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Using Maximum Entropy Modeling to Identify and Prioritize Red Spruce Forest Habitat in West Virginia

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Abstract

Red spruce forests in West Virginia are found in island-like distributions at high elevations and provide essential habitat for the endangered Cheat Mountain salamander and the recently delisted Virginia northern flying squirrel. Therefore, it is important to identify restoration priorities of red spruce forests. Maximum entropy modeling was used to identify areas of suitable red spruce habitat, with a total of 32 variables analyzed. Maximum temperature of the warmest month and minimum temperature of the coldest month were identified as variables explaining the most information about red spruce forest habitat. In addition, habitat maps identifying areas of high, medium, and low suitability were created and quantified at the county level. These results will benefit current and future conservation and restoration management activities as they identify core areas that possess the necessary environmental conditions for supporting future complex red spruce communities. Restoration efforts focused in areas possessing high suitability ensure peak potential of success and will ultimately give red spruce forests in West Virginia the greatest resilience to future climatic conditions by establishing connectivity between red spruce forests and increasing genetic diversity.

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Cover Photo

A high-elevation landscape of red spruce mixed with northern hardwoods in the spring before leaf out in Pocahontas County, West Virginia. Photo by Nathan Beane, U.S. Army ERDC.

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INTRODUCTION

Red spruce (*Picea rubens* Sarg.) characterizes niche communities at higher elevations throughout the Appalachian Mountain Region and is a relict species of the central and southern Appalachians whose range was much larger in a previous geologic epoch (Audley et al. 1998, Davis 1981, Delcourt and Delcourt 1987, Stephenson and Clovis 1983). In West Virginia, red spruce forests once held a prominent status at higher elevations, occupying 190,000 ha or more (Clarkson 1964, Hopkins 1891, Millspaugh 1891). However, during the logging era (ca. 1880-1920), much of the original old-growth forest in the State was harvested. With the expansion of railroads and the development of the band sawmill and Shay locomotive, the exploitation of timber and pulpwood led to an almost complete removal of West Virginia's red spruce forests (Clarkson 1964). Over 30 years, more than 4,800 km of railroad tracks were laid (Lewis 1998) and 48 band sawmills (Brooks 1910) were constructed to remove and process this timber. The loss of seed trees following exploitative harvest, destructive wildfires, and wind and water erosion produced a new landscape where uneven-aged red-spruce-hardwood mixtures were largely replaced by even-aged stands of hardwood species. Today, less than 10,000 ha of spruce forests remain, primarily throughout the highest elevations of the State.

Red spruce forests provide essential habitat for the federally endangered Cheat Mountain salamander (*Plethodon nettingi* Green) and the recently delisted Virginia northern flying squirrel (VNFS) (*Glaucomys sabrinus fuscus* Miller) (Menzel et al. 2006a,b; Odom et al. 2001). VNFS habitat has been described as high elevation islands surrounded by a matrix of lower quality or unsuitable forest habitat (Menzel et al. 2006a, Wiegl 2007). This island-like distribution has been found to restrict gene flow in VNFS and is most likely a result of reduced population size and isolation (Menzel et al. 2006a, Wiegl 2007). Red spruce habitat restoration may be critical to maintaining genetic diversity of future VNFS populations.

Other high elevation species of conservation concern in West Virginia are the saw-whet owl (*Aegolius acadicus* Gmelin), snowshoe hare (*Lepus americanus* Erxleben), northern goshawk (*Accipiter gentilis* L.), and fisher (*Martes pennanti* Erxleben) (Menzel et al. 2006b). Restoration of red spruce forests has the potential to enhance or increase habitat availability for these species and is likely to benefit an array of insects and other invertebrates that have been poorly researched and possibly not yet described (Acciavatti et al. 1993, Schuler et al. 2002). These species all play important roles in red spruce forest ecosystems and stress the need for restoration of this rare forest type in West Virginia. Modeling efforts focused on identifying areas best suited for red spruce restoration would therefore be of great importance.

Ecological researchers have shown much interest in species distribution models (SDMs) used for predicting suitable habitat for a given species (e.g., Baldwin 2009, Bollinger et al. 2000, Elith et al. 2011, Phillips et al. 2006, Raxworthy et al. 2003). SDMs are useful not only in generating maps that identify areas of suitable habitat but also in determining which variables are the primary drivers for a species' occurrence on the landscape. SDMs provide a valuable tool for many ecological studies and may also be used to guide future field surveys for species with limited ranges (Phillips et al. 2006).

The SDM incorporated in this study is Maximum Entropy (Maxent, version 3.3.2), a presence-only modeling technique used to characterize a species' niche in environmental space, accomplished by relating observed occurrences to a suite of environmental variables (Pearson 2007, Phillips et al. 2006). Although many techniques are now available for modeling species distributions, Maxent has been identified in many studies to be a strongly competitive or superior modeling method, particularly for species with limited distribution (e.g., Elith et al. 2011, Hernandez et al. 2006, Hijmans and Graham 2006, Pearson 2007, Phillips et al. 2006). Maxent software is a general purpose machine learning method that may be freely downloaded (http://www.cs.princeton.edu/~schapire/maxent/) (Phillips et al. 2004, 2006). Maxent is a novel modeling method with many advantages: (1) characterizes probability distributions from incomplete information, (2) does not require absence data, (3) uses continuous and categorical variables, and (4) produces output that is a continuous prediction ranging from zero to one, with higher values indicating higher suitability for a given species. In comparison with traditional regression-based techniques, Maxent does not violate a model assumption if variables that possess multicollinearity or spatial autocorrelation are incorporated.

The goal of this research was to identify areas on the landscape that possessed the environmental and site-specific parameters necessary for red spruce habitat. Furthermore, we wanted to identify the range of values for each environmental and site-specific variable where suitable red spruce habitat occurred and further refine modeled results to identify areas of high, medium, and low habitat suitability. For state and local agencies interested in conservation and restoration of unique forest habitats, this effort would help by identifying areas best suited on the landscape based on environmental and site-specific variables.

MATERIALS AND METHODS

The upland forests of West Virginia (i.e., elevations over 915 m) comprise two distinct physiographic regions that possess red spruce forest communities: