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Wiley
International Journal of Forestry Research
Volume 2025, Article ID 4526136, 9 pages
https://doi.org/10.1155/ijfr/4526136

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Research Article

Red Spruce Forest Stand Structure and Virginia Northern Flying Squirrel Habitat Suitability

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Received 18 July 2025; Revised 12 August 2025; Accepted 19 September 2025

Academic Editor: Poorani Gurumallesh

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The Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*; VNFS) is a rare, Pleistocene-relict, disjunct subspecies of the northern flying squirrel. The squirrel occurs only in high-elevation red spruce (*Picea rubens*) forests of the central Appalachian Mountains of Virginia and West Virginia—a forest type that was substantially reduced by exploitative logging and wildfire in the 1890s–1930. Owing to its cryptic nature and difficulty of capture, managers have relied on an evolving series of predicted habitat suitability models that primarily have used topographic measures and red spruce cover class to assess potential occupancy on the landscape. Currently, VNFS is considered the sentinel species in the region whereby its predicted presence indicates red spruce forests with higher relative habitat integrity, and unsuitable habitat highlights where red spruce restoration or enhancement should occur. However, extant VNFS models only use red spruce percent composition and do not provide insights into forest structure, such as forest canopy height or basal area, that are needed by managers to implement restoration or assess effectiveness. We examined recent historical VNFS observations from nest-box surveys and radiotelemetry data (natural dens and foraging points) relative to random pseudoabsence points across red spruce cover classes from the most current VNFS predicted probability habitat model. Using generalized linear models in an information-theoretic approach, we found that within each red spruce composition class, suitable VNFS habitat was related to increased forest canopy height (m), basal area ($m^2 \cdot ha^{-1}$), quadratic mean diameter (cm), and stem density (number of trees ha^{-1}), indicating that, within red spruce and mixed red spruce–northern hardwood forests, VNFS is associated most with mature forest conditions. Accordingly, our results could be recombined with habitat suitability models to prioritize where, for example, red spruce forest structural enhancement would facilitate shifting a given stand to a higher probability condition for VNFS use.

1. Introduction

Red spruce (*Picea rubens*) forests once occupied as much as 600,000 ha in the central Appalachian Mountains of West Virginia and portions of western Virginia and western Maryland, USA [1, 2]. At the turn of the 20th century, red spruce was exploitatively harvested, and postharvest areas often experienced extensive wildfires that eliminated regeneration and seed sources [3]. These events shifted forest conditions from a boreal-like, red spruce-dominated forest to northern hardwood forests comprised primarily of birch (*Betula* spp.), American beech (*Fagus grandifolia*), red maple (*Acer rubra*), and sugar maple (*A. saccharum*) [4]. Currently, much of the region's red spruce is reduced to small,

aggregated patches or as a mixed component within the northern hardwood type. Nonetheless, red spruce seedlings and saplings are now found widely in the midstory of the northern hardwood cover types [5].

Within this regional habitat type, the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*; VNFS), a disjunct subspecies of the northern flying squirrel, occurs in northwestern Virginia and eastern West Virginia [6] largely in the Monongahela National Forest, Canaan Valley National Wildlife Refuge, Kumbrabow State Forest, and surrounding private lands above 800 m in elevation [7]. The VNFS forages for hypogeal fungi on the forest floor underneath red spruce or other montane conifer canopies and dens in tree cavities or dreys [8–10]. Relative to other subspecies of northern flying squirrel [6, 11], home range sizes of VNFS can exceed 50 ha owing to the overall degraded red spruce forest condition and poor habitat connectivity in the region [9]. In 1985, the U.S. Fish and Wildlife Service listed the VNFS as endangered [12] due to historical habitat loss and fragmentation. The contemporary rarity of the VNFS was also correlated with the slow recovery of Central Appalachian red spruce forests from industrial-derived atmospheric deposition of S and N in the 1940s–1980s [7]. However, after roughly three decades since listing, population stability and regional persistence of VNFS were reached as was the recognition that red spruce recovery was occurring naturally, albeit slowly [13] which led to the VNFS being delisted in 2013 [14]. Nonetheless, VNFS remains a species of greatest conservation need as red spruce forests continue to be vulnerable to habitat degradation from climate change impacts or direct habitat conversion [7, 15]. As a mature red spruce forest obligate, the VNFS is considered a "sentinel" species indicative of functioning, high integrity conditions and is used as an indicator species for current red spruce restoration and enhancement efforts in the region [16, 17].

Due to the rare and cryptic nature of the VNFS, traditional live-trapping and monitoring methods are difficult [7]. Since the 1990s, managers have relied on predictive habitat modeling to delineate potentially suitable habitat and the quality thereof for VNFS and the red spruce forest it inhabits. Using elevation and landform indices models, Odom et al. [18] were highly precise in identifying areas unsuitable for VNFS, but their model provided ambiguous results for suitable areas. From artificial nest box records, Ford et al. [19] and Menzel et al. [20] determined that VNFS habitat suitability was associated with forest stands with > 30% red spruce composition and elevations > 1000 m. Radiotelemetry data from Menzel et al. [9] and Diggins and Ford [10] provided additional VNFS natural den and foraging observations that Ford et al. [7] used in conjunction with better landform and forest cover class inputs [21], to create a more robust predictive habitat model for VNFS. The Ford et al. [7] model further cemented the link between VNFS habitat suitability and increasing percent red spruce cover, elevation, and, in some contexts, presence of highly sheltered, concave landforms. Although an improvement over earlier work, this effort did not incorporate forest stand-level structure measures found to be biologically important to the VNFS or the closely related endangered Carolina northern flying squirrel (*Glaucomys sabrinus coloratus*; CNFS) in similar habitat in the southern Appalachian Mountains [10, 11].

Standard forest structure metrics, i.e., forest height, stand basal area, stand density, and tree diameter, could be used to prioritize red spruce restoration or stand enhancement in the central Appalachian Mountains as well as provide benchmarks for restoration success [5]. Accordingly, the purpose of our study was to explore the relationships between VNFS presence as denoted by the Ford et al. [7] resource selection spatial model with added forest stand structure metrics in the central Appalachian Mountains above 800 m across four red spruce cover composition classes (0%, 1%–10%, 10%–50%, and > 50%). Based on previous work [7, 9, 10, 22], we hypothesized that predicted habitat suitability would increase for stands that had late-successional structural characteristics, such as tall, large-diameter trees and high stand density, which may be more indicative of preharvest and prefire conditions that historically occurred in the central Appalachian Mountains [23].

2. Methods

Our study was centered in the Allegheny Highlands of the central Appalachian Mountains, primarily within eastern West Virginia (Figure 1). This region is characterized by high elevations (600–1482 m), steep slopes, broad valleys, and often planar, plateau-like ridges [7]. Owing to the elevation, the climate is relatively cool, with average annual temperatures ranging from 6.7° to 9.4°C. For the majority of the region from the Allegheny Front west, annual precipitation is high (≥ 120 cm), much of which falls as snow during the winter months [21]. Soils are rocky, shallow, acidic silt loams due to the sandstone and shale parent materials [4]. Prior to harvesting and fire, a montane, boreal-like forest of red spruce dominated at the highest elevations and then occurred in pure to mixed northern hardwood stands downslope in sheltered ravines and riparian areas at midelevations. Minor associates in these systems include eastern hemlock (*Tsuga canadensis*), yellow birch (*B. alleghaniensis*), and American beech with an understory mostly comprised of ericaceous shrubs, such as great rhododendron (*Rhododendron maximum*) and various blueberries (*Vaccinium* spp.). As elevation decreases or where post-logging fire removed red spruce seed sources and advanced regeneration, the dominant forest composition shifts to a northern hardwood association with common species such as American beech, yellow birch, red and sugar maple, black cherry (*Prunus serotina*), and Fraser magnolia (*Magnolia fraseri*), with some red spruce in the mid- and understory [21, 23, 24].

2.1. Data Collection. To examine the relationship of VNFS presence with forest stand structure metrics, we used the 2173 VNFS presence records from Ford et al. [7], which included contemporary nest box, natural den, and foraging location data. Since true absence points for VNFS were

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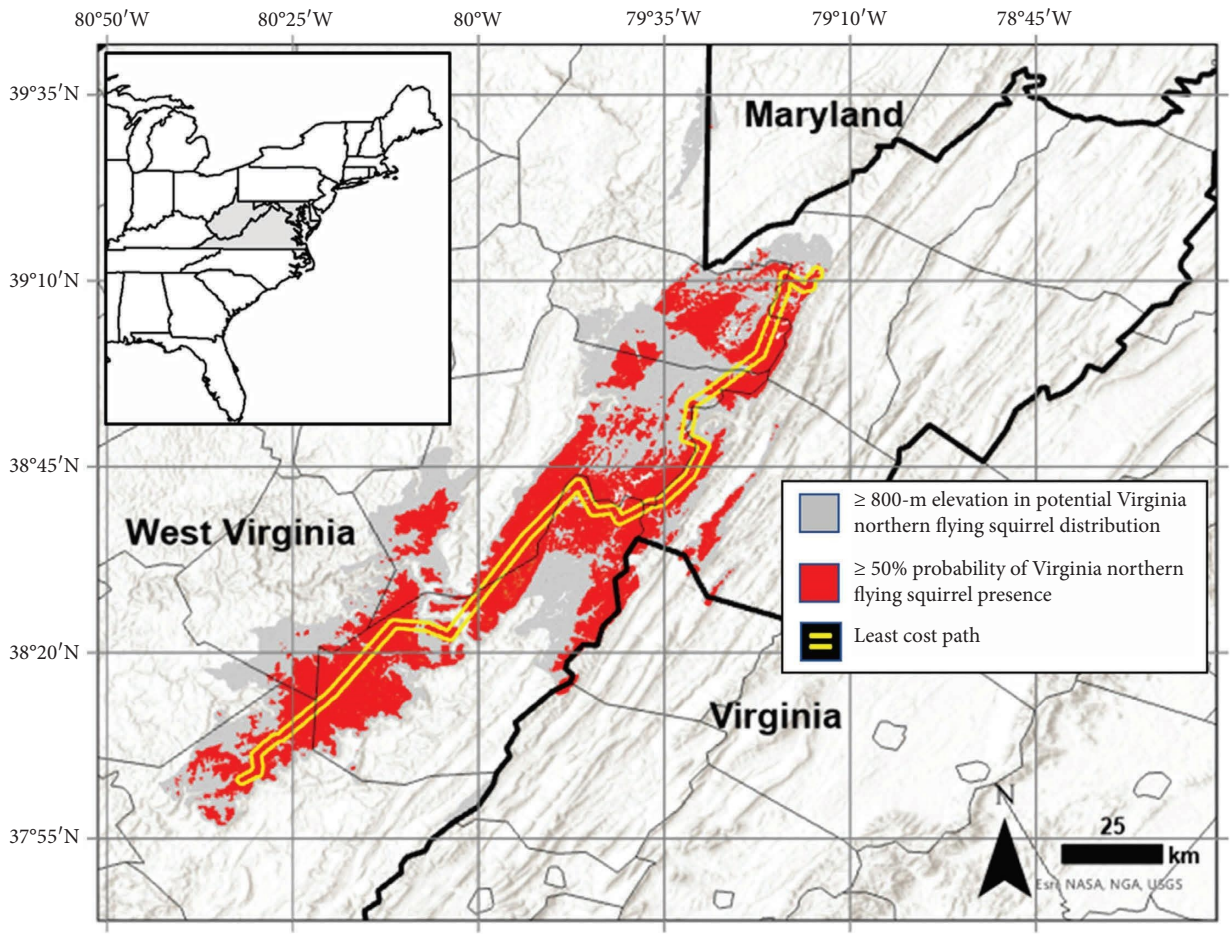


FIGURE 1: Map of the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*; VNFS) and red spruce (*Picea rubens*) potential distribution in the central Appalachian Mountains of Maryland, West Virginia, and Virginia. Regions in red are predicted VNFS high habitat suitability (≥ 50%) from Ford et al. [7], whereas the remaining gray areas are in the wider landscape that are ≥ 800 m in elevation, where red spruce and VNFS occurrence is possible. Yellow lines denote a computed least cost path connecting VNFS habitat patches on the landscape (see text).

unknown [7], we generated 10,865 pseudoabsence points, five times the number of presence records, for comparison [25]. To assign presence and pseudoabsence points to a red spruce cover class value, we acquired spatial data provided by Byers et al. [21], which delineated red spruce percent composition classes on the landscape as: None (0) = 0%, Low (1) = 0.1%–10%, Medium (2) = 10.1%–50%, and High (3) = > 50.1%. We then joined the red spruce cover classes with the U.S. Forest Service's raster product, "TreeMap 2022," which provided structure metrics for all trees irrespective of species, such as number of trees ha^{-1} (TPH), basal area ($m^2 \cdot ha^{-1}$; BA), stand average dominant tree height (m; TH), and quadratic mean diameter (> 2.5 cm; QMD) that is a measure of the diameter of average tree per tree basal area [26]. To preserve all VNFS presence records, we filled missing values in the TreeMap layers using the *focal* function, defining a 9-cell moving window, in the *terra* package [27] of R.

