composition variables
 366 predicting the likelihood of presence of Virginia northern flying squirrel (*Glaucomys*
 367 *sabrinus fuscus*; VNFS) in Central Appalachian Mountains of Maryland, Virginia, and West
 368 Virginia using nest-box (n = 279) and live-trapping captures (n = 279), den sites (n = 71),
 369 and foraging points from previous radio-telemetry studies (n = 1823). * Basal area (BA)
 370 (m²/ha), Quadratic Mean Diameter (QMD) (cm), Stand height (TH) (m), and Spruce canopy
 371 composition Classifications (>50%, 10 – 50%, 0 – 10%, and 0%), Akaike information
 372 criterion (AIC_c), difference of Akaike information criterion from lowest score (Δ AIC_c), Root
 373 Mean Square Error (RMSE), Coefficient of Determination (R²). * I(X²) notates a quadratic
 374 term. (2015 – 2022). * Variance Inflation Factors based on the quadratic global model do
 375 not exceed 2.3; Spruce (1.04), QMD (2.20), BA (1.60), TH (1.20), TPH (2.20).

376

Model Name	Formula	AIC	RMSE	R ²	AUC	Δ AIC
Quadratic BA, TH, and QMD	VNFS ~ Spruce + QMD + I(QMD ²) + BA + I(BA ²) + TH + I(TH ²)	2727.109	0.324	0.480	0.917	0.000
Quadratic Global	VNFS ~ Spruce + QMD + I(QMD ²) + BA + I(BA ²) + TH + I(TH ²) + TPH + I(TPH ²)	2730.862	0.324	0.480	0.917	3.753
Quadratic BA and Height	VNFS ~ Spruce + BA + I(BA ²) + TH + I(TH ²)	2740.377	0.324	0.476	0.917	13.269
Standard Global	VNFS ~ Spruce + QMD + BA + TH + TPH	2774.552	0.328	0.470	0.915	47.443
Standard BA and TH	VNFS ~ Spruce + BA + TH	2792.113	0.330	0.466	0.915	65.005
Standard BA and TH with QMD	VNFS ~ Spruce + QMD + BA + TH	2792.840	0.330	0.466	0.916	65.732

377

378

379 Table 2. The most supported generalized linear model (VNFS ~ Spruce + QMD + I(QMD²)
 380 + BA + I(BA²) + TH + I(TH²)) for predicting the likelihood of the presence of the Virginia
 381 Northern Flying Squirrel (*Glaucomys sabrinus fuscus*; VNFS) in the Central Appalachian
 382 Mountains of Maryland, Virginia, and West Virginia. *The Spruce canopy composition
 383 classifications (>50%, 10 – 50%, 0 – 10%, and 0%), Quadratic Mean Diameter (QMD) (cm),
 384 Basal Area (BA) (m²/ha), and Stand Height (TH) (m). *I(X²) notates a quadratic term. (2015 –
 385 2022).

Term	Estimate	Std Error	t-Statistic	P-Value
> 50%	2.635	0.219	12.027	<0.001
10 – 50%	-0.269	0.256	-1.049	0.294
0 – 10%	-0.956	0.237	-4.03	<0.001
0%	-3.595	0.227	-15.847	<0.001
QMD	0.028	0.073	0.386	0.7
I(QMD ²)	-0.147	0.043	-3.439	<0.001
BA	0.977	0.072	13.53	<0.001
I(BA ²)	0.22	0.057	3.875	<0.001
TH	-0.445	0.067	-6.643	<0.001
I(TH ²)	-0.186	0.034	-5.433	<0.001

386

387

388 Table 3. The area and proportion of additive forest structure and composition categories that
 389 meet the optimum metrics outlined by the most supported generalized linear model for
 390 predicting the likelihood of presence of the Virginia Northern Flying Squirrel (*Glaucomys*
 391 *sabrinus fuscus*) in the Central Appalachian Mountains of Maryland, Virginia, and West
 392 Virginia. *Basal area (BA) (m²/ha), Quadratic Mean Diameter (QMD) (cm), Stand height
 393 (TH) (m), and Spruce canopy composition 10 – 100%. (2015 – 2022).

Optimums Met	Area (ha)	% Proportion	Total Area Above 800m (ha)
TH	308.688	2.368	13037.802
BA+TH	93.327	0.716	
QMD	0.855	0.007	
QMD+TH	4714.332	36.157	
QMD+BA+TH	5946.678	45.609	
Spruce+TH	34.344	0.263	
Spruce+BA+TH	252.282	1.935	
Spruce+QMD	0.006	0.000	
Spruce+QMD+TH	450.249	3.453	
Spruce+QMD+BA+TH	1237.746	9.493	

394

395

References

- Ali, A. (2019). Forest stand structure and functioning: Current knowledge and future challenges. *Ecological Indicators*, 98, 665–677. <https://doi.org/https://doi.org/10.1016/j.ecolind.2018.11.017>
- Anderson-Sprecher, R. (1994). Model comparisons and R^2 . *The American Statistician*, 48, 113–117. <https://doi.org/https://doi.org/10.1080/00031305.1994.10476036>
- Boyce, M.S., Vernier, P.R., Nielsen, S.E., & Schmiegelow, F.K.A. (2002). Evaluating resource selection functions. *Ecological Modelling*, 157, 281–300. <https://doi.org/https://doi.org/10.1016/S0304-3800>
- Bozdogan, H. (1987). Model selection and Akaike's Information Criterion (AIC): The general theory and its analytical extensions. *Psychometrika*, 52, 345–370. <https://doi.org/https://doi.org/10.1007/BF02294361>
- Byers, E.A. (2010). Natural communities of the Central Appalachian red spruce ecosystem and their conservation significance. In J.S. Rentch & T.M. Schuler (Eds.), *Proceedings from the conference on the ecology and management of high-elevation forests in the central and southern Appalachian Mountains (2009 May 14-15; Slatyfork, WV)* (p. 206). U.S. Department of Agriculture, Forest Service, Northern Research Station.
- Cook, N.R. (2007). Use and misuse of the receiver operating characteristic curve in risk prediction. *Circulation*, 115, 928–935. <https://doi.org/https://doi.org/10.1161/CIRCULATIONAHA.106.672402>
- Curtis, R.O. (1970). Stand density measures: An interpretation. *Forest Science*, 16, 403–414.
- Curtis, R.O., & Marshall, D.D. (2000). Why quadratic mean diameter? *Western Journal of Applied Forestry*, 15, 137–139.
- Dale, P.E., Chapman, H., Brown, M.D., Ritchie, S.A., Knight, J., & Kay, B.H. (2002). Does habitat modification affect oviposition by the salt marsh mosquito (*Ochlerotatus vigilax*) (Skuse) (Diptera: Culicidae)? *Australian Journal of Entomology*, 41, 49–54. <https://doi.org/https://doi.org/10.1046/j.1440-6055.2002.00258.x>
- De La Cruz, J. L., Ford, W. M., Jones, S., Johnson, J. B., & Silvis, A. (2023). Distribution of northern long-eared bat summer habitat on the Monongahela National Forest, West Virginia. *Journal of the Southeastern Association of Fish and Wildlife Agencies*, 10, 114–124.
- Diggins, C.A., & Ford, W.M. (2017). Microhabitat selection of the Virginia Northern Flying Squirrel (*Glaucomys sabrinus fuscus*) in the Central Appalachians. *Northeastern Naturalist*, 24, 173–190. <https://doi.org/https://doi.org/10.1656/045.024.0209>
- Diggins, C.A., Gilley, L.M., Kelly, C.A., & Ford, W.M. (2020). Using ultrasonic acoustics to detect cryptic flying squirrels: Effects of season and habitat quality. *Wildlife Society Bulletin*, 44, 300–308. <https://doi.org/https://doi.org/10.1002/wsb.1083>
- Ford, W.M., Kelly, C.A., Rodrigue, J.L., Odom, R.H., Newcomb, D., Gilley, L.M., & Diggins, C.A. (2014). Late winter and early spring home range and habitat use of the endangered Carolina northern flying squirrel in western North Carolina. *Endangered Species Research*, 23, 73–82. <https://doi.org/https://doi.org/10.3354/esr00561>
- Ford, W.M., Diggins, C.A., De La Cruz, J.L., & Silvis, A. (2022). Distribution probability of the Virginia Northern Flying Squirrel in the high Allegheny Mountains. *Journal of the Southeastern Association of Fish and Wildlife Agencies*, 9, 168–175.

- Ford, W.M., Mertz, K.N., Menzel, J.M., & Sturm, K.K. (2007). Late winter home range and habitat use of the Virginia Northern Flying Squirrel (*Glaucomys sabrinus fuscus*). Research Paper NRS-4. U.S. Forest Service, Northern Research Station, Newtown Square, PA. <https://doi.org/https://doi.org/10.2737/NRS-RP-4>
- Ford, W.M., Stephenson, S.L., Menzel, J.M., Black, D.R., & Edwards, J.W. (2004). Habitat characteristics of the endangered Virginia Northern Flying Squirrel (*Glaucomys sabrinus fuscus*) in the Central Appalachian Mountains. *The American Midland Naturalist*, 152, 430–438. <https://doi.org/https://doi.org/10.1674/0003-0031>
- Hayes, R.L., Summers, C., & Seitz, W. (1981). Estimating habitat variables. U.S. Fish and Wildlife Service, FWS/OBS-81/47.
- Hodson, T.O. (2022). Root-mean-square error (RMSE) or mean absolute error (MAE): When to use them or not. *Geoscientific Model Development*, 15, 5481–5487. <https://doi.org/https://doi.org/10.5194/gmd-15-5481-2022>
- Johnson, D.H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, 65–71. <https://doi.org/https://doi.org/10.2307/1937156>
- Menzel, J.M. (2003). An examination of the habitat requirements of the endangered Virginia Northern Flying Squirrel (*Glaucomys sabrinus fuscus*) by assessing nesting sites, habitat use, and developing a habitat model. (Master's Thesis). West Virginia University.
- Menzel, J.M., Ford, W.M., Edwards, J.W., & Menzel, M.A. (2004). Nest tree use by the endangered Virginia Northern Flying Squirrel in the Central Appalachian Mountains. *The American Midland Naturalist*, 151, 355–368.
- NOAA, U.S.D. of C. (2025). Climate. <https://doi.org/https://www.weather.gov/wrh/Climate?wfo=rlx> (accessed 2.7.25).
- Northrup, J.M., Vander Wal, E., Bonar, M., Fieberg, J., Laforge, M.P., Leclerc, M., Prokopenko, C.M., & Gerber, B.D. (2022). Conceptual and methodological advances in habitat-selection modeling: Guidelines for ecology and evolution. *Ecological Applications*, 32, e02470. <https://doi.org/https://doi.org/10.1002/eap.2470>
- Nudds, T.D. (1977). Quantifying the vegetative structure of wildlife cover. *Wildlife Society Bulletin (1973-2006)*, 5, 113–117.
- Riley, K.L., Grenfell, I.C., Finney, M.A., & Shaw, J.D. (2021). TreeMap 2016: A tree-level model of the forests of the conterminous United States circa 2016. <https://doi.org/https://doi.org/10.2737/RDS-2021-0074>
- Rollins, A.W., Adams, H.S., & Stephenson, S.L. (2010). Changes in forest composition and structure across the red spruce-hardwood ecotone in the Central Appalachians. *Castanea*, 75, 303–314. <https://doi.org/https://doi.org/10.2179/09-052.1>
- RStudio, T. (2024). RStudio: Integrated development for R. RStudio. PBC. MA. <https://doi.org/http://www.rstudio.com/>
- Schuler, T.M., Ford, W.M., & Collins, R.J. (2002). Successional dynamics and restoration implications of a montane coniferous forest in the Central Appalachians, USA. *Natural Areas Journal*, 22, 88–98.
- Smith, W.P. (2012). Sentinels of ecological processes: The case of the Northern Flying Squirrel. *BioScience*, 62, 950–961. <https://doi.org/https://doi.org/10.1525/bio.2012.62.11.4>
- Thomas-Van Gundy, M., & Morin, R. (2021). Change in montane forests of east-central West Virginia over 250 years. *Forest Ecology and Management*, 479, 118604. <https://doi.org/https://doi.org/10.1016/j.foreco.2020.118604>

- U.S. Fish and Wildlife Service. (1985). Determination of end status for 2 kinds of Northern flying squirrel. Federal Register, 50 FR 26999-27002. Retrieved from <https://doi.org/https://www.fws.gov/species-publication-action/determination-end-status-2-kinds-northern-flying-squirrel-50-fr-26999> (accessed 2.6.25).
- U.S. Fish and Wildlife Service. (2013). Endangered and threatened wildlife and plants; reinstatement of removal of the Virginia Northern flying squirrel from the list of endangered and threatened wildlife. Federal Register, 78 FR 14022. Retrieved from <https://doi.org/https://www.federalregister.gov/documents/2013/03/04/2013-04932/endangered-and-threatened-wildlife-and-plants-reinstatement-of-removal-of-the-virginia-northern> (accessed 2.6.25).
- Weigl, P. D. (1978). Resource overlap, interspecific interactions and the distribution of the flying squirrels, *Glaucomys volans* and *G. sabrinus*. The American Midland Naturalist, 100(1), 83–96. Retrieved from <https://doi.org/10.2307/2424779>

CHAPTER TWO

Crop tree release accelerates growth of understory *Picea rubens* to midstory – 20-year results

Tanner Humbert, Department of Forest Resources and Environmental Conservation; College of Natural Resources and Environment, Virginia Polytechnic Institute and State University, Blacksburg, VA 24060

Abby W. McKellips, Department of Forest Resources and Environmental Conservation; College of Natural Resources and Environment, Virginia Polytechnic Institute and State University, Blacksburg, VA 24060W.

James Rentch, Division of Forestry and Natural Resources, West Virginia University, Morgantown, WV 26506

David R. Carter, Department of Forestry; College of Agriculture and Natural Resources, Michigan State University, East Lansing, MI 48824

P. Corey Green, Department of Forest Resources and Environmental Conservation; College of Natural Resources and Environment, Virginia Polytechnic Institute and State University, Blacksburg, VA 24060

Mark Ford, U.S. Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit, Blacksburg, VA 24060

Abstract

As a Pleistocene relic, red spruce (*Picea rubens*) once co-dominated > 300,000 ha of forest across the central Appalachian Mountains of West Virginia and Virginia. Due to broad-scale, exploitative logging followed by uncontrolled wildfires at the turn of the 20th century, atmospheric acid deposition, and expansive surface mining for coal production, red spruce-dominated forests now occupy approximately 21,000 ha. The loss and fragmentation of red spruce forests have led to a decline in numerous rare, sensitive, and/or endemic species of concern. In 2005, a silvicultural restoration study was implemented to observe the response of individual red spruce to various percent basal area (BA; m²) removal treatments of competing hardwood species. These treatments consisted of four different basal area removals: control = 0%, low ≈ 33%, medium ≈ 67%, and high ≈ 100% around individual understory trees. Crop tree response was measured in 2007, 2010, 2013, and 2024. In each revisit, the diameter at breast height (DBH) and total height (TH) were collected. By 2016, trees in the three release treatments had a significantly greater increase in DBH and TH growth relative to controls. In 2024, we observed that all classes' average annual growth rates had increased. Similar to the 2016 findings, the growth of the trees in the removal treatments increased more than that of the controls. However, by 2024, there was no significant difference in the responses of the crop trees in the low and medium removal classes. Nonetheless, there was a significant difference between the growth of the high-treatment class and all other classes. Based on the slope of the control treatment's growth line, we suggest that over 17 years, there has been either a decrease in response rate with a single-release treatment or unmeasured environmental attributes exerted stronger controls on growth than the treatments. Nonetheless, our results indicate that release treatments are a viable technique to promote understory red spruce accession to a competitive canopy position.

Introduction

With a historical extent estimated to be as much as 300,000 ha of forest in the central Appalachians prior to the turn of the 20th Century, red spruce (*Picea rubens*) dominated forests have been reduced to approximately 21,000 ha following exploitative logging and subsequent wildfires, as well as surface mining for coal and recreational development (Rentch et al., 2016; Thomas-Van Gundy and Morin, 2021). Though red spruce was capable of regenerating on logged sites, due to post-logging fires, most advanced red spruce regeneration and seed sources were eliminated. Consequently, these high-elevation landscapes were converted to northern hardwoods consisting of sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), white ash (*Fraxinus americana*), yellow birch (*Betula alleghaniensis*), and eastern hemlock (*Tsuga canadensis*) (Rentch et al., 2010a). This loss and fragmentation of red spruce forests led to the decline of spruce-obligate species endemic to the region, such as the Virginia northern flying squirrel (VNFS) (*Glaucomys sabrinus fuscus*), Cheat Mountain salamander (*Plethodon nettingi*), the saw-whet owl (*Aegolius acadicus*), and the southernmost population in Eastern North America of the snowshoe hare (*Lepus americanus*) in eastern North America (Ford et al., 2022; Rentch et al., 2016). As a result, the Central Appalachian red spruce ecosystem was

labeled as “one of the most endangered forest systems in the United States” in the mid-1990s (Noss and Scott, 1995).

Despite projections that suggest future red spruce distribution contraction (Beane et al., 2013; Iverson et al., 2008), red spruce appears to be naturally recovering from past stressors despite climate change (Rollins et al., 2010). Unfortunately, this recovery occurs slowly with natural succession. Central Appalachian mature red spruce ring growth widths from 1930–85 showed decreased growth, perhaps attributable to atmospheric deposition and drought impacts (Adams et al., 1985). However, by the 1990s, growth declines had stabilized, and research suggested that stand thinning and crop-tree release might reverse these trends and re-accelerate growth (Hornbeck and Kochenderfer 1998, Schuler et al. 2002). Rollins et al. (2010) provided evidence suggesting that red spruce is increasing across all size classes and is beginning to recapture adjacent northern hardwood forests. However, these optimistic findings only consider current and past climatic conditions. Under more optimistic climate scenarios, red spruce loses more than 52% of the current available suitable range and, in the most severe scenarios, > 85% loss of suitable habitat by 2099 (Beane, 2010). Further evidence suggests that red spruce cannot capture the maximum suitable habitat under natural succession before seeing large climate-related losses (Beane et al., 2013). Therefore, securing a resilient red spruce system in the Central Appalachians may require management or artificial disturbance before large climate change effects occur (Beane et al., 2013; Schuler et al., 2002).

Red spruce obligate species have become rare due to the loss and fragmentation of the red spruce range in the Central Appalachian Mountains. Being listed as endangered in 1985 (but de-listed in 2013), the Virginia Northern Flying Squirrel remains a species of conservation concern and forest management focus in Virginia and West Virginia (Ford et al., 2022). The Virginia Northern Flying Squirrel population loss historically is tied to the loss and fragmentation of mature red spruce cover (Menzel *et al.*, 2006). The Virginia Northern Flying Squirrel, along with other red spruce-obligate biota, will be impacted by the presumed loss of red spruce suitable habitat due to environmental change (Beane et al., 2013). These communities would benefit from accelerating the red spruce canopy ascension to retain and expand habitat quality and to more quickly create a more resilient red spruce-dominated cover on a broader scale than with natural succession. A more resilient community helps ensure its long-term viability in this landscape.

Red spruce is a shade-tolerant tree that can persist for decades in the understory, providing a “stockpile” of potential new canopy recruits (Dumais and Prévost, 2007). This growth strategy allows red spruce, even after long periods of suppression, to be responsive to release events (Schuler et al., 2002). Rentch et al. (2007) demonstrated that released red spruce exhibits rapid growth and can achieve canopy co-dominance relatively quickly as compared to natural succession and stand dynamic processes. Still, near-full sunlight conditions are needed for optimal growth response (Dumais and Prévost, 2007). Many mid to high elevation (850 – 1,400 m) second-growth forests in the Central Appalachian Mountains are now northern hardwood-dominated overstories with a montane conifer element beneath the canopy (Rentch et al., 2007a). Most management efforts to support red spruce forest restoration or enhancement occur primarily through silvicultural crop-tree release, a technique widely used in the Central

Appalachians for high-value hardwood sawtimber, i.e., black cherry (*Prunus serotina*) (Brose and Hutchinson, 2019; Rentch et al., 2010b; Schuler, 2006; Ward, 2017). This restoration technique focuses on single trees or small groups where competing hardwoods within a certain radius of the crop-tree are removed via cutting or herbicide application (Dey, 2014). This removal of dominant canopy competitors then allows the crop-tree more access to sunlight and other resources for accelerated growth (Dey, 2014). In hardwoods, tree width and height development vary by species under a crop tree release regime. In shade-tolerant species such as oaks (*Quercus spp.*), DBH increases with time at a greater rate than controls, a similar trend to that outlined in Rentch et al. (2007, 2010, 2016), demonstrating growth responses over 35 years of record (Vogel et al., 2022). The height of oaks also saw a significant increase when released in stands dominated by other species such as black cherry (Schuler, 2006). Looking at the growth response of residual red spruce following a diameter-limit harvest of black cherry and northern red oak (Schuler et al., 2002), researchers concluded that it might be feasible to use crop tree release as a restoration tool for red spruce in the Central Appalachian Mountains.

