Distribution Probability of the Virginia Northern Flying Squirrel in the High Allegheny Mountains

W. Mark Ford[1], *U.S. Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit, Blacksburg, VA 24061*

Corinne A. Diggins, *Department of Fish and Wildlife Conservation, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061*

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*

Abstract: In the central Appalachians of Virginia and West Virginia, the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*; VNFS) is a subspecies of northern flying squirrel generally associated with red spruce (*Picea rubens*)-dominated forests at high elevations. Listed as endangered by the U.S. Fish and Wildlife Service from 1985 to 2013, the VNFS currently is the subject of a 10-year post-delisting assessment. Still considered a state-listed species in Virginia and a species of greatest conservation need in West Virginia, the VNFS serves as a focal target for red spruce restoration activities in the High Allegheny Region (HAR) of the two states. Owing to the cryptic nature of VNFS and its low detection probability in live-capture surveys, managers in the region rely on habitat models to assess probable presence. Using long-term nest-box, live-trapping, and radio-telemetry data matched with updated high elevation forest-type coverage data for the region, we created a new VNFS resource selection function and spatial coverage map. Inputting red spruce cover, increasing elevation, and decreasing landform index (increasing site shelteredness) composed the best model explaining VNFS occurrence. The calculated amount of low-quality habitat was congruent with previous modeling efforts; however, inclusion of more VNFS occurrence records in the current effort indicated that previous efforts substantially underestimated the amount (>400%) of extant high quality VNFS habitat. We estimate the HAR to contain approximately 197,952 ha with ≥0.50 predicted probability of occurrence of VNFS. In addition to potentially improving current and future VNFS live-capture surveys, with this model managers may better target forests for red spruce restoration to increase high elevation forest ecological integrity and to improve habitat patch connectedness for VNFS.

Key words: elevation, *Glaucomys sabrinus fuscus*, landform index, red spruce

Journal of the Southeastern Association of Fish and Wildlife Agencies 9: 168–175

The Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*; VNFS) is a nocturnal, arboreal montane forest, primarily red spruce (*Picea rubens*), obligate subspecies that occurs in the High Allegheny Region (HAR) of the central Appalachian Mountains of eastern West Virginia and northwestern Virginia (Ford et al. 2007b). Due to loss of historic habitat, perceived low population densities, and low detection probability, the VNFS was listed as endangered in 1985 under the 1973 Endangered Species Act (ESA) by the U.S. Fish and Wildlife Service along with Carolina northern flying squirrel (*G. s. coloratus*; CNFS) in the southern Appalachians (Menzel et al. 2006b, Ford et al. 2015). Endangered species listing spurred almost three decades of multi-agency supported monitoring and research that demonstrated that distribution of VNFS was greater than originally believed and that long-term site-persistence was high (Ford et al. 2010). Additional research showed red spruce forests exhibiting continued signs of recovery and expansion following industrial logging activities and landscape-level wildfires that took place from 1890 until 1930 (Nowacki et al. 2010). Accordingly, the VNFS was delisted in 2013 and has been undergoing a post-delisting monitoring period (2013–2023) to determine if any change in status is warranted at the federal level. However, as of 2021 the VNFS is still listed as state endangered in Virginia and is considered a species of greatest conservation need in West Virginia. The VNFS serves as an indicator for assessing high elevation forest community condition and integrity in the region and is the primary impetus for increased red spruce forest enhancement and restoration efforts (Thomas-Van Gundy and Sturtevant 2014). Nonetheless, threats to the long-term viability of VNFS exist from potential future loss of red spruce forests from climate change, atmospheric acid deposition, and second-home/recreational development (Beane and Rentch 2015).

In the HAR, VNFS primarily have been observed at elevations >800 m. Though observations exist from northern hardwood communities, particularly those with a substantial eastern hemlock (*Tsuga canadensis*) component, most occurrences are associated with red spruce presence in the overstory. Ford et al. (2004) noted that the likelihood of VNFS presence rose dramatically when red spruce composition exceeded 35% of forest composition. Similarly, individual VNFS, as well as CNFS, display smaller home-range sizes as the red spruce forest component increases (Menzel et al. 2006b, Dig-

1. E-mail: wmford@vt.edu

gins et al. 2017). Menzel et al. (2004) demonstrated near exclusive use of hardwood tree and snag cavities in the HAR that suggested a hardwood component was needed by VNFS for denning. However subsequent work on VNFS and CNFS in red spruce dominated stands revealed high use of dreys in conifers across seasons (Ford et al. 2007b, 2014; Diggins et al. 2017) and that den use was mainly a function of stand composition and den site availability (Menzel et al. 2004). The VNFS has a mycophagist feeding strategy and the preponderance of foraging occurs under or adjacent to red spruce boles where symbiotic hypogeal fungi associated with red spruce roost systems occur (Diggins and Ford 2017, Diggins et al. 2020a). Moreover, the dense overstory provided by red spruce can provide additional protection from avian predators (Carey et al. 1992).

Despite the need to identify VNFS habitat to protect and actively improve habitat conditions (Schuler et al. 2002), early efforts were hindered by lack of high-quality, high resolution forest composition and condition data for the HAR (Odom et al. 2001). Because extant red spruce distribution could be modeled relatively well in the southern Appalachians from physical variables such as elevation, aspect, and landform index, Odom et al. (2001) attempted to correlate VNFS nest-box occupancy with environmental conditions believed conducive to red spruce in the HAR. However, owing to the 90% reduction in red spruce coverage from earlier logging and high intensity wildfires that removed red spruce advance regeneration and seed sources (Korstian 1937, Thomas-Van Gundy and Morin 2021), modeling results were equivocal. At best, this has only allowed managers to know where VNFS does not occur at low to mid-elevations with unfavorable aspects (southern and western) or exposed landforms as opposed to where they were likely to occur. With an expanded nest-box occupancy dataset, Menzel et al. (2006a) modeled potential VNFS habitat in the HAR using elevation and a binary red spruce presence/absence variable from Landsat-derived remotely sensed data. Subsequent validation efforts showed the Menzel et al. (2006a) model performed reasonably well where the red spruce coverage layer was correct (Ford et al. 2010) and could be used in localized areas to implement red spruce enhancement and restoration efforts (Rentch et al. 2007, 2016). Although an improvement on the Odom et al. (2001) model, the Menzel et al. (2006a) model was similarly constrained by limited occurrence data (Menzel et al. 2006b, Diggins and Ford 2017).

To delineate extant red spruce extent and provide a reconstruction of former red spruce distribution in the HAR, an updated red spruce forest community classification and an associated red spruce coverage was created by the West Virginia Division of Natural Resources (Byers et al. 2010, Byers 2013). These data were derived from >4000 vegetation plots and aerial imagery analysis of >500,000 ha and greatly improved the spatial coverage for this forest type regionally. Accordingly, this new vegetation layer along with VNFS foraging and additional den site and nest-box locations not included in earlier modeling efforts (Ford et al. 2007a, Diggins and Ford 2017) provide an opportunity to update and improve VNFS predicted probability coverages that can inform VNFS management efforts and guide red spruce enhancement and restoration efforts. The objective of our study was to use available VNFS foraging locations, natural den-site locations (2000–2015), and expanded nest-box occurrences (1990–2015) with the Byers (2013) red spruce habitat data along with physical environmental variables (i.e., elevation, aspect, slope, and landform index) to create an updated VNFS resource selection function for the HAR.

Study Area

Our study area approximated the southern High Allegheny and northern High Allegheny sub-sections covering ~1,625,400 ha in the Allegheny Mountains and Plateau and westernmost Ridge and Valley physiographic provinces in Maryland (Garrett County), Virginia (Alleghany, Bath and Highland counties) and West Virginia (Barbour, Grant, Greenbrier, Mineral, Nicholas, Pendleton, Pocahontas, Preston, Upshur, and Webster counties) (Byers 2013, Thomas-Van Gundy and Sturtevant 2014). The region is characterized by broad plateau-like ridges, steep slopes, and narrow valleys in the Allegheny Mountains and Plateau and long, linear ridges with wider valleys in the Ridge and Valley physiographic provinces (Fenneman 1938, Byers et al. 2010). Elevations range from 200 to 1482 m. The mountains of the region are capped with erosion-resistant sandstone with soils that are rocky, highly acidic, and generally low in productivity except in valley bottoms (Allard and Leonard 1952, Pyle et al. 1982). Forest community composition varies widely throughout the region depending on elevation, aspect, and land use history, but higher elevations of VNFS habitat are comprised of red spruce, mixed red spruce-northern hardwoods, or northern hardwoods with an eastern hemlock component. Small areas of balsam fir (*Abies balsamea*) occur in the HAR and are also regarded as VNFS habitat (Ford et al. 2004). In addition to red spruce, common overstory species include eastern hemlock, sugar maple (*Acer saccharum*), red maple (*A. rubrum*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), and black cherry (*Prunus serotine*; Rentch et al. 2010). Most of the region is second- and third-growth forest following the period of railroad logging from 1890 until 1930. For a more detailed study area description of the HAR, see Byers et al. (2010) and Thomas-Van Gundy and Sturtevant (2014).

Methods

To create a VNFS second-order (within the putative subspecies distribution) resource selection function (Boyce et al. 2002) for the

HAR, we assembled all available nest-box survey records of presence from Odom et al. (2001) and Menzel et al. (2006a) as updated by West Virginia Division of Natural Resources in 2015, along with foraging and den-site locations of 45 individuals obtained from recent VNFS radio-telemetry studies (Menzel et al. 2006b, Ford et al. 2007a, Diggins and Ford 2017). Because some nest-box records of occurrence did not include sex of the VNFS observed and that previous studies found no difference in male versus female habitat use and selection (Menzel et al. 2006b, Diggins and Ford 2017, Diggins et al. 2017), we omitted sex as a possible covariate to maximize the number observations and spatial distribution examined. Using ArcMap 10 (ERSI, Redlands, California), we added 1635 random points throughout the study area to serve as pseudo-absences for comparison to VNFS observations. From a 10-m U.S. Geological Survey Digital Elevation Model, we calculated elevation (m), aspect (degrees), and slope (%) for each observation and pseudo-absence. None of these variables were correlated ($r < 0.1$) and therefore were considered available for model inclusion. Prior to analysis, we used a cosine transformation of aspect to linearize this circular variable (Odom and McNab 2000). Prior to the logging era, red spruce was often associated with sheltered landforms at mid- to low-elevations (Odom et al. 2001, Ford et al. 2015). Therefore, following Odom and McNab (2000), we calculated a 100-m radius landform index from the DEM whereby negative values are indicative of sheltered, concave landform (i.e., ravines and coves), and positive values are indicative of exposed, convex landforms (i.e., planar side slopes and ridgelines). For red spruce coverage, we used the West Virginia Division of Natural Resource's potential and current red spruce ecosystem map for Virginia and West Virginia which assigned discrete forest stand polygons to one of four overstory cover classes: no red spruce present, red spruce present (>0% but <10% of stand composition), mixed red spruce-northern hardwood (10%–50% of stand composition), and red spruce dominant (>50% of stand composition). However, this coverage did not encompass the entire HAR where some random points occurred above our minimum elevation threshold of 615 m that constitutes the lowest elevation for red spruce (Beane and Rentch 2015). Therefore, we also examined forest cover outside the potential and current red spruce coverage to determine if any extant red spruce or mixed red spruce-northern hardwood existed using the 2016 West Virginia Land Use Land Cover datasets (Strager 2020).

To determine which combination of variables resulted in the most parsimonious VNFS resource selection function, we used the PROC HPGENSELECT generalized linear model backwards stepwise model function in SAS 9.4 (SAS Inc, Cary, North Carolina) with a variable exit threshold of $P < 0.25$ and model retention based on the lowest Akaike's Information Criteria score (Yamashita et al. 2007). We tested all combinations of elevation, aspect, slope, and landform index, including all 2-variable interactions, along with forest overstory cover as a fixed, class variable. To provide parameter estimates, we then reran the selected model using the PROC GENMOD generalized linear model function to calculate model intercept and beta estimates. We assessed model discrimination by examining the model's receiver operating curve using the logistic regression function in PROC LOGISTIC with observed versus predicted values as a *post-hoc* validation. To create a VNFS resource selection function layer, we input the selected model intercept and covariate beta estimates into 'raster calculator' using ArcMap 10.7.1 (ERSI Inc., Redlands, California). Lastly, for comparison purposes (overlap, inclusion, and exclusion) with the Menzel et al. (2006a) predicted occurrence map, we calculated area amounts in three predicted probability of occurrence categories for VNFS: 0–<0.50, 0.50–0.75, and >0.75 corresponding to low, medium, and high, respectively.

Results

Our best supported model for predicting second-order VNFS occurrence in the HAR from nest-box and live-trapping captures ($n = 279$), den sites ($n = 79$), and foraging points ($n = 1823$) from radio-telemetry studies included forest cover class, elevation, landform index, aspect and percent slope and an elevation*landform index interactive term (Tables 1, 2). Predicted probability of VNFS occurrence increased with increasing elevation among all four forest cover types (Table 2, Figure 1) and decreased as landform index went from sheltered to exposed values (Figure 2). Presence of red spruce was the primary driver of presence of VNFS with almost all of forest cover classes with either 10–50% and >50% red spruce stand composition containing >75% of predicted VNFS occurrence (Table 3). Model discrimination between known VNFS locations and random pseudo-absences was high with a receiver operating characteristic curve area of 0.923. At the >0.50 probability cutoff, model sensitivity (true positive rate) and specificity (true negative rate) were 87.3% and 85.1%, respectively, whereas at the >0.75 probability cutoff, model sensitivity and specificity were 85.0% and 90.5%, respectively. Overall model performance in terms of false positive and negative rates was largely constant from 0.15 to 0.90, although uncertainty below and above that range increased with false positive and false negative rates (Table 3). In terms of area with ≥0.50 probability of VNFS occurrence, overlap with our model was largely congruent with the Menzel et al. (2006a) model. However, above that threshold, our model considered a far larger percentage of that area to be very high quality (>0.75 probability of occurrence) than did Menzel et al. (2006a; Table 4, Figure 3). For the HAR, our model predicted that approx-

Table 1. Backward stepwise generalized linear model selection of environmental variables predicting the probabilistic occurrence of Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the High Allegheny Region of Virginia and West Virginia using nest-box ($n = 279$) and live-trapping captures ($n = 279$), den sites ($n = 71$), and foraging points from radio-telemetry studies ($n = 1823$), 1990–2015 (see text). Variables were retained for inclusion if significant at $P < 0.25$.

Model	Parameters	−2 loglikelihood	ΔAIC
Elevation + Landform index + (no red spruce, >0–<10% red spruce, 10–50% red spruce, >50% red spruce) + Elevation*Landform index[a]	7	2555.32	0.00
Elevation + Landform index + Aspect + (no red spruce, >0–<10% red spruce, 10–50% red spruce, >50% red spruce) + Elevation*Landform index	8	2554.68	1.36
Elevation + Landform index + Aspect + (no red spruce, >0–<10% red spruce, 10–50% red spruce, >50% red spruce) + Elevation*Landform index + Aspect*Landform index	9	2553.56	2.24
Elevation + Landform index + Aspect + Percent slope + (no red spruce, >0–<10% red spruce, 10–50% red spruce, >50% red spruce) + Elevation*Landform index + Aspect*Landform index	10	2552.79	3.47
Elevation + Landform index + Aspect + Percent slope + (no red spruce, >0–<10% red spruce, 10–50% red spruce, >50% red spruce) + Elevation*Landform index + Aspect*Landform index + Landform index*Percent slope	11	2551.95	4.63

a. Selected model

Table 2. Best supported generalized linear model for predicting the probability of Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) occurrence in the High Allegheny Region of Virginia and West Virginia using nest-box and live-trapping captures ($n = 279$), den sites ($n = 79$) and foraging points ($n = 1823$) from radio-telemetry studies, 1990–2015 (see text).

Parameter	*df*	Estimate	SE	χ^2	*P*
Intercept	1	−5.11	0.48	112.53	<0.0001
No red spruce	1	−3.06	0.22	187.96	<0.0001
>0–<10% red spruce	1	−1.18	0.23	26.69	<0.0001
10–50% red spruce	1	−0.07	0.25	0.07	0.79
>50% red spruce[a]	.	.	.	.	.
Elevation (m)	1	0.01	0.0003	346.50	<.0001
Landform index	1	0.15	0.08	3.14	0.08
Elevation*Landform Index	1	−0.0002	0.0001	6.27	0.01

a. Reference condition

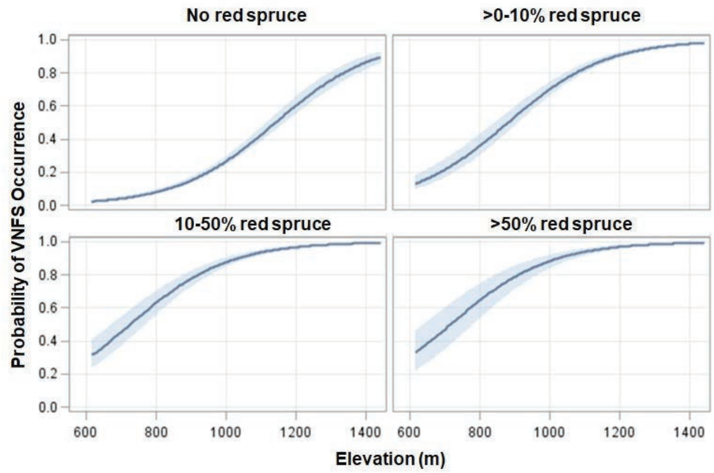

Figure 1. Generalized linear model fit plot of the probability and 95% confidence interval of Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*; VNFS) occurrence relative to red spruce (*Picea rubens*) cover class and elevation in the High Allegheny Region of Virginia and West Virginia using nest-box and live-trapping captures ($n = 279$), den sites ($n = 79$) and foraging points ($n = 1823$) from radio-telemetry studies, 1990–2015 (see text). Plots computed at landform index = −0.22.

Table 3. Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) predicted probability model performance in the High Allegheny Region of Virginia and West Virginia using nest-box and live-trapping captures ($n = 279$), den sites ($n = 79$), and foraging points ($n = 1823$) from radio-telemetry studies, 1990–2015 (see text). Performance was evaluated in 0.05 increments of probability level (0.05–0.95); levels with identical performance are binned.

Probability levels	Correct classification (%)	Sensitivity (%)	Specificity (%)	False positive rate (%)	False negative rate (%)
0.05–0.15	57.1	100	0.0	42.9	0.0
0.20–0.55	86.4	87.3	85.1	11.3	16.5
0.60–0.90	87.3	85.0	90.5	7.7	18.1
0.95	42.9	0.0	100	0.0	57.1

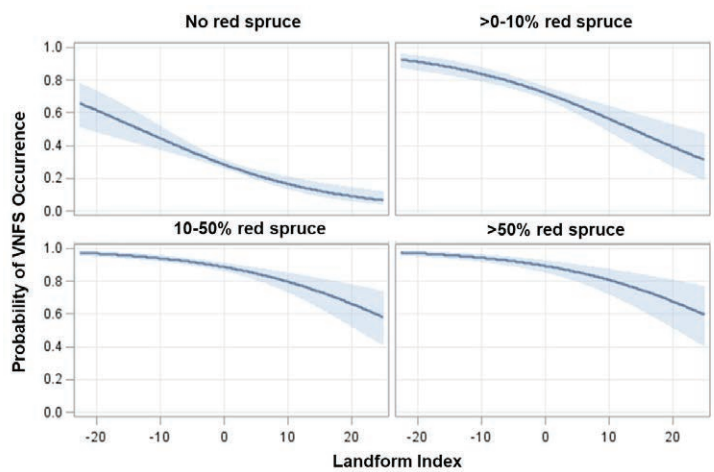

Figure 2. Generalized linear model fit plot of the probability and 95% confidence interval of Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*; VNFS) occurrence relative to red spruce (*Picea rubens*) cover class and landform index in the High Allegheny Region of Virginia and West Virginia using nest-box and live-trapping captures ($n = 279$), den sites ($n = 79$) and foraging points ($n = 1823$) from radio-telemetry studies, 1990–2015 (see text). Negative landform index values indicate more sheltered positions (i.e., ravines and coves), whereas positive values indicate exposed positions (i.e., planar sideslopes, and ridgelines). Plots computed at elevation = 1022 m.

Table 4. Area and percent composition of low, medium and high probability of Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*; VNFS) occurrence in the 1,625,436 ha High Allegheny Region (HAR) of Virginia and West Virginia among red spruce (*Picea rubens*) cover classes and percent difference relative to low, medium, and high probability categories as reported in Menzel et al. (2006a).

VNFS suitability	Area (ha) in HAR	% area in no red spruce	% area in >0–<10% red spruce	% area in 10–50% red spruce	% area in >50% red spruce	% change from Menzel et al. (2006a)
Low probability (0–<0.50)	1,427,485	86.2	1.8	0.0	0.0	+4.0
Medium probability (0.50–0.75)	71,833	12.8	24.9	0.5	0.1	−69.0
High probability (>0.75)	126,119	0.9	73.3	99.5	99.9	+477.4

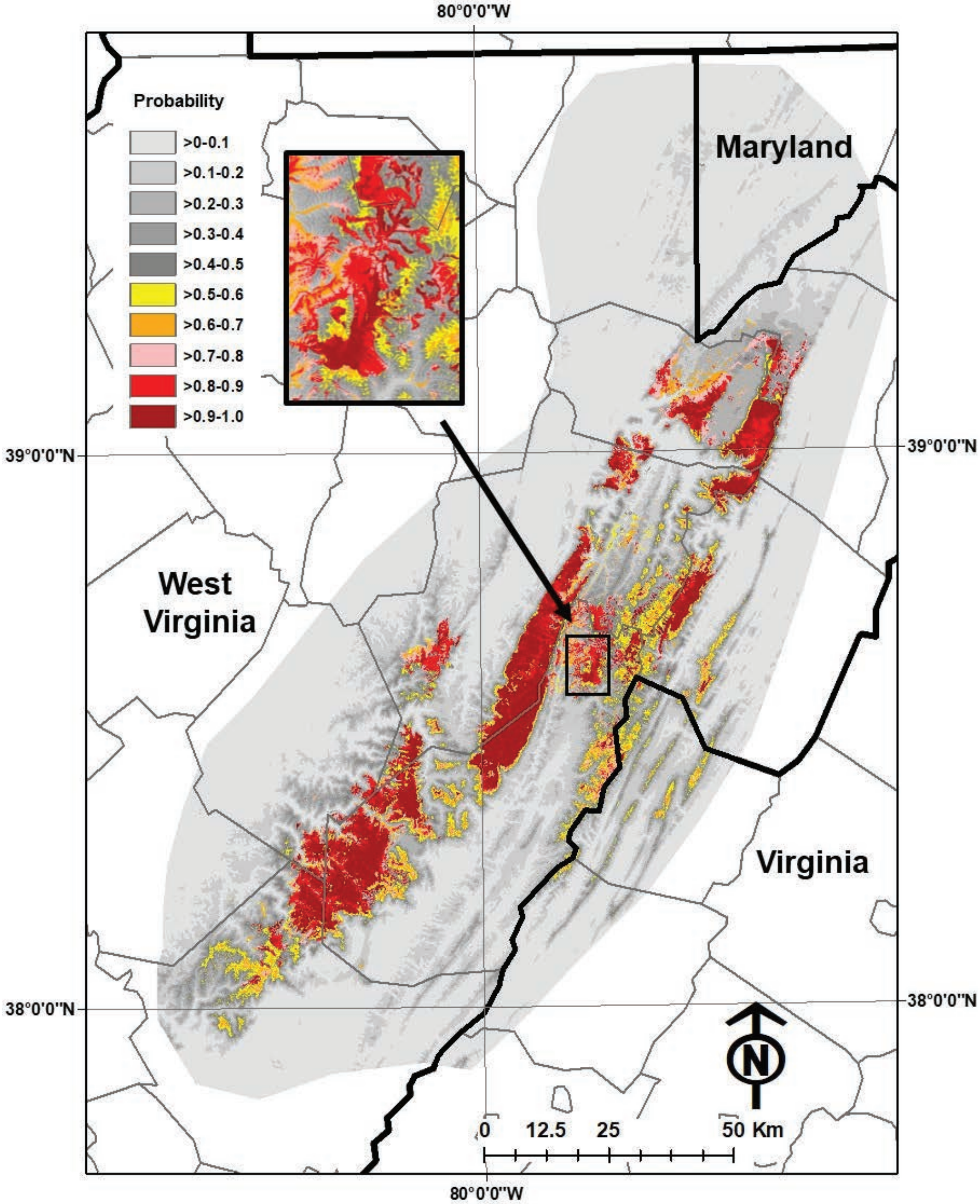

Figure 3. Predicted probability of Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) occurrence in the High Allegheny Region of Maryland, Virginia, and West Virginia. Inset shows the Middle Mountain area of the Monongahela National Forest, Pocahontas County, West Virginia.

imately 87.8% of the region showed low predicted probability of VNFS occurrence (<0.50) whereas approximately 4.4% of medium probability (0.50–0.75) and 7.7% of high probability (>0.75) of predicted occurrence (Table 4, Figure 3).

Discussion

The results of our modeling effort continue to confirm that increased red spruce composition and higher elevations are indicators of higher-quality VNFS habitat in the HAR of Virginia and West Virginia. Our inclusion of landform index along with an improved red spruce layer as model covariates added increased precision that was not provided by Menzel et al. (2006a). Indeed, our model determined that potential high quality VNFS habitat has been greatly underestimated by the Menzel et al. (2006a) model that management agencies in the region currently use for stewardship project planning to benefit VNFS or red spruce forests. This disparity stemmed from the earlier reliance on nest-box records whereby a large placement bias within high quality habitat was evident (Ford et al. 2010). The earlier Odom et al. (2001) model relied more on landform index and elevation following the assumptions from Odom and McNab (2000) in the southern Appalachians that edaphic conditions largely dictate forest composition. However, the post-logging burning intensity and extent in the HAR were far greater than in the southern Appalachians (Korstian 1937, Yarnell 1998), hence Odom et al. (2001), while foundational in a sense as a first approximation, was useful to managers only for determining where VNFS did not occur. As such, our model should provide an improved template for identifying areas where red spruce stand improvement (e.g., thinning of overstocked stands to increase old-growth attributes) or restoration (e.g., hardwood overstory removal to release red spruce or in some cases red spruce planting) could occur to maximize VNFS habitat patch size and connectivity (Menzel et al. 2006a, Rentch et al. 2016).

Our final model identified several disjunct medium probability patches where no VNFS nest-box or live-trapping surveys have occurred. Owing to the continued presence of the closely-related CNFS in the southern Appalachians in patches <500 ha (Arbogast et al. 2006, Ford et al. 2015), expanded surveys to validate our VNFS model or to determine necessary patch size and configuration seems warranted. Although traditional methods were essential in determining the general distribution and basic ecology of VNFS (Stihler et al. 1995, Reynolds et al. 1999), unfortunately additional establishment of VNFS nest-box transects is unlikely and live-trapping has low detection probability (Ford et al. 2010). Advances in the uses of ultrasonic acoustic sampling that are efficient to determine site occupancy of northern flying squirrels (Diggins et al. 2016, 2020b, 2020c) may lessen the need to employ nest-box and live-trapping surveys. For example, these survey methods have been used to document four additional presence locations CNFS in the southern Appalachians where past trapping efforts produced no captures (Diggins et al. 2016). Nonetheless, maintenance of existing VNFS nest-box transects is still valuable to provide demographic information that is unobtainable through acoustic surveys.

Although our VNFS resource selection model is an improvement over the Odom et al. (2001) and Menzel et al. (2006a) models, we still urge caution in its application. One consideration is that little forest structure data beyond stand establishment time currently exists for red spruce forests in much of the HAR. Whereas forest stand age can serve broadly as a surrogate for rating VNFS habitat quality (i.e., older forests beyond the stem exclusion phase or entering the canopy gap re-initiation phase provide better northern flying squirrel foraging and denning habitat; Smith 2007, Ford et al. 2014, Diggins and Ford 2017, Diggins et al. 2017), stand age alone may not predict structural conditions (Hornbeck and Kochenderfer 1998, Schuler et al. 2002) for red spruce in the HAR. Ford et al. (2014) noted that in the southern Appalachians, CNFS use of red spruce stands of taller canopy heights (>20 m) with multi-layered mid-story development and numerous canopy gaps was greater than in shorter red spruce with more homogeneous stand structure. Inclusion of forest stand metrics such as basal area, stocking, diameter class distribution, and measures of canopy height invariably would improve future VNFS habitat models. These factors may indicate stand age and help determine other limiting resources, such as cavity trees for denning, which may be more limited in younger stands. Secondly, VNFS hypogeal fungi "dig" sites often are associated with spodozol soil types and fungi consumed by VNFS occur near conifer host trees such as red spruce and eastern hemlock (Mitchell 2001, Diggins and Ford 2017, Diggins et al. 2020a). Nauman et al. (2015) mapped soil conditions for a portion of the HAR linking the current and former presence of red spruce on the landscape to spodic conditions. Inclusion of spodozol presence as a habitat component when soil mapping is complete may help explain some VNFS occurrence in northern hardwood forests with no red spruce that formerly may have had a significant red spruce component but that still contain some habitat characteristics that support VNFS foraging (Diggins and Ford 2017).

The improved model provided by our study also can be used as the basis for understanding the potential impacts of climate change on VNFS. One factor for listing under the ESA was the endangerment of its habitat from climate change (Ford et al. 2007b). Past modeling efforts have determined increased temperatures may drastically reduce the range of red spruce forests from at the southern extent of its range (Beane and Rentch 2015, Koo et al. 2015, Walter et al. 2017). Consequently, northern flying squirrels, particularly CNFS in the southern Appalachians (Burns et al. 2003), may see range reductions or shifts. However, no effort has been made to model the potential effects of climate change on VNFS habitat, *per se*. Understanding future climate-induced habitat change may help distinguish red spruce restoration priority areas or determine areas that may be most vulnerable to upslope range shifts of southern flying squirrels (*G. volans*). Southern flying squirrels are known to compete for den sites with VNFS and carry a parasitic nematode (*Strongyloides robustus*) that is deleterious to northern flying squirrels (Wetzel and Weigl 1994). Climate-induced range shifts and hybridization have already been observed in northern flying squirrels and southern flying squirrels in New England and the Great Lakes region (Bowman et al. 2005, Myers et al. 2009, Garroway et al. 2010, 2011, Wood et al. 2016), highlighting the need to document and understand mechanisms of potential range shifts in VNFS and southern flying squirrels due to climate change. Further work to determine potential sympatric tension zones between the species in the HAR could be informative.

Because the VNFS is a subspecies of high conservation concern that serves as an indicator for high elevation forests in the HAR, our improved resource selection model should be valuable to managers tasked with delineating potential habitat. With appropriate consideration of caveats, our results can help facilitate stand- and landscape-level management efforts to support red spruce restoration efforts in the near-term and that hopefully promotes landscape resistance and resilience to climate change in the longer-term. Such efforts would not only benefit VNFS, but ostensibly other montane boreal wildlife that occurs in the HAR. Lastly, inclusion of additional environmental covariates such as soils to further improve our efforts also would be beneficial for VNFS habitat assessment.

Acknowledgments

We thank the West Virginia Division of Natural Resources, West Virginia Division of Forestry, West Virginia Division of Highways, U.S. Forest Service Monongahela National Forest, U.S. Fish and Wildlife Service West Virginia Ecological Services Field Office, Intrawest Corporation, and Westvaco Corporation for their cooperation and support of VNFS research over the past 25 years. Barbara Breshock, Barbara Douglas, Edward Galford, Shane Jones, Jennifer Menzel, Jane Rodrigue, Ella Rowan, William Tolin, Craig Stihler, and Jack Wallace provided invaluable help and guidance over the duration of this effort. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Literature Cited

Allard, H. A. and E. C. Leonard. 1952. Canaan and Stony River Valleys of West Virginia, their former magnificent spruce forests, their vegetation and floristics today. Castanea 17:1–60

Arbogast, B. S., R. A. Browne, P. D. Weigl, and G. J. Kenagy. 2006. Conservation genetics of endangered flying squirrels (*Glaucomys*) from the Appalachian Mountains of eastern North America. Animal Conservation 8:123–133

Beane, N. R. and J. S. Rentch. 2015. Using known occurrences to model suitable habitat for a rare forest type in West Virginia under select climate change scenarios. Ecological Restoration 33:178–189.