2.2. Data Analysis. We conducted our structurally based resource selection analysis [28] update to the Ford et al. [7] model using R Version 4.3 [29]. To determine the relationship between VNFS habitat suitability and forest structural variables, we compared VNFS presence versus pseudoabsences using generalized linear models (GLMs) with a binomial error distribution. We combined historical presence data and extracted environmental data using the *dplyr* package of R [30]. We tested 32 GLMs that contained various combinations of TH, TPH, BA, and QMD (Table 1). For TH and QMD, we examined quadratic polynomials because wildlife responses to these measures often are not linear [31]. Prior to modeling, we ensured that no continuous variable exceeded a variable inflation score of 5 using the *vifcor* function in the *usdm* package of R [32]. Models were compared with the corrected *Akaike information criterion* (AIC_c) and ΔAIC_c to select the best-approximating model that was the most parsimonious and contained

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Table 1: Generalized linear model selection using Akaike information criterion (AIC_c) with coefficient of determination (R^2) and area under the curve (AUC) of forest structure and composition variables predicting the likelihood of habitat suitability for the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*; VNFS) in central Appalachian Mountains of Maryland, Virginia, and West Virginia comparing recent historical and contemporary used locations (nest boxes, live-trapping captures, natural den sites, and foraging points from radiotelemetry) and random pseudoabsence points, 2015–2022.

Model	AIC_c	ΔAIC_c	R^2	AUC
SPRUCE + QMD + I (QMD^2) + BA + TPH + TH + I (TH^2)	5913.56	0.00	0.52	0.85
SPRUCE + QMD + I (QMD^2) + BA + TH + I (TH^2)	5916.50	2.95	0.52	0.86
SPRUCE + BA + TH + I (TH^2)	5923.36	9.81	0.52	0.86
SPRUCE + BA + TPH + TH + I (TH^2)	5925.26	11.70	0.52	0.86

Note: Forest stand structure and composition variables were as follows: basal area ($m^2 \cdot ha^{-1}$; BA), quadratic mean diameter (cm; QMD), stand average dominant tree height (m; TH), trees ha^{-1} (TPH), and red spruce (*Picea rubens*) canopy composition (> 50%, 10%–50%, 0%–10%, and 0%). Quadratic terms are noted by I (TERM^2). Only models within 12 ΔAIC_c shown.

informative covariates of significance [33]. We used spatially explicit (10,000 m) 10-fold cross-validation using package *blockCV* [34] to calculate Tjur's R^2 for explained variation via *performance* [35] and area under the curve (AUC) for accuracy via *Metrics* [36, 37].

Following model selection, we utilized the single-variable structure optimums produced from the modeling efforts to make a categorical raster [38]. These categorical rasters were then combined in three categories of varying size from largest to smallest: within the spatial footprint of the region's collective area ≥ 800-m elevation, within the areas described as ≥ 50% suitable VNFS habitat per Ford et al. [7], and a 1.9-km-wide "least cost path" [39] based on maximum VNFS home range width [9]. This path, created using the *grainscape* R package [40], efficiently connected high-probability VNFS habitat patches from south to north, highlighting areas of suboptimal red spruce cover and stand structure to guide enhancement or restoration efforts. We accomplished this using the red spruce class vector [41] and packages *terra* [27] and *dplyr* [30] in R Studio (Figure 2). Once the categorical map was created, we derived area estimates (ha) by single optimal for red spruce cover and forest structure variables or optimal combinations thereof.