Beginning in 2005, a series of long-term monitoring plots in red spruce or mixed northern hardwood-red spruce forests were established at Canaan Valley National Wildlife Refuge, the Monongahela National Forest, and Kumbrow State Forest, West Virginia, to investigate the response of experimental mid-story red spruce crop-tree methods (Rentch et al., 2007a). Rentch et al. (2007) selected potential red spruce crop-trees and measured initial diameter at breast height (DBH; 1.37m), tree height (TH), and surrounding stand basal area. At each crop-tree, a 6.1 m vertical cylinder was projected through the canopy, for which all competing deciduous trees whose crowns intersected the cylinder were tallied and identified for a simulation of basal area removal therein. Their results indicated that a basal area removal of $\approx 50\%$ would, at least in the short term, successfully release suppressed red spruce in older-aged stands and potentially decrease the time needed to increase the percentage of the overstory canopy of red spruce. At these same crop-trees, release treatments of four BA removals (0%, 33%, 67%, and 100%) were performed (Rentch et al., 2016). Post-release red spruce DBH and TH responses were measured in 2007, 2010, and 2013 (Rentch et al., 2016). Observations from the 2013 remeasurement showed that all treatment class red spruce showed growth responses that were significantly greater than the control. The 100% release performed significantly better than all other treatment classes, whereas the 33% and 67% releases were not significantly different. Rentch et al. (2016) suggested that a complete 100% release would be the most effective strategy for managers in the future seeking to accelerate red spruce entry into a canopy position.

Single tree release treatments have been shown to be successful in increasing target tree competitiveness; however, the literature on crop-tree release treatments on montane conifers remains scarce. However, in Bhutan fir (*Picea densa*), a study found that single tree selection underperformed in ring width when compared to group selection cuts (Dukpa et al., 2012). Furthermore, in eastern white pine (*Pinus strobus*), crop tree release efforts showed a significant increase in the diameter of crop trees (Desmarais and Leak, 2005). Beyond the Rentch studies, red spruce release work has been limited to observational studies of spruce

growth over time that ended with suggestions of management, yet none had outlined the performance of any one management implementation (Adams et al., 1985; Hornbeck and Kochenderfer, 1998; Schuler et al., 2002). Consequently, we remeasured these red spruce crop trees in 2024 to document the continued response of released red spruce across the four treatments. We hypothesized that the complete release would continue to outperform the low and medium-release treatments. In contrast, the distinction between controls, the low and medium release, would become less apparent as competing and hardwood competition would fill in available growing space.

Study Area

We conducted our study in the Allegheny Highlands portion of the Central Appalachians in east-central West Virginia, USA (Figure 1). This region is characterized by steep slopes, broad valleys, and spanning plateaus (Ford et al., 2022). Soils across this region are often shallow, sandy, silty loams high in acidic deposition due to the sandstone and shale parent materials (Rollins et al., 2010). Elevations range from 600 to > 1,400 m, but red spruce and northern hardwood-red spruce forests typically occur at elevations > 950 m, depending on slope and aspect (Rollins et al., 2010). The region experiences high annual precipitation of > 100 cm, much of which falls as snow (> 400 cm annually) in winter. The growing season is short, with a frost-free season averaging ~145 days in Elkins, WV, and ~99 days in Canaan, exhibiting a variability of ± 22 days due to climate change (Gaertner et al., 2019; Vogel and Leffler, 2015; Pan et al., 1997). As an effect of the regionally high elevations and montane boreal conditions, the climate is cool, with mean annual summer highs (2000 – 2024) of 23.56° C and lows of 17.56° C and mean annual winter highs (2000 – 2024) of 7.72° C and winter lows of -6.61° C (NOAA, 2025). For most of the region west of the Allegheny Front, the average annual precipitation accumulation is high (110 - 170 cm; depending on elevation and location) and falls evenly throughout the year (NOAA, 2025; Thomas-Van Gundy and Morin, 2021; Rentch et al., 2010a; Vogel and Leffler, 2015). Though past disturbances have determined the current forest extent and composition, generally, elevations lower than 900m are comprised of northern hardwood associations with a minor spruce component, and higher elevations are typically red spruce-dominated (Adams et al., 1985; Diggins and Ford, 2017; Hornbeck and Kochenderfer, 1998; Menzel et al., 2006b; Rentch et al., 2007b; Rollins et al., 2010, 2010). Due to high variations in landform, history, and climate, the forest composition is broadly diverse, second in extent to the red spruce in the higher elevation, species such as northern red oak, sugar maple, American beech, white ash, yellow birch, black cherry and eastern hemlock (Diggins and Ford, 2017; Menzel et al., 2006b; Rentch et al., 2007b; Rollins et al., 2010). Our study locations were located at Canaan Valley #1 39° 1'26.91"N 79°23'49.11" W, Canaan Valley #2 39° 0'36.86"N 79°24'38.65"W, Briery Knob 38° 8'58.68"N 80°20'55.92"W, and Williams River 38°13'8.56"N 80°11'57.56"W, Kumbrabow State Forest #1 38°38'21"N 80°05'34"W, and Kumbrabow State Forest #2 38°38'23"N 80°05'23" W (Figure 1). These sites were selected as they represent the portion of the Central Appalachians that supports approximately 66% of the region's available and potential dominant red spruce (Rentch et al., 2016).

Field Methods

In the summer of 2024, we revisited the Rentch et al. (2007) crop-tree release plots to remeasure the 188 released red spruce crop-trees. For additional details on plot establishment and crop-tree release, see Rentch et al. (2007, 2010, 2016). At establishment, plots and crop trees were monumented with aluminum tags (Adams, 2004; Thomas-Van Gundy, 2022), and locations were georeferenced. We recorded crop-tree DBH using Spencer's logger's diameter tape (Model 950DC, US Tape Company, Pennsburg, PA, USA) and TH with a Haglöf's hypsometer (Vertex laser Geo 2, Haglöf Sweden, Långsele, Sweden).

Data Analysis

Data analysis was conducted using the statistical software R to assess changes in DBH and HT over time. Across release treatments, we developed a linear mixed-effects model. Then, we examined response data with repeated measures Analysis of Variance using function *anova* in R version 5.24 (RStudio, 2024). Using 2005 as the baseline, we developed three variables: measurement change, absolute change over time, and growth rate per year. The latter was achieved by subtracting the measurement value from the previous measurement year's value for the change variable and then dividing that value by the number of years since the last measurement to obtain the mean value change rate per measurement year. Following the Analysis of Variance testing, we performed *post hoc* treatment comparisons using predicted means and standard errors with the *LSMEANS* in package R. Additionally, we developed metrics of cumulative percent change by subtracting the measurement value in 2024 from the baseline value, then dividing that value by the baseline, and multiplying by 100. Finally, using the predicted mean values derived from the DBH and height models, we made all graphical figures using *GGPLOT2* in R.

Results

Across our study areas, we were able to relocate 182 of 188 (140 treated and 42 controls) red spruce trees for remeasurement. The crop trees that were not found likely suffered mortality from wind-throw or other disturbances. There was an increase in DBH and HT across all treatments from the study's inception through 2024 (Table 1, Figure 2). Overall, crop trees in the 100% release had the greatest gain of DBH and HT (Table 1, Figure 2), whereas the 67% and 33% release treatments had no significant difference from each other across all years, but still saw growth (Table 2, Figure 2). Furthermore, in HT, the 100% release was not significantly different from the 67% release treatment in 2024 and was only significantly different from controls in 2013-24 (Table 2, Figure 2). In HT, all treatments differed significantly from the controls in 2024 (Table 2). The 33% treatment was only significantly different from the controls in TH in 2024 (Table 2). In DBH, all treatments and controls from 2005 to 2013 were not significantly different (Table 2). Likewise, in TH, all treatments and controls are not different from 2005 – 2010 (Table 2). Finally, all covariates significantly contribute to the modeled values of both DBH and TH since released (Table 1).

Similar to the differences in tree sizes among treatments, there was a positive linear relationship for absolute change in all classes spanning from before release (2005) to the most recent year of measurement (2024) (Table 3 & 4, Figure 3). Unlike the change in measurements, the *post hoc* comparisons illustrated a different relationship of significance between the treatment effects on DBH. The only significant contrasts for DBH were 100% - 33% and 100% - controls (Table 4). For HT, all treatment comparisons were significantly different except for the 100% - 67% and 67% - 33% (Table 4). Similar to the measurements of DBH and TH since release, the cumulative absolute change in measurements over time had a significant interaction between treatment and year for DBH and HT (Table 3). The cumulative percent change in height in 2024 per treatment was: High = $94\% \pm 4.04$ SE, Medium = $92\% \pm 4.21$, Low = $89\% \pm 3.99$ SE, Control = 78.3 ± 4.28 and DBH in 2024 is: High = $89\% \pm 0.31$ SE, Medium = $78\% \pm 0.32$ SE, Low = $76\% \pm 0.30$ SE, Control = $68\% \pm 0.32$. In total, HT under the 100% treatment cumulative response in 2024 was 2% higher than the 67% treatment, 5% greater than the 33% removal, and 14% better than the control specimen. The DBH patterns were similar, with 100% treatment being 11% more than the 67% removal, 13% over the 33% treatment, and a 21% greater cumulative response than the controls.

The mean growth rate since the release rose from 2010 to 2013 and then decreased in rate by 2024 for both measurements across treatments (Table 5 & 6, Figure 5). Though this trend is evident in Figure 5, the only significant difference of rate across treatments for DBH and TH lies between the 100% treatment and the controls (Table 7). However, the difference between 67% release and the controls was only marginally significant (Table 7). The growth rate across the years for DBH is only significantly different from the year of release (2007), with a marginal difference between the growth rates in 2010 and 2013 (Table 5). In TH, however, only a significant difference between 2013 and 2024 supported the regression in growth rate illustrated in Figure 5 (Table 6). Furthermore, there were marginal differences between 2010 and 2013 and 2007 and 2024 (Table 6).

Discussion

Our results suggest that 100% removal is the best strategy if the goal is to release individual red spruce to an ascended structural position at least throughout our study, from the initial release to the present. With only two remeasurements, Rentch et al. (2016), also concluded that “full overhead release” would produce significantly more height and DBH growth than controls. Whereas the partial releases did elicit a positive growth trend, the 100% release significantly outperformed them over the period examined. We note that we have no data on growth in the 11 years between 2013 and 2024, so the timing and patterns of growth rates are unknown. Future research could use tree-ring analysis to conduct a more precise response to treatment analysis.

Our observation that the treated trees and controls changed similarly, albeit with differing endpoints, was surprising under the assumption that shade-tolerant, suppressed red spruce growth would be far slower than unsuppressed trees (Yetter et al., 2021). Although active release will still accelerate canopy capture, this suggests that unmanaged natural red spruce may be more viable than previously thought. However, an alternative is that our release

treatments still had a positive impact on our control trees. Yet, using a suggested zone of influence formula ($3.5 \times$ mean crown radius; Lorimer, 1983), we determined that the > 20 m between the plots was beyond the zone of influence by an average excess of 4 m. This suggests, rather than our controls are performing better than expected, that the results of the treatments were not as dramatic as previously anticipated. Rollins et al. (2010) noted an increase in unmanaged spruce growth in both suppressed spruce zones and ecotones in West Virginia. This trend of unmanaged growth is not unique to montane conifers; in red oaks, researchers found that controls increased growth on the same timeline with a similar slope, albeit growing less than the managed trees (Vogel et al., 2022). Further research is needed to understand the potential of external and unaccounted effects of changes in microclimate from nearby releases, weather trends during the study period, and any other stochastic events influencing the growth of suppressed red spruce.

The growth rate change in the released red spruce we observed gave insight into details that can bolster more robust management timelines. The treated trees' growth rate lowered 3 years (2010) after release, after which DBH and height growth rates increased in 2013 (year 6 after release). From 2013 to 2024, growth decreased (for height); this suggests that either peak growth occurred at or beyond 2013 and ceased before 2024. To maintain the highest growth rate, our data indicates that another release six years post-treatment could increase growth. This suggests that managers could consider a second visit to maintain the canopy gap around the target crop tree.

In 2024, the average height of the 100% release trees was approximately 11 m. Mature Central Appalachian red spruce forests are characterized by a canopy height exceeding 20 m (Moores et al., 2007). Based on the findings of Humbert et al. (in press) and Ford et al. (2014), the southern subspecies of the northern flying squirrel, the Carolina northern flying squirrel (*Glaucomys sabrinus coloratus*) in the Southern Appalachians selected for both a higher percentage of red spruce composition and mature forest conditions with tree heights exceeding 20 m. Our results of 11 m for the best-performing treatment fall short of producing these conditions over this period. In a single release, it would take over 30 years from release to develop a mature red spruce stand and meet the sentinel species' habitat requirements, and unmanaged trees may take 60 – 80 years (Schuler et al., 2002). We also observed numerous hardwood tree stump sprouts or saplings that were not removed during the 2007 treatments, many of which have now overtopped some red spruce crop trees. Suggesting a need for a second release treatment. This gradual decline to a steady state following a single release was observed in the diameter-limit harvested stands studied by Schuler et al. (2002). We suggest that additional research is warranted not only on the response of targeted red spruce over time but also on the response of residual competitors and their in-growth.

Red spruce is predominantly recruited to the canopy via natural release from competing tree mortality and disturbance-created gaps (Dumais and Prévost, 2007). In the northern portion of its range, red spruce height growth responds best to 50% exposure to the open sky (Moores et al., 2007). Though our study directly examined height and DBH change relative to basal area removal, Rentch et al. (2007) and Rentch et al. (2016) focused on canopy

openness and understory light responses to the treatments. The results of Rentch et al. 2016 suggest that 100 and 67% basal area removals resulted in 22.5% canopy openness and 43% in understory light 3 years after treatment. These metrics are close to the suggested optimal release condition indicated by other studies (Dumais and Prévost, 2007; Moores et al., 2007; Seymour, 1995, 1992). This and other research *suggest* that while all release treatments elicited a positive response, the heavier the removal, the greater the effect, and the longer the duration of the gap (Figure 1-3).

The application of additional techniques that could eliminate unwanted regeneration or slow the encroachment of surrounding competition could be beneficial. Group selection (larger than those used), larger area basal area releases, or an additional release post-treatment could optimize this process for red spruce in the right conditions (Butler et al., 2022; Dumais and Prévost, 2007). In situations requiring non-commercial treatments, managers could utilize single-tree release with a reasonable expectation of a response. However, where a commercial release was feasible, group selection harvest could allow producers to extract valuable species in the region, such as black cherry, northern red oak, and sugar maple, to offset the cost to managers of red spruce release and to potentially create small patches of habitat heterogeneity on the landscape valuable for wildlife such as ruffed grouse (*Bonasa umbellus*), mourning warblers (*Geothlypis philadelphia*) and the snowshoe hare (*Lepus americanus*).

Acknowledgment

This research was funded by Grant G23AC00621-00 Research Work Order 211 from the U.S. Geological Survey Northeast Climate Adaptation Science Center and the Cooperative Research Unit Program at Virginia Tech.

We would like to graciously thank all who helped support this project. Matt Boarman of the U.S. Fish and Wildlife Service, Canaan Valley National Wildlife Refuge, Shane Jones, Jason Teets, and Kris Henning of the U.S. Forest Service, Monongahela National Forest, Steven Evans of the West Virginia Division of Forestry, Kumbrabow State Forest, Will Evans of The Nature Conservancy, West Virginia Office, and Virginia Tech, Forest Resources and Environmental Conservation for all logistical, planning, access and mapping help. Furthermore, I acknowledge my field technicians and computer support group from the Virginia Tech Department of Forest Resources and Conservation: Christopher Harris, Henry Coddington, Benjamin Protzman, Dan Putnum, and Christen Beasley.

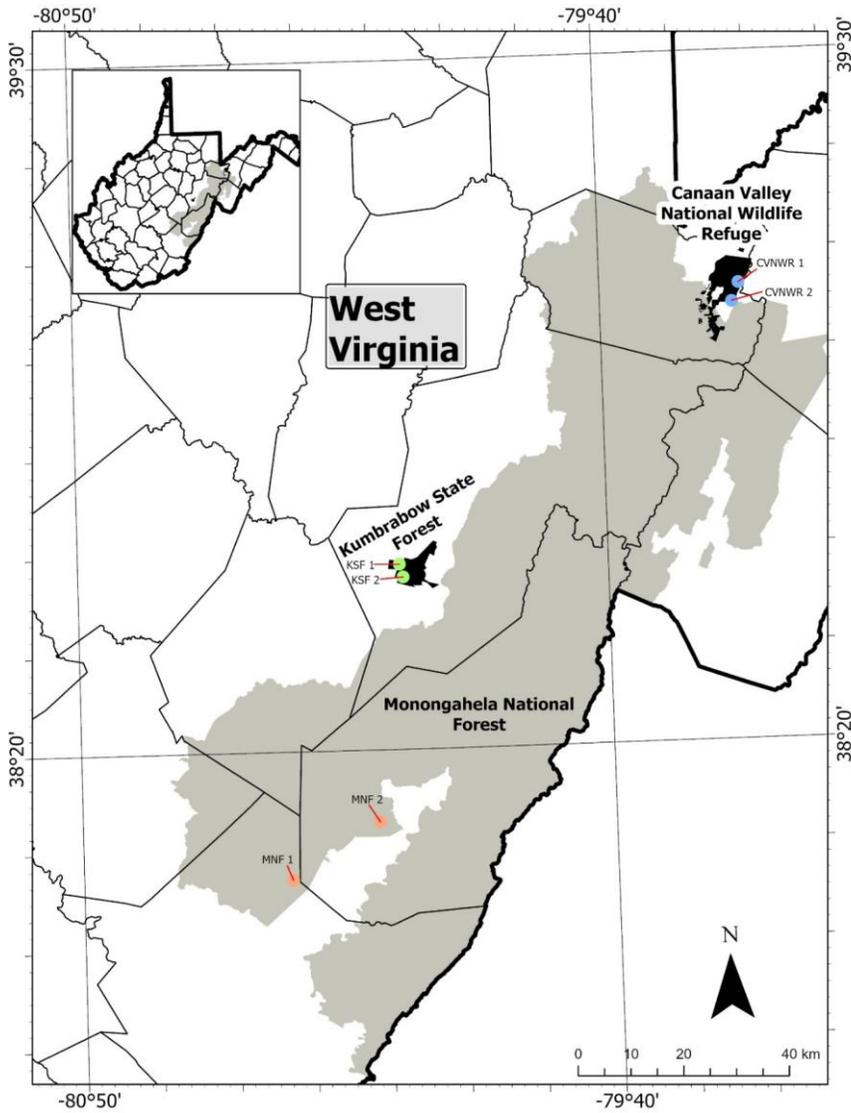
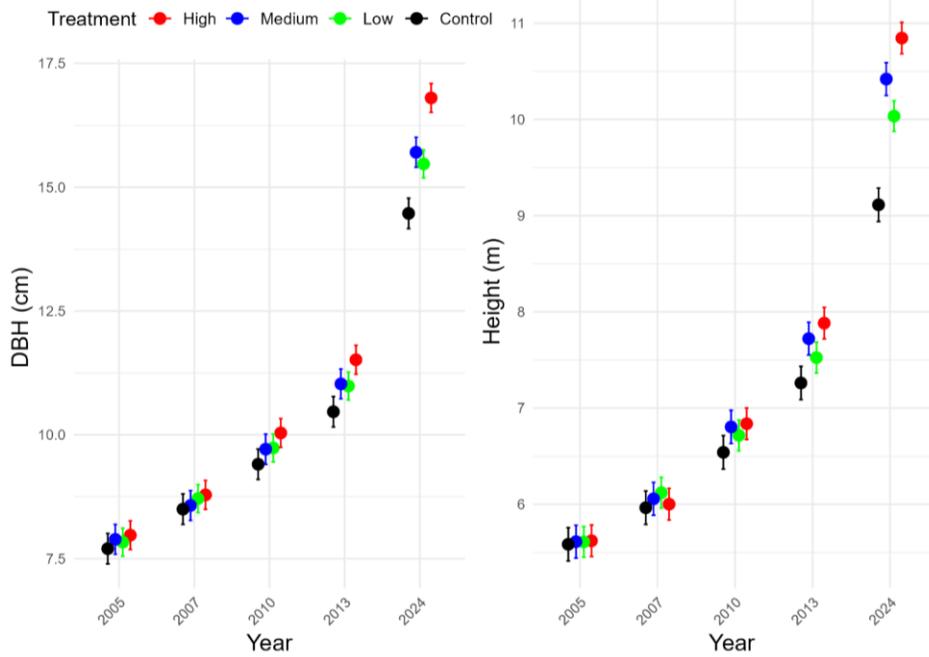


Figure 1. Map of study area and six study sites of sing tree red spruce (*Picea rubens*) release across the Central Appalachian Mountains of West Virginia, June 2024. * Monongahela National Forest (MNF), Kumbrow State Forest (KSF), and Canaan Valley National Wildlife Refuge (CVNWR). (2005–2024).