Bowman, J., G. L. Holloway, J. R. Malcolm, K. R. Middel, and P. J. Wilson. 2005. Northern range boundary dynamics of southern flying squirrels: evidence of an energetic bottleneck. Canadian Journal of Zoology 83:1486–1494.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmieglow. 2002. Evaluating resource selection functions. Ecological Modeling 157:281–300.

Burns, C. E., K. M. Johnston, and O. J. Schmitz. 2003. Global climate change and mammalian species diversity in US national parks. Proceedings of the National Academy of Sciences 100:11474–11477.

Byers, E. A. 2013. Red spruce (*Picea rubens*) cover in West Virginia 2013. West Virginia Division of Natural Resources, Elkins, West Virginia. <http://wvgis.wvu.edu/data/dataset.php?ID=455> Accessed on 3 September 2020.

_____, J. P. Vanderhorst, and B. P. Streets. 2010. Classification and conservation assessment of upland red spruce communities in West Virginia. West Virginia Natural Heritage Program, West Virginia Department of Natural Resources (WVDNR), Elkins, West Virginia.

Carey, A. B., S. P. Horton, and B. L. Biswell. 1992. Northern Spotted Owls: Influence of prey base and landscape character. Ecological Monographs 62:223–250.

Diggins, C. A., M. A. Castellano, and W. M. Ford. 2020a. Hypogeous, sequestrate fungi (Genus *Elaphomyces*) found at small-mammal foraging sites in high-elevation conifer forests of West Virginia. Northeastern Naturalist 27:N40–N47.

_____, and W. M. Ford. 2017. Foraging microhabitat of the Virginia Northern Flying Squirrel (*Glaucomys sabrinus fuscus*) in the central Appalachians. Northeastern Naturalist 24:173–190.

_____, L. M. Gilley, G. G. Turner, and W. M. Ford. 2020b. Ultrasonic acoustic surveys of state endangered northern flying squirrels in the Pocono Mountains, Pennsylvania. Journal of Fish and Wildlife Management 11: 644–653.

_____, _____, C. A. Kelly, and W. M. Ford. 2016. Comparison of survey techniques on detection of northern flying squirrels. Wildlife Society Bulletin 40:654–662.

_____, _____, _____, and W. M. Ford. 2020c. Using ultrasonic acoustics to detect cryptic flying squirrels: seasonality and survey length. Wildlife Society Bulletin 44:300–308.

_____, A. Silvis, C. A. Kelly, and W. M. Ford. 2017. Home range, den selection and habitat use of Carolina northern flying squirrels (*Glaucomys sabrinus coloratus*). Wildlife Research 44:427–437.

Fenneman, N. M. 1938. Physiography of eastern United States. McGraw-Hill, New York, New York.

Ford, W. M., A. M. Evans, R. H. Odom, J. L. Rodrigue, C. A. Kelly, N. Abaid, C. A. Diggins, and D. Newcomb. 2015. Predictive habitat models derived from nest-box occupancy for the endangered Carolina northern flying squirrel in the southern Appalachians. Endangered Species Research 27: 131–140.

_____, C. A. Kelly, J. L. Rodrigue, R. H. Odom, D. Newcomb, L. M. Gilley, and C. A. Diggins. 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 2:73–82.

_____, K. M. Mertz, J. M. Menzel, and K. K. Sturm 2007a. Winter home range and habitat use of the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*). USDA Forest Service Research Paper NRS-4. Newtown Square, Pennsylvania.

_____, K. R. Moseley, C. W. Stihler, and J. W. Edwards. 2010. Area occupancy and detection probabilities of the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) using nest-box surveys. Pages 37–47 *in* J. S. Rentch and T. M. Schuler, editors. Proceedings from the Conference on the Ecology and Management of High Elevation Forests in the Central and Southern Appalachian Mountains. USDA Forest Service General Technical Report NRS-P-64. USDA Forest Service, Northern Research Station, Newtown Square, Pennsylvania.

_____ and J. L. Rodrigue. 2007b. Northern flying squirrel. Pages 389–394 *in* M. K. Trani, W. M. Ford and B. R. Chapman, editors. The land manager's guide to mammals of the South. The Nature Conservancy, Durham, North Carolina, and U.S. Forest Service, Atlanta, Georgia.

_____, S. L. Stephenson, J. M. Menzel, D. R. Black, and J. W. Edwards. 2004. Habitat characteristics of the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the central Appalachian Mountains. American Midland Naturalist 152:430–438.

Garroway, C. J., J. Bowman, T. J. Cascaden, G. L. Holloway, C. G. Mahan, J.R. Malcolm, M.A. Steele, G. Turner, and P.J. Wilson. 2010. Climate change induced hybridization in flying squirrels. Global Change Biology 16:113–121.

_____, _____, G.L. Holloway, J.R. Malcolm, and P.J. Wilson. 2011. The genetic signature of rapid range expansion by flying squirrels in response to contemporary climate warming. Global Change Biology 17:1760–1769.

Hornbeck, J.W. and J.N. Kochenderfer. 1998. Growth trends and management implications for West Virginia's spruce forests. Northern Journal of Applied Forestry 15:197–202.

Koo, K.A., B.C. Patten, and M. Madden. 2015. Predicting the effects of climate change on habitat suitability of red spruce (*Picea rubens* Sarg.) in the southern Appalachian Mountains of the USA: understanding complex systems mechanisms through modeling. Forests 6:1208–1226.