3. Results

The full model, including all variables, had the strongest support for predicting VNFS habitat, though a model excluding TPH was within three ΔAIC (Table 1). All forest structural covariates included in the top model were significant contributors to predicting VNFS habitat suitability. However, the percent spruce composition classes originally used in the Ford et al. [7] model were still the primary driver of model performance and accuracy as reflected by the similar R^2 and AUC scoring among models (Tables 1 and 2). VNFS habitat suitability increased across all red spruce classes, consistent with previous findings [7, 20]; specifically, habitat suitability was highest for TH between 10 and 30 m and for QMD of 15–25 cm (Table 2; Figure 2) and further increased with BA and TPH, with higher suitability when BA was ≥ 30 m^2/ha and TPH exceeded > 2500 stems per hectare (Table 2; Figure 3).

Following model selection, our spatial analyses revealed that the specific optima generated by the model accounted for the variation in structure under low, medium, and high red spruce canopy compositions. The specific optima used for area calculations were Spruce 10%–100%, TH 10–20 m, QMD 15–25 cm, BA ≥ 30, and TPH ≥ 2500. Within the ≥ 50% predicted probability area for VNFS from Ford et al. [7], where red spruce restoration activities would provide the most conservation contribution, approximately 21% of the landscape met red spruce cover and at least 1+ of the forest structural optima. Conversely, most of the remaining area (79%) lacked sufficient extant overstory red spruce (Figure 3, Table 3). For the least cost path of 38,222 ha, approximately 1237 ha was below 800 m in elevation and outside the probable VNSF distribution. Of the remaining 36,985 ha, 41% of the area met both red spruce cover and contained 1+ forest structure optima.

4. Discussion

The results of our study demonstrate that habitat suitability for VNFS is linked primarily to red spruce cover, but forest stand structure metrics are significant components of habitat suitability and, presumably, occupancy. Similar to the CNFS subspecies in the southern Appalachian Mountains, our results confirm that VNFS habitat suitability increases in red spruce forests with mature characteristics such as forest canopy height. However, in contrast to the CNFS, our model indicates a predicted probability decline for VNFS habitat with TH exceeding 25 m [11]. First, we believe this is an artifact of sampling bias introduced in utilizing pseudoabsent points. The limited data points we had to represent VNFS presence captured a smaller range of TH than the pseudoabsence points used in Ford et al. [7]. Invariably, the pseudoabsence points captured areas of mature or highly productive northern and Allegheny hardwood stands with taller tree heights than might be found on extant spruce stands. Second, false negatives likely were produced by pseudoabsence points that randomly fell in a red spruce stand with an average height taller than 25 m. Lastly and more importantly, past harvesting and wildfires in the central Appalachian Mountains eliminated much of the original old growth, and presumably tall, red spruce, whereby residuals or postharvest regeneration had not reached preharvest potential height yet. The rarity of these conditions may create an illusion of avoidance by VNFS to the few areas with a red spruce component > 25 m in height,

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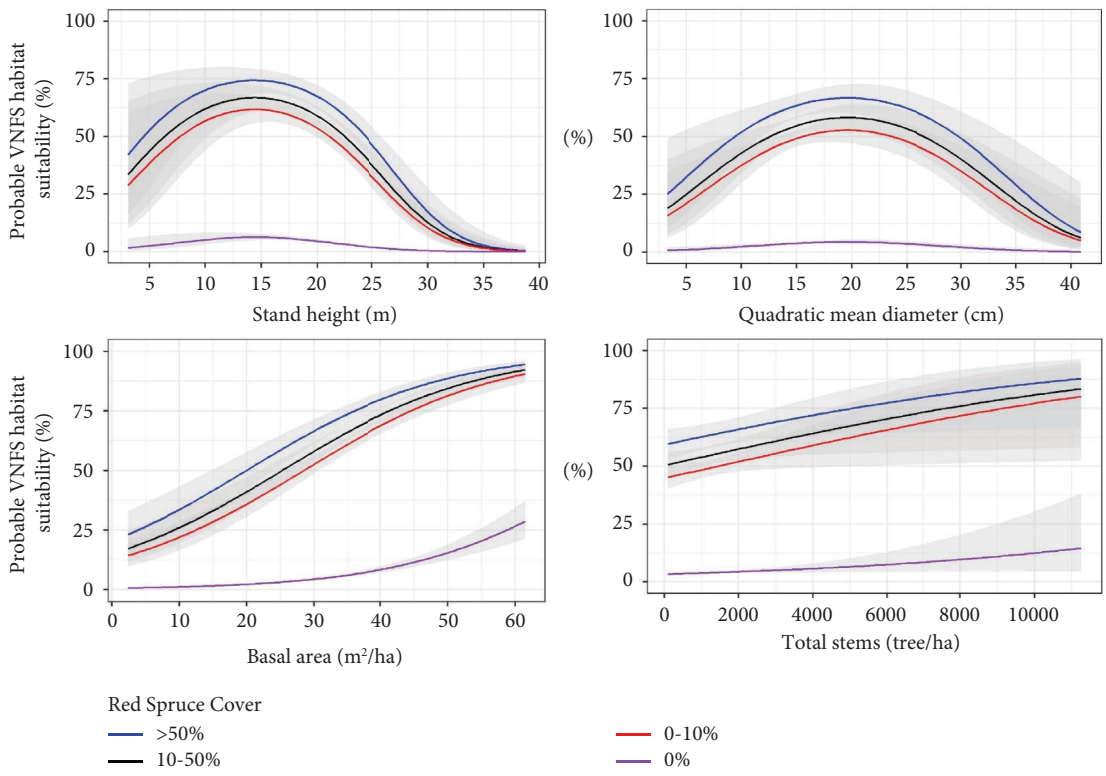