Formatted: Space After: 0 pt

Figure 2. Mean by year (\pm SE) of diameter at breast height cm (DBH; 1.37m) and total height m (Height) for three crop tree release treatments and a control group of red spruce (*Picea rubens*) at two study sites in Kumbrabow State Forest, two sites at Monongahela National Forest, and two sites at Canaan Valley National Wildlife Refuge. * High = 100 % basal area removal treatment, Medium = 67% basal area removal treatment, and Low = 33% basal area removal treatment (2005-2024).

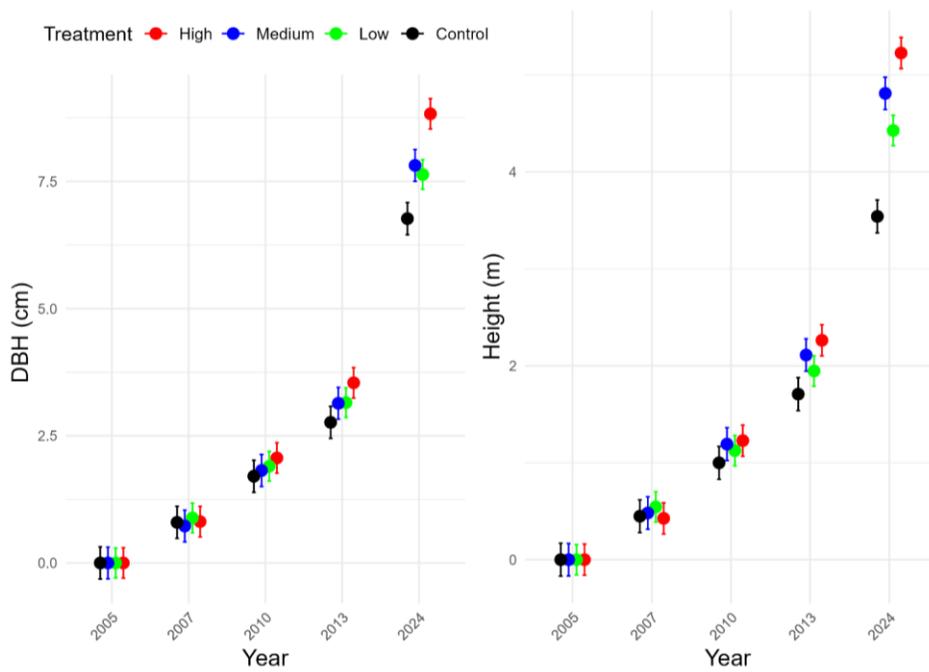


Figure 3. Absolute change of the mean by year (\pm SE) relative to 2005 of diameter at breast height cm (DBH; 1.37m) and total height m (Height) for three treatments and a control group of red spruce (*Picea rubens*) at two study sites in Kumrabow State Forest, two sites at Monongahela National Forest, and two sites at Canaan Valley Nation Wildlife Refuge. * High = 100 % basal area removal treatment, Medium = 67% basal area removal treatment, and Low = 33% basal area removal treatment (2005-2024).

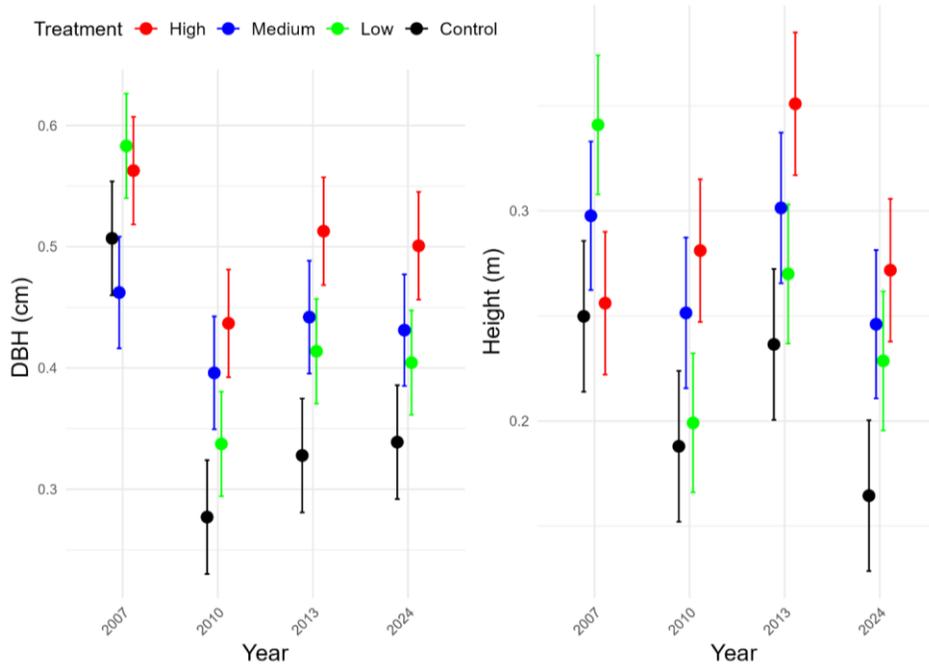


Figure 4. Rate of difference of mean growth by year (\pm SE) relative to the previous measurement year of diameter at breast height cm (DBH; 1.37m) and total height m (Height) for three treatments and a control group of red spruce (*Picea rubens*) at two study sites in Kumbrabow State Forest, two sites at Monongahela National Forest, and two sites at Canaan Valley Nation Wildlife Refuge. * High = 100 % basal area removal treatment, Medium = 67% basal area removal treatment, and Low = 33% basal area removal treatment (2005-2024).

Table 1. Repeated measures analysis of variance of tree height and diameter at breast height by basal area removal treatment level and measurement year (2007–2024) regarding the pre-treatment measurement values (2005) of red spruce (*Picea rubens*) target trees in east-central West Virginia. * Tree Height (TH), Diameter at Breast Height (DBH), Degrees of Freedom (DF), Sum of Squares (Sum Sq), Mean Sum of Squares (Mean Sq), * The interaction of the treatment and measurement year (*Treatment: Year*). * *Model: (Value (TH or DBH) ~ Baseline (measurement) + Treatment: Year + (1|Tree Number)). (2005–2024).* * Standard Error (SE), Degrees of Freedom (DF), Sum of Squares (Sum Sq.), Mean Squares (Mean Sq.).

Variable (TH)	Sum Sq	Mean Sq	DF	F-value	p-value
Pre-treatment HT	575.554	575.554	1	719.096	<0.001
Treatment	10.698	3.566	3	4.455	0.005
Year	1862.030	465.508	4	581.604	<0.001
Treatment: Year	38.909	3.242	12	4.051	<0.001
Variable (DBH)	Sum Sq	Mean Sq	DF	F-value	p-value
Pre-treatment DBH	1123.334	1123.334	1	480.475	<0.001
Treatment	23.990	7.997	3	3.420	0.019
Year	5481.400	1370.350	4	586.129	<0.001
Treatment: Year	55.509	4.626	12	1.979	0.024

Table 2. Tukey’s Honest Significant Difference contrast of mean \pm SE tree height and diameter at breast height by % basal area removal treatment level and measurement year (2007–2024) regarding the pre-treatment measurement values (2005) of red spruce (*Picea rubens*) target trees in east-central West Virginia. * Tree Height (TH), Diameter at Breast Height (DBH)* The interaction of the treatment and measurement year (*Treatment: Year*). * *Model*: (Value (TH or DBH) ~ Baseline (measurement) + Treatment: Year + (1|Tree Number)). Values that do not share a letter vary significantly within years across treatments. (2005–2024).

YEAR (TH)	CONTROL	33%	67%	100%
2005	5.6a \pm 0.17	5.6a \pm 0.16	5.6a \pm 0.17	5.6a \pm 0.16
2007	6.0a \pm 0.17	6.1a \pm 0.16	6.5a \pm 0.17	6.0a \pm 0.16
2010	6.5a \pm 0.17	6.7a \pm 0.16	6.8a \pm 0.17	6.8a \pm 0.16
2013	7.3a \pm 0.17	7.5ab \pm 0.16	7.7ab \pm 0.17	7.9b \pm 0.16
2024	9.1a \pm 0.17	10.0b \pm 0.16	10.4bc \pm 0.17	10.8c \pm 0.16
YEAR (DBH)	CONTROL	33%	67%	100%
2005	7.7a \pm 0.31	7.8a \pm 0.28	7.9a \pm 0.30	8.0a \pm 0.29
2007	8.5a \pm 0.31	8.7a \pm 0.28	8.5a \pm 0.30	8.8a \pm 0.29
2010	9.4a \pm 0.31	9.7a \pm 0.28	9.8a \pm 0.30	10.0a \pm 0.29
2013	10.5a \pm 0.31	11.0a \pm 0.28	11.0a \pm 0.30	11.5a \pm 0.29
2024	14.5a \pm 0.31	15.5ab \pm 0.28	15.7b \pm 0.30	16.8c \pm 0.29

1. Means in rows not followed by the same letter are significantly different ($P < 0.05$) in the transformed data.
2. (n = 182) per year

Table 3. Repeated measures analysis of variance of cumulative tree height and diameter at breast height by basal area removal treatment level and measurement year (2007–2024) regarding the pre-treatment measurement values (2005) of red spruce (*Picea rubens*) target trees in east-central West Virginia. * Tree Height (TH), Diameter at Breast Height (DBH), Degrees of Freedom (DF), Sum of Squares (Sum Sq), Mean Sum of Squares (Mean Sq), * The interaction of the treatment and measurement year (*Treatment: Year*). * Model: (Absolute Value (TH or DBH) ~ Baseline (measurement) + Treatment: Year + (1|Tree Number)). (2005–2024). * Standard Error (SE), Degrees of Freedom (DF), Sum of Squares (Sum Sq.), Mean Squares (Mean Sq.).

Variable (TH)	Sum Sq	Mean Sq	DF	F-value	p-value
Treatment	8.959	2.986	3	3.813	0.012
Year	1848.097	462.024	4	589.929	<0.001
Treatment: Year	39.018	3.251	12	4.152	<0.001
Variable (DBH)	Sum Sq	Mean Sq	DF	F-value	p-value
Treatment	10.226	3.409	3	1.460	0.228
Year	5474.577	1368.644	4	586.365	<0.001
Treatment: Year	55.405	4.617	12	1.978	0.024

Table 4. Tukey’s Honest Significant Difference contrast of mean ± SE cumulative tree height and diameter at breast height by % basal area removal treatment level and measurement year (2007–2024) regarding the pre-treatment measurement values (2005) of red spruce (*Picea rubens*) target trees in east-central West Virginia. * Tree Height (TH), Diameter at Breast Height (DBH)* The interaction of the treatment and measurement year (*Treatment: Year*). * *Model*: (Absolute Value (TH or DBH) ~ Baseline (measurement) + Treatment: Year + (1|Tree Number)). Values that do not share a letter vary significantly within years across treatments. (2005–2024).