Korstian, C.F. 1937. Perpetuation of spruce on cut-over and burned lands in the higher southern Appalachian Mountains. Ecological Monographs 7:125–167.

Menzel, J.M., W.M. Ford, J.W. Edwards, and L.J. Ceperley. 2006a. A habitat model for the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the central Appalachian Mountains. USDA Forest Service Research Paper-NE-729. USDA Forest Service, Northern Research Station, Newtown Square, Pennsylvania.

_____, _____, _____, and M.A. Menzel. 2004. Nest tree use by the endangered Virginia northern flying squirrel in the central Appalachian Mountains. American Midland Naturalist 151:355–368.

_____, _____, _____, and T.M. Terry. 2006b. Home range and habitat use of the vulnerable Virginia northern flying squirrel *Glaucomsy sabrinus fuscus* in the Central Appalachian Mountains, USA. Oryx 40:204–210.

Mitchell, D. 2001. Spring and fall diet of the endangered West Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*). American Midland Naturalist 146:439–443.

Myers, P., B.L. Lundrigan, S.M. Hoffman, A.P. Haraminac, and S.H. Seto. 2009. Climate-induced changes in the small mammal communities of the Northern Great Lakes Region. Global Change Biology 15:1434–1454.

Nauman T.W., J.A. Thompson, S.J. Teets, T.A. Dilliplane, J.W. Bell, S.J. Connolly, H.J. Libermann, and K.M. Yoastac. 2015. Ghosts of the forest: mapping pedomemory to guide forest restoration. Geoderma 248:51–64

Nowacki, G., R. Carr, R., and M. Van Dyck. 2010. The current status of red spruce in the eastern United States: distribution, population trends, and environmental drivers. In Pages 140–162 in J.S. Rentch and T.M. Schuler, editors. Proceedings from the Conference on the Ecology and Management of High Elevation Forests in the Central and Southern Appalachian Mountains. USDA Forest Service General Technical Report NRS-P-64. USDA Forest Service Northern Research Station, Newtown Square, Pennsylvania.

Odom, R.H., W.M. Ford, J.W. Edwards, C. Stihler, and J.M. Menzel. 2001. Modeling Virginia northern flying squirrel habitat in the central Appalachians. Biological Conservation 99:245–252.

_____ and W.H. McNab. 2000. Using digital terrain modeling to predict ecological types in the Balsam Mountains of western North Carolina. USDA Forest Service Research Note SE-8. USDA Forest Service Southern Research Station, Asheville, North Carolina.

Pyle, R.E., W.W. Berveage, T. Yoakum, D.P. Amick, W.F. Hatfield, and D.E. McKinney. 1982. Soil survey of Randolph County area, main part, West Virginia. USDA Soil Conservation Service, Morgantown, West Virginia.

Rentch, J.S., W.M. Ford, T.S. Schuler, J. Palmer, and C.A. Diggins. 2016. Release of suppressed red spruce using canopy gap creation–ecological restoration in the Central Appalachians. Natural Areas Journal 36:29–37.

_____, T.M. Schuler, W.M. Ford, and G.J. Nowacki. 2007. Red spruce dynamics, simulation and restoration opportunities in the central Appalachians. Restoration Ecology 15:440–452.

_____, _____, _____, N.R. Beane and W.M. Ford. 2010. Canopy gap dynamics of second-growth red spruce-northern hardwood stands in West Virginia. Forest Ecology and Management 260:1921–1929.

Reynolds, R.J., J.F. Pagels, and M.L. Fies. 1999. Demography of northern flying squirrels in Virginia. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 53:340–349.

Schuler, T.M., W.M. Ford, and R.J. Collins. 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. 2007. Ecology of *Glaucomys sabrinus*: habitat, demography and community relations. Journal of Mammalogy 88:862–881.

Stihler, C.W., J.L. Wallace, E.D. Michael, H. Pawelczyk. 1995. Range of *Glaucomys sabrinus fuscus*, a federally endangered subspecies of northern flying squirrel in West Virginia. Proceedings of the West Virginia Academy of Science 67:13–20.

Strager, M.P. 2020. WV Land Use Land Cover (NAIP 2016). Morgantown, West Virginia, USA. <http://wvgis.wvu.edu/data/dataset.php?ID=489> Accessed on 15 December 2020.

Thomas-Van Gundy, M. and R. Morin. 2021. Change in montane forests of east-central West Virginia over 250 years. Forest Ecology and Management 479:118604.

_____ and B.R. Sturtevant. 2014. Using scenario modeling for red spruce restoration planning in West Virginia. Journal of Forestry 111(5):457–466.

Walter, J.A., J.C. Neblett, J.W. Atkins, and H.E. Epstein. 2017. Regional- and watershed-scale analysis of red spruce habitat in the southeastern United States: implications for future restoration efforts. Plant Ecology 218:305–316.

Wetzel, E.J. and P.D. Weigl. 1994. Ecological implications for flying squirrels (Glaucomys spp.) of effects of temperature on the in vitro development and behavior of Strongyloides robustus. American Midland Naturalist 131:43–54.

Wood, C.M., J.W. Witham, and M.L. Hunter. 2016. Climate-driven range shifts are stochastic processes at a local level: two flying squirrel species in Maine. Ecosphere 7(2):e01240.

Yamashita, T., K. Yamashita, and R. Kaminura. 2007. A stepwise AIC method for variable selection in linear regression. Communications in Statistics–Theory and Methods 36:2395–2403.

Yarnell, S.L. 1998. The southern Appalachians: a history of the landscape. USDA Forest Service General Technical Report SRS-18. USDA Forest Service, Southern Research Station, Asheville, North Carolina.