Figure 2: Fit plot of the generalized linear model probability and 95% confidence interval of Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*; VNFS) likelihood of presence in the central Appalachian Mountains of Maryland, Virginia, and West Virginia relative to stand height, quadratic mean diameter, and basal area by the red spruce (*Picea rubens*) canopy cover composition classification.

Table 2: The most supported generalized linear model (VNFS ~ SPRUCE + QMD_M + I (QMD_M^2) + BA_M + TPH + TH_M + I (TH_M^2)) for predicting the likelihood of habitat suitability for the Virginia Northern Flying Squirrel (*Glaucomys sabrinus fuscus*; VNFS) in the central Appalachian Mountains of Maryland, Virginia, and West Virginia using red spruce (*Picea rubens*) canopy composition (> 50%, 10%–50%, 0%–10%, and 0%), quadratic mean diameter (cm; QMD), basal area ($m^2 \cdot ha^{-1}$; BA), trees per hectare (TPH), and stand average dominant tree height (m; TH).

Covariate	Estimate	Std. error	*Z*-value	*p* value
Intercept	0.62	0.12	5.18	< 0.01
Spruce 10%–50%	−0.36	0.12	−2.95	< 0.01
Spruce 0%–10%	−0.58	0.12	−4.68	< 0.01
Spruce 0%	−3.75	0.13	−29.40	< 0.01
QMD	0.20	0.10	1.94	0.05
I (QMD^2)	−0.15	0.04	−3.59	< 0.01
BA	0.63	0.06	10.40	< 0.01
TPH	0.20	0.09	2.17	0.03
TH	−0.49	0.06	−4.70	< 0.01
I (TH^2)	−0.14	0.03	2.17	< 0.01

Note: I (^2) notates a quadratic term.

where no VNFS surveys occurred. Similarly, it is also probable that these residual, presumably high-quality red spruce stands existed as small isolates within the larger, less suitable northern hardwood forest matrix that are barriers to movement or colonization [42].

Our QMD optima do match earlier VNFS research, showing that the den site selection occurred in stands with conventional overstory mean DBHs of approximately 15 cm [8]. Furthermore, the bell-like curve relating habitat suitability to QMD could be attributable to the same biases as TH. Few data exist on stand density characteristics for conditions selected by VNFS. Ford et al. [19] and Menzel et al. [8] observed average overstory basal areas of approximately 34 $m^2\,ha^{-1}$ surrounding natural VNFS den trees or snags. Although this is less than direct evidence about VNFS habitat relationships to stand density, it does align with our findings that stands with basal area ≥ 30 m^2/ha are more likely to support VNFS habitat. Moreover, VNFS habitat suitability increases with basal area in all spruce canopy classes, suggesting that even compositionally poor