YEAR (TH)	CONTROL	33%	67%	100%
2005	0a ± 0.17	0a ± 0.16	0a ± 0.17	0a ± 0.16
2007	0.4a ± 0.17	0.5a ± 0.16	0.5a ± 0.17	0.4a ± 0.16
2010	1.0a ± 0.17	1.1a ± 0.16	1.2a ± 0.17	1.2a ± 0.16
2013	1.7a ± 0.17	1.9a ± 0.16	2.1a ± 0.17	2.3a ± 0.16
2024	3.5a ± 0.17	4.4b ± 0.16	4.8bc ± 0.17	5.2c ± 0.16
YEAR (DBH)	CONTROL	33%	67%	100%
2005	0a ± 0.31	0a ± 0.29	0a ± 0.31	0a ± 0.30
2007	0.8a ± 0.31	0.9a ± 0.29	0.7a ± 0.31	0.8a ± 0.30
2010	1.7a ± 0.31	1.9a ± 0.29	1.9a ± 0.31	2.1a ± 0.30
2013	2.8a ± 0.31	3.2a ± 0.29	3.1a ± 0.31	3.5a ± 0.30
2024	6.8a ± 0.31	7.6a ± 0.29	8.9ab ± 0.31	6.8b ± 0.30

1. Means in rows not followed by the same letter are significantly different ($P < 0.05$) in the transformed data.
2. (n = 182) per year

Table 5. Repeated measures analysis of variance of the rate of mean growth difference of tree height and diameter at breast height by basal area removal treatment level and measurement year (2007–2024) regarding the pre-treatment measurement values (2005) of red spruce (*Picea rubens*) target trees in east-central West Virginia. * Tree Height (TH), Diameter at Breast Height (DBH), Degrees of Freedom (DF), Sum of Squares (Sum Sq), Mean Sum of Squares (Mean Sq), * The interaction of the treatment and measurement year (*Treatment: Year*). * *Model*: (Growth rate (TH or DBH) ~ Baseline (measurement) + Treatment: Year + (1|Tree Number)). (2005–2024). * Standard Error (SE), Degrees of Freedom (DF), Sum of Squares (Sum Sq.), Mean Squares (Mean Sq.).

Variable (TH)	Sum Sq	Mean Sq.	DF	F-value	p-value
Pre-treatment HT	598.544	598.544	1	765.501	<0.001
Treatment	10.937	3.646	3	4.663	0.004
Year	1911.851	477.963	4	611.285	<0.001
Treatment: Year	39.977	3.331	12	4.261	<0.001
Variable (DBH)	Sum Sq	Mean Sq	DF	F-value	p-value
Pre-treatment DBH	1.043	1.043	1	22.111	<0.001
Treatment	0.406	0.135	3	2.868	0.039
Year	2.175	0.725	3	15.364	<0.001
Treatment: Year	0.561	0.062	9	1.321	0.224

Table 6. Tukey’s Honest Significant Difference contrast of the growth rate tree height and diameter at breast height by measurement year (2007–2024) regarding the pre-treatment measurement values (2005) of red spruce (*Picea rubens*) target trees in east-central West Virginia. * Tree Height (TH), Diameter at Breast Height (DBH), Degrees of Freedom (DF), Standard Error (SE)* The interaction of the treatment and measurement year (*Treatment: Year*). * *Model*: (Growth Rate (TH or DBH) ~ Baseline (measurement) + Treatment: Year + (1|Tree Number)). (2005–2024). * Standard Error (SE), Degrees of Freedom (DF).

Contrast TH	Estimate	SE	DF	t-ratio	p-value
2007 – 2010	0.056	0.024	440.031	2.336	0.092
2007 – 2013	-0.004	0.024	440.031	-0.149	0.999
2007 – 2024	0.058	0.024	439.217	2.431	0.073
2010 – 2013	-0.060	0.024	439.217	-2.481	0.064
2010 – 2024	0.002	0.024	440.031	0.090	1.000
2013 – 2024	0.062	0.024	440.031	2.575	0.050
Contrast DBH	Estimate	SE	DF	t-ratio	p-value
2007 – 2010	0.167	0.025	439.617	6.648	0.000
2007 – 2013	0.105	0.025	439.617	4.167	0.000
2007 – 2024	0.110	0.025	439.050	4.388	0.000
2010 – 2013	-0.062	0.025	439.050	-2.477	0.065
2010 – 2024	-0.057	0.025	439.617	-2.270	0.107
2013 – 2024	0.005	0.025	439.617	0.211	0.997

Table 7. Tukey’s Honest Significant Difference contrast of the growth rate tree height and diameter at breast height by % basal area removal treatment level regarding the pre-treatment measurement values (2005) of red spruce (*Picea rubens*) target trees in east-central West Virginia. * Tree Height (TH), Diameter at Breast Height (DBH), Degrees of Freedom (DF), Sum of Squares (Sum Sq), Mean Sum of Squares (Mean Sq), * The interaction of the treatment and measurement year (*Treatment: Year*). * *Model*: (Growth rate (TH or DBH) ~ Baseline (measurement) + Treatment: Year + (1|Tree Number)). (2005–2024). * Standard Error (SE), Degrees of Freedom (DF).

Contrast (TH)	Estimate	SE	DF	t-ratio	p-value
100 - 33	0.030	0.025	145.285	1.217	0.617
100 - 67	0.016	0.026	146.322	0.613	0.928
100 - RC	0.080	0.026	145.290	3.071	0.013
33 - 67	-0.014	0.025	146.396	-0.568	0.941
33 - RC	0.050	0.026	145.287	1.944	0.215
67 - RC	0.064	0.027	146.406	2.420	0.078
Contrast (DBH)	Estimate	SE	DF	T-ratio	P-value
100 - 67	0.070	0.047	146.302	1.505	0.437
100 - 33	0.069	0.045	145.605	1.511	0.434
100 - RC	0.141	0.048	145.612	2.931	0.020
67 - 33	-0.002	0.046	146.411	-0.040	1.000
67 - RC	0.070	0.048	146.420	1.448	0.472
33 - RC	0.072	0.047	145.605	1.542	0.415

References

- Adams, H. S., Stephenson, S. L., Blasing, T. J., & Duvick, D. N. (1985). Growth-trend declines of spruce and fir in Mid-Appalachian subalpine forests. [https://doi.org/10.1016/S0098-8472\(85\)90029-2](https://doi.org/10.1016/S0098-8472(85)90029-2)
- Adams, M. B. (2004). Description of the Fork Mountain long-term soil productivity study: site characterization. USDA Forest Service. <https://doi.org/10.2737/NE-GTR-323>
- Beane, N. R. (2010). Using environmental and site-specific variables to model current and future distribution of red spruce (*Picea rubens* Sarg.) forest habitat in West Virginia (Ph.D. dissertation). West Virginia University. <https://doi.org/10.33915/etd.3177>
- Beane, N. R., Rentch, J. S., & Schuler, T. M. (2013). Using maximum entropy modeling to identify and prioritize red spruce forest habitat in West Virginia. <https://doi.org/10.2737/NRS-RP-23>
- Brose, P.H. & Hutchinson, T.F. (2019). The fundamentals of release burning in mixed oak forests with emphasis on the shelterwood-burn technique. In D.C. Dey, M.C. Stambaugh, S.L. Clark, & C.J. Schweitzer (Eds.), *Oak Symposium: Sustaining Oak Forests in the 21st Century through Science-Based Management* (pp. 79–90). USDA Forest Service, Southern Research Station.
- Butler, P.R., Iverson, L., Thompson, F.R., Brandt, L., Handler, S., Janowiak, M., Shannon, P.D., Swanston, C., Karriker, K., Bartig, J., Connolly, S., Dijak, W., Bearer, S., Blatt, S., Brandon, A., Byers, E., Coon, C., Culbreth, T., Daly, J., Dorsey, W., Ede, D., Euler, C., Gillies, N., Hix, D.M., Johnson, C., Lyte, L., Matthews, S., McCarthy, D., Minney, D., Murphy, D., O’Dea, C., Orwan, R., Peters, M., Prasad, A., Randall, C., Reed, J., Sandeno, C., Schuler, T., Sneddon, L., Stanley, B., Steele, A., Stout, S., Swaty, R., Teets, J., Tomon, T., Vanderhorst, J., Whatley, J., & Zegre, N. (2022). Central Appalachians forest ecosystem vulnerability assessment and synthesis: A report from the Central Appalachians Climate Change Response Framework project. Gen. Tech. Rep. NRS-146. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA. <https://doi.org/10.2737/NRS-GTR-146>
- Desmarais, K.M. & Leak, W.B. (2005). Ten-year performance of eastern white pine under a crop tree release regime on an outwash site. *Northern Journal of Applied Forestry*, 22, 139–142. <https://doi.org/10.1093/njaf/22.2.139>
- Dey, D.C. (2014). Sustaining oak forests in eastern North America: Regeneration and recruitment, the pillars of sustainability. *Forest Science*, 60, 926–942. <https://doi.org/10.5849/forsci.13-114>
- Diggins, C.A. & Ford, W.M. (2017). Microhabitat selection of the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus* Miller) in the central Appalachians. *Northeastern Naturalist*, 24, 173–190. <https://doi.org/10.1656/045.024.0209>
- Dukpa, D., Khandu, Y., Darabant, A., & Cook, E.R. (2012). Growth release of retained fir (*Abies densa*) trees in the group opening and single tree selection logging. *Bhutan Journal of Renewable Natural Resource*, 8, 113–119. <https://doi.org/10.1016/j.dendro.2018.03.003>
- Dumais, D. & Prévost, M. (2007). Management for red spruce conservation in Québec: The importance of some physiological and ecological characteristics – A review. *The Forestry Chronicle*, 83, 378–391. <https://doi.org/10.5558/tfc83378-3>

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

- Ford, W.M., Diggins, C.A., De La Cruz, J.L., & Silvis, A. (2022). Distribution probability of the Virginia northern flying squirrel in the High Allegheny Mountains. *Journal of the Southeastern Association of Fish and Wildlife Agencies*, 9, 168–175.
- Gaertner, B.A., Zegre, N., Warner, T., Fernandez, R., He, Y., & Merriam, E.R. (2019). Climate, forest growing season, and evapotranspiration changes in the central Appalachian Mountains, USA. *Science of The Total Environment*, 650, 1371–1381. <https://doi.org/10.1016/j.scitotenv.2018.09.129>
- Hornbeck, J.W. & Kochenderfer, J.N. (1998). Growth trends and management implications for West Virginia's red spruce forests. *Northern Journal of Applied Forestry*, 15, 197–202. <https://doi.org/10.1093/njaf/15.4.197>
- Iverson, L.R., Prasad, A.M., Matthews, S.N., & Peters, M. (2008). Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management*, 254, 390–406. <https://doi.org/10.1016/j.foreco.2007.07.023>
- Lorimer, C.G. (1983). Tests of age-independent competition indices for individual trees in natural hardwood stands. *Forest Ecology and Management*, 6, 343–360. [https://doi.org/10.1016/0378-1127\(83\)90042-7](https://doi.org/10.1016/0378-1127(83)90042-7)
- Menzel, J.M., Ford, W.M., Edwards, J.W., & Terry, T.M. (2006). Home range and habitat use of the vulnerable Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the central Appalachian Mountains, USA. *Oryx*, 40, 204–210. <https://doi.org/10.1017/S0030605306000494>
- Moore, A.R., Seymour, R.S., & Kenefic, L.S. (2007). Height development of shade-tolerant conifer saplings in multi-aged Acadian forest stands. *Canadian Journal of Forest Research*, 37, 2715–2723. <https://doi.org/10.1139/X07-110>
- Noss, R. F., Scott, J. M., LaRoe, E. T., & U.S. Fish and Wildlife. Research and Development. (1995). *Endangered ecosystems of the United States: A preliminary assessment of loss and degradation*. Washington, D.C.: U.S. Dept.
- NOAA, U.S. Department of Commerce. (2025). *Climate*. <https://www.weather.gov/wrh/Climate?wfo=rlx> (accessed 2.7.25).
- Pan, C., Tajchman, S.J., & Kochenderfer, J.N. (1997). Dendroclimatological analysis of major forest species of the central Appalachians. *Forest Ecology and Management*, 98, 77–87. [https://doi.org/10.1016/S0378-1127\(97\)00087-X](https://doi.org/10.1016/S0378-1127(97)00087-X)
- Rentch, J.S., Ford, W.M., Schuler, T.S., Palmer, J., & Diggins, C.A. (2016). Release of suppressed red spruce using canopy gap creation—ecological restoration in the Central Appalachians. *Natural Areas Journal*, 36, 29–37. <https://doi.org/10.3375/043.036.0108>
- Rentch, J.S., Schuler, T.M., Ford, W.M., & Nowacki, G.J. (2007). Red spruce stand dynamics, simulations, and restoration opportunities in the Central Appalachians. *Restoration Ecology*, 15, 440–452. <https://doi.org/10.1111/j.1526-100X.2007.00240.x>
- Rentch, J.S., Schuler, T.M., Nowacki, G.J., Beane, N.R., & Ford, W.M. (2010). Canopy gap dynamics of second-growth red spruce-northern hardwood stands in West Virginia. *Forest Ecology and Management*, 260, 1921–1929. <https://doi.org/10.1016/j.foreco.2010.08.043>
- Rollins, A.W., Adams, H.S., & Stephenson, S.L. (2010). Changes in forest composition and structure across the red spruce-hardwood ecotone in the Central Appalachians. *Castanea*, 75, 303–314. <https://doi.org/10.2179/09-052.1>

Formatted: Font: Italic

- RStudio, T. (2024). RStudio: Integrated Development for R*. RStudio PBC. Boston, MA <http://www.rstudio.com/>.
- Schuler, T.M. (2006). Crop tree release improves competitiveness of northern red oak growing in association with black cherry. <https://doi.org/10.1093/njaf/23.2.77>
- Schuler, T.M., Ford, W.M., & Collins, R.J. (2002). Successional dynamics and restoration implications of a montane coniferous forest in the Central Appalachians, USA. *Natural Areas Journal*, 22, 88–98.
- Seymour, R.S. (1995). The northeastern region. In J.W. Barrett (Ed.), *Regional Silviculture of the United States* (3rd ed., pp. 31–79). John Wiley & Sons, New York, NY.
- Seymour, R.S. (1992). The red spruce-balsam fir forest of Maine: Evolution of silvicultural practice in response to stand development patterns and disturbances. In M.J. Kelty, B.C. Larson, & C.D. Oliver (Eds.), *The Ecology and Silviculture of Mixed-Species Forests* (pp. 217–244). Springer Netherlands, Dordrecht. ISBN 0-7923-1643-6.
- Thomas-Van Gundy, M. (2022). Twenty-year trends in running buffalo clover (*Trifolium stoloniferum* Muhl. Ex A. Eaton; Fabaceae) on a managed forest in northeastern West Virginia. *Natural Areas Journal*, 42, 79–88. <https://doi.org/10.3375/21-19>
- Thomas-Van Gundy, M. & Morin, R. (2021). Change in montane forests of east-central West Virginia over 250 years. *Forest Ecology and Management*, 479, 118604. <https://doi.org/10.1016/j.foreco.2020.118604>
- Vogel, P.J., Lhotka, J.M., & Stringer, J.W. (2022). Long-term effects of crop tree release on growth and quality in white-oak (*Quercus alba* L.)-dominated stands. *Forest Science*, 68, 343–352. <https://doi.org/10.1093/forsci/xfac015>
- Vogel, C.A. & Leffler, R.J. (2015). Climate of Canaan Valley. *Southeastern Naturalist*, 14 (sp7), 18–32. <https://doi.org/10.1656/058.014.sp705>
- Ward, J.S. (2017). Twenty-five year response of non-crop trees to partial release during precommercial crop tree management. *Forest Ecology and Management*, 387, 12–18. <https://doi.org/10.1093/forsci/xfac015>
- Yetter, E., Brown, J., & Chhin, S. (2021). Anamorphic site index curves for central Appalachian red spruce in West Virginia, USA. *Forests*, 12, 94. <https://doi.org/10.3390/f12010094>

Formatted: Font: Italic

Appendix A.

In June and July 2024, I traveled to the Central Appalachian Mountains of West Virginia (Figure 1, Chapter 2) to test the utility of lidar-derived products in forest restoration and wildlife habitat management. In doing so, I collected ground heights utilizing a Haglöf's hypsometer (see Methods, Chapter 2) to measure the total tree heights of 271 trees. Of those measured, 66 trees were dominant or codominant red spruce (*Picea rubens*). All red spruce were GPS-located with approximately 1m accuracy using Juniper Systems Geode GNS2. In 2025, 3 DEP point clouds were acquired from USGS (apps.nationalmaps.gov) for the plots where these 66 trees are located. Using R version 5.24 (see Chapters 1&2) and the package *lidR*, we normalized the heights of these point clouds. Then, I used the `pixel_metrics` function to develop a 5m rasterized canopy height model, limiting the z-axis maximum to 40m to avoid unclassified noise. To perform statistical analysis, I utilized the *ggplot2* package and the base function *t.test* to examine the relationships between ground heights, LiDAR heights, and Treemap 2016 heights (see Chapter 1).

I used a paired *t-test* to show a mean difference of 0.618 m (p-value <0.001) between the ground heights and the z-axis maximums of the LiDAR data. There was a slight positive relationship between LiDAR-derived heights and the ground heights (Figure A). However, a paired t-test revealed a mean difference of 3.71 m between ground-measured heights and Treemap 2016 heights (p< 0.001). Furthermore, there is no linear relationship between ground heights and Treemap 2016 heights (Figure B).

The results demonstrate the expected relationship between LiDAR heights and ground-verified heights, indicating that LiDAR-derived heights can be used as substitutes for ground-verified heights in specific applications. However, this brief study raises questions about the accuracy of Treemap 2016 at this resolution. For fine modeling and precision-based applications, Treemap 2016 may be too coarse to be sufficient and would be better substituted for LiDAR-derived metrics.

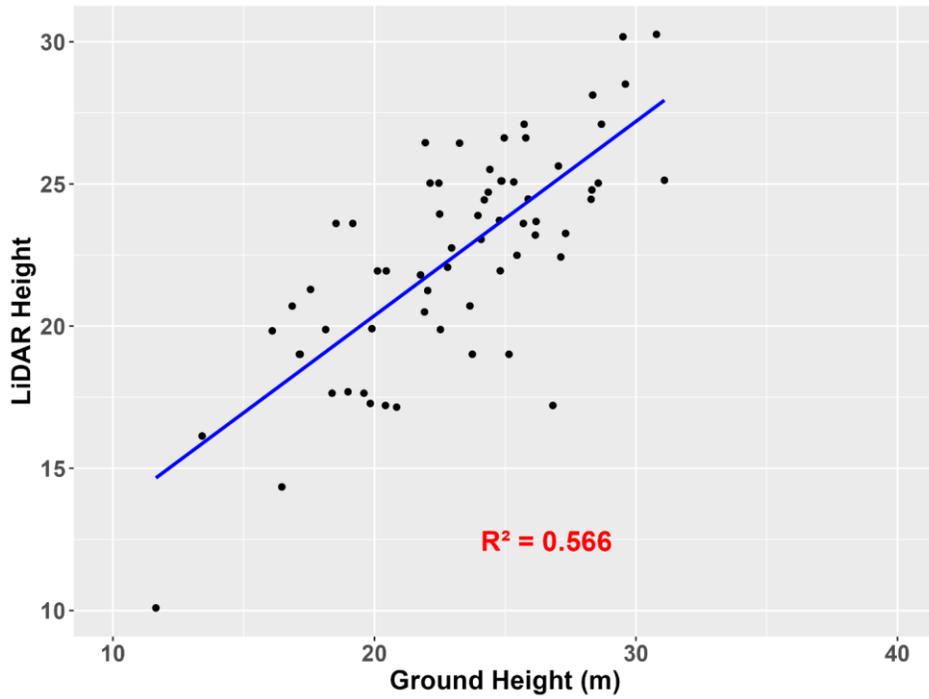


Figure A. Scatter plot and regression line of the relationship between Z-axis maximum values (m) derived from LiDAR and ground measured heights (m) at 66 dominant/co-dominant red spruce (*Picea rubens*) trees on the Monongahela National Forest in the Central Appalachian Mountains of West Virginia. * Coefficient of Determination (R^2). (June, 2024).