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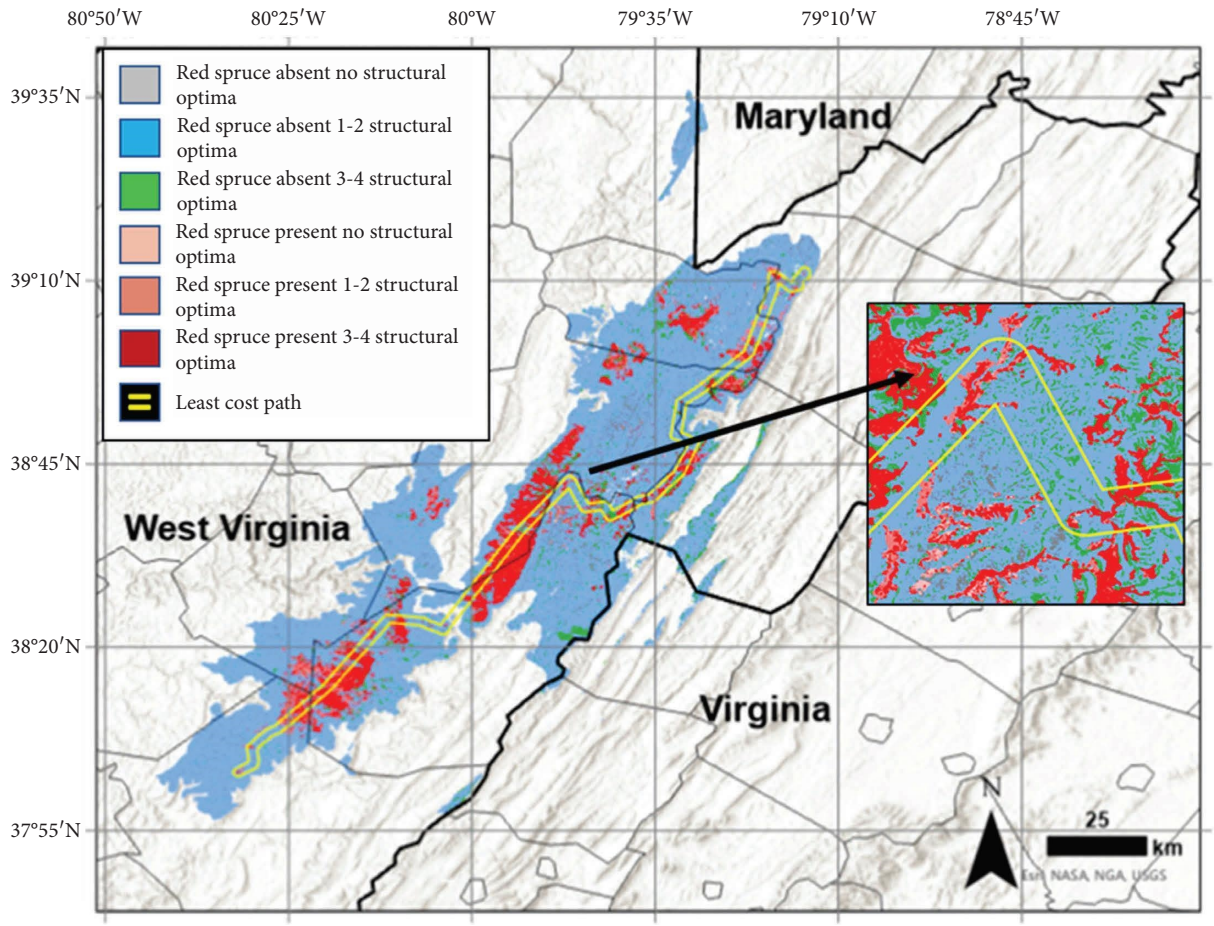


FIGURE 3: Categorical map of the additive accumulations of the forest stand structure and red spruce (*Picea rubens*) canopy cover optima (see text) for Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*; VNFS) habitat in the central Appalachian Mountains of Maryland, Virginia, and West Virginia with an inset of a portion of the VNFS least cost path in the northern Cheat Mountain and Middle Mountain massifs of central West Virginia.

TABLE 3: The area and proportion of additive forest structure and red spruce (*Picea rubens*) overstory 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 (*Glaucomys sabrinus fuscus*; VNFS) in the central Appalachian Mountains across the three landscape scales.