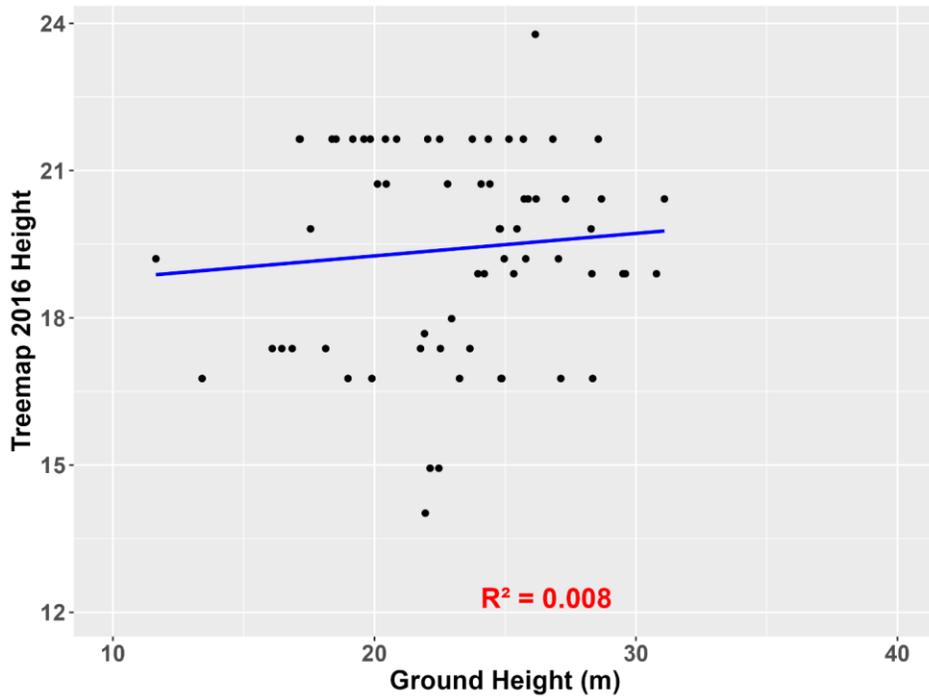


Figure B. Scatter plot and regression line of the relationship between Treemap 2016 average dominant stand height (m) raster cell values and ground measured heights (m) at 66 dominant/co-dominant red spruce (*Picea rubens*) trees on the Monongahela National Forest in the Central Appalachian Mountains of West Virginia. * Coefficient of Determination (R^2). (June 2024).

Appendix B.

In 2025, I acquired rasterized canopy height models derived from USGS 3 DEP LiDAR sourced across the Monongahela National Forest in West Virginia. With these products, I sought to test whether the canopy surface roughness is related to the Virginia Northern Flying Squirrel (*Glaucomys sabrinus fuscus*; VNFS). To accomplish this, I utilized the *raster* package in R. I isolated the z-axis maximum heights (Z-Max) band and then used the function *focal* with the nearest eight cells to extract the standard deviation of maximum heights and the average height. I then used the Canopy Roughness Index formula (CRI) (*Standard Deviation of Heights* ÷ *Average Heights*), or $\left(CRI = \frac{\sigma}{\mu}\right)$ (Zhang et al., 2022). This coefficient of variation offers a normalized quantification of canopy surface textural complexity independent of absolute canopy heights. This canopy roughness index was then extracted to the VNFS capture and pseudo-random points (see Methods Chapter 1). A generalized linear model (GLM) was then made to determine the significance of the included covariates. Finally, I developed relationship graphs using *ggplot2* and the *anova* function in base R to create an Analysis of Variance for the included variables.

The output of the GLM demonstrates that rugosity has a significant relationship with the probability of VNFS occurrence and interaction with the red spruce canopy class (Figure C, Table A). Furthermore, Lidar-derived heights further support the findings from Treemap 2016 in Humbert et al. (in press; Chapter 1), which indicate that the occurrence probability of VNFS is linked to spruce stands taller than 20m (Figure D).

These findings suggest that canopy surface roughness affects the VNFS habitat structure. Specifically, the VNFS selects higher horizontal and vertical variability, which can be inferred from Humbert et al. (in press; see Figures & Discussion Chapter 1). Finally, the relationship between VNFS and LiDAR-derived heights resembles the maximum suggested height in Humbert et al. (in press), which adds validity to the findings of the model used in that study, despite the inaccuracies of the forest structure data (Treemap 2016) used. Future research using LiDAR-derived metrics of forest structure and ground validation data is needed to understand the connections between roughness and traditional forest structure measurements (Diameter at breast height, tree height, and Basal area) and further realize VNFS structure selection.

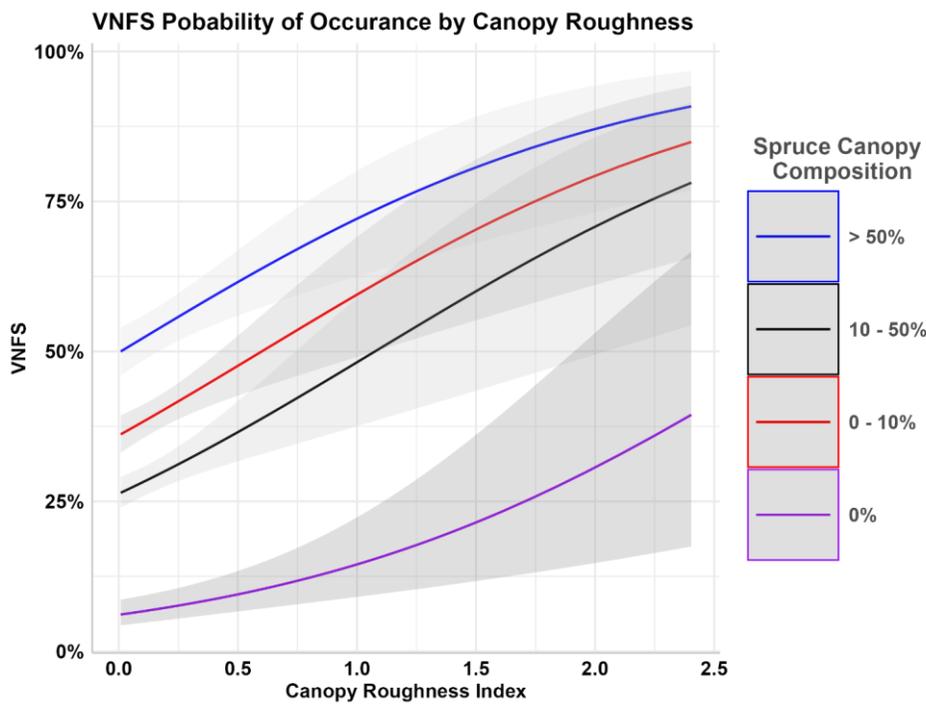


Figure C. The fit plot of the generalized linear modeled probability and 95% confidence interval of Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*; VNFS) likelihood of presence in the Central Appalachian Mountains of Virginia and West Virginia relative canopy rugosity colored by the spruce canopy composition classifications (>50%, 10 – 50%, 0 – 10%, and 0%). Model: VNFS~ Z-Max + Canopy Roughness Index + Spruce Class. (March 2025).

Formatted: Font: Italic

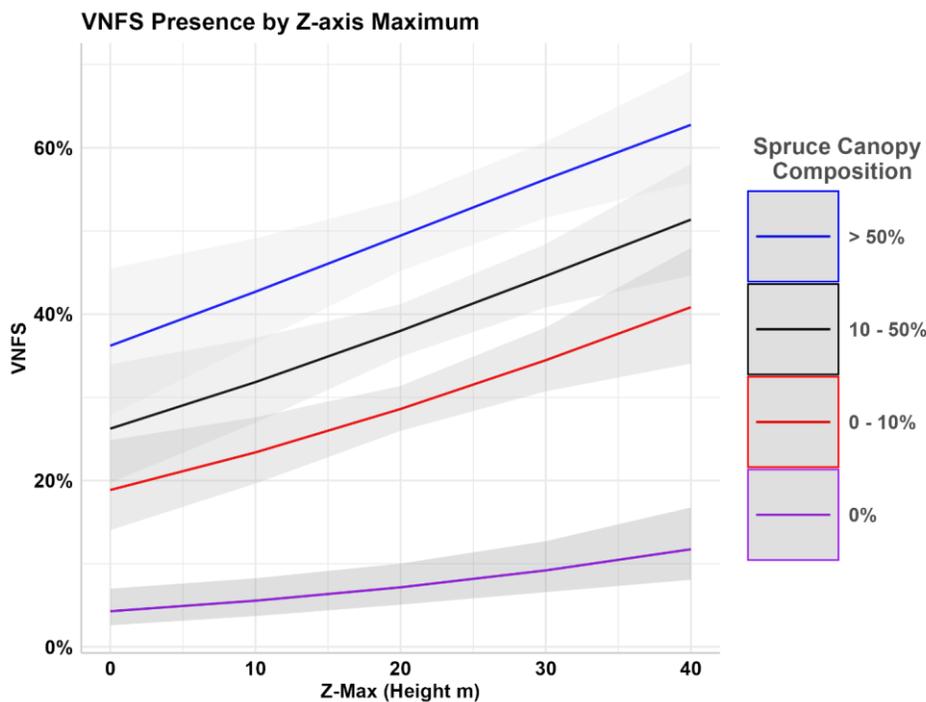


Figure D. The fit plot of the generalized linear modeled probability and 95% confidence interval of Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*; VNFS) likelihood of presence in the Central Appalachian Mountains of Virginia and West Virginia LiDAR-derived canopy height (z-axis maximum) colorized by the spruce canopy composition classifications (>50%, 10 – 50%, 0 – 10%, and 0%). * Model: VNFS~ Z-Max (Z – Axis Maximum (Tree height m)) + Canopy Roughness Index * Spruce Class. (March 2025)

Formatted: Font: Italic

Table A. Analysis of variance of the generalized linear model of the Virginia Northern Flying Squirrel (*Glaucomys sabrinus fuscus*) likelihood of presence as predicted by LiDAR-derived canopy heights (Z-Max), basal area, canopy roughness, and spruce canopy composition class (>50%, 10 – 50%, 0 – 10%, and 0%). * Model: VNFS~ Z-Max + Canopy Roughness Index (Roughness) + Spruce Class. (March 2025). * Degrees of Freedom (DF), Residual Degrees of Freedom (Resid. DF), Residual Deviation (Resid. Dev).

Variable	DF	Deviance	Resid. DF	Resid. Dev.	p-value
Z-Max	1	35.49	3719	4749.400	<0.001
Roughness	1	12.82	3718	4736.500	<0.001
Spruce Class	3	329.99	3715	4406.500	<0.001

References

- Zhang, X., Zhang, Z., Zhang, Y., Zhang, Q., Liu, X., Chen, J., Wu, Y., & Wu, L. (2022). Influences of fractional vegetation cover on the spatial variability of canopy SIF from unmanned aerial vehicle observations. *International Journal of Applied Earth Observation and Geoinformation**, 107, 102712. <https://doi.org/10.1016/j.jag.2022.102712>