Condition	Within landscape > 800 m·(ha)	Within > 50% VNFS probability (ha)	Within least cost path (ha)
No red spruce + No structure optima	37,806.05	10,457.54	1731.99
No red spruce + 1-2 structure optima	392,487.95	181,314.93	1,7243.76
No red spruce + 3-4 structure optima	21,688.59	133,76.97	2375.56
Red spruce + no structure optima	1228.14	1226.25	229.92
Red spruce + 1-2 structure optima	56,333.94	36,832.73	11,885.71
Red spruce + 3-4 structure optima	16,772.47	16,772.38	3907.06
< 800-m elevation (no data)	*	*	1237.17

stands could potentially support VNFS if the structure is optimal—though whether that would be a "sink" habitat is unknown. Finally, optimal ranges for each variable validate the assertion that the VNFS prefers mature red spruce stands with heterogeneity in horizontal and vertical structures as has been shown for CNFS [11].

Although our results using a forest structure approach has merit for better relating quantifiable forest conditions to VNFS presence, the habitat suitability functions developed in this study performed somewhat equivocally and their performance of these models was essentially no different than those presented by Ford et al. [7] and Menzel et al. [20] that both used primarily red spruce cover class and elevation as input covariates. Furthermore, TreeMap is a spatial raster that combines extrapolated data from U.S. Forest Service's forest inventory analysis plots and LANDFIRE cover data to make coarse collective assessments of structural and compositional conditions at a 30-m^2 scale. With the resolution of

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this spatial product and the inherent limitations of the input sources, there are likely inaccuracies and biases in the TreeMap product that may become more apparent at finer scales.

Despite our results' probable biases and the coarseness of TreeMap data, the similarity of both statistics and spatial distribution of probability to the previous models would indicate that our structural model does have utility to inform management. Land management work beneficial to VNFS over this large landscape will occur primarily through red spruce midstory release and variable retention thinning or group selection harvests that remove deciduous species and retain red spruce residuals to eventually reach minimum red spruce overstory compositions of > 30% and conceivably accelerate height and diameter growth of red spruce residuals [5, 19]. However, because the Ford et al. [7] model does not incorporate forest stand structure components, the results of our work can help managers delineate and examine forest stands of high suitability that do not, at current, meet optimal volume or height metrics. Moreover, managers could use our findings to prioritize enhancing structure to increase mature red spruce patch area and interpatch connectivity in the region.

For example, the ranges of forest composition and stand structures along portions of the VNFS least cost path exhibited more variable conditions within the Ford et al. [7] ≥ 50% predicted VNFS habitat suitability area than anticipated (Figure 3). Managers could use our findings to better target restoration efforts in a more efficient manner such as locating areas that contain the appropriate composition of red spruce but not the suitable structure, delineating stands for red spruce midstory release treatments, or identifying areas for red spruce planting where the species is currently absent.

Though our work provides new insight into VNFS habitat suitability, it does not assess what red spruce forest structure was optimal for VNFS habitat before the exploitative logging and wildfires in the early 1900s. A complete understanding of the previous pre-European conditions in this landscape is not currently possible [43]. The contemporary range of VNFS can only be used to describe its present structural requirements, while truly optimal conditions may require more time to develop. However, continued acoustic and telemetry monitoring along with continued collection of forest stand- and plot-level data may continue to add to our understanding of VNFS habitat needs as red spruce coverage expands and develops late-successional characteristics. Additionally, ongoing monitoring studies of CNFS in the unharvested and unburned areas in the southern Appalachian Mountains [44], such as the Great Smoky Mountains National Park in North Carolina and Tennessee, might provide suitable pre-European condition analogs to facilitate a better understanding of VNFS habitat for the central Appalachian Mountains.

Data Availability Statement

Data are available from the U.S. Geological Survey: https://www.sciencebase.gov/catalog/item/68c810f9d4be02503201632e.

Disclosure

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Conflicts of Interest

The authors declare no conflicts of interest.

Author Contributions

Tanner R. Humbert, Jesse L. De La Cruz, Corinne A. Diggins, and W. Mark Ford conducted the primary data gathering, analysis, and drafting of the paper. Abigail W. McKellips, David R. Carter, and P. Corey Green assisted in providing the technical advice relating to study methods and reviewing the paper draft. Jesse L. De La Cruz provided technical help in the data gathering, analysis, and reviewing the paper draft. Contributions from all authors made this research work and manuscript a success.

Funding

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 to Virginia Tech.

Acknowledgments

We graciously thank all who helped support this project: Matt Boarman (U.S. Fish and Wildlife Service); Shane Jones, Jason Teets, and Kris Henning (U.S. Forest Service); Steven Evans (West Virginia Division of Forestry); and Will Evans (The Nature Conservancy).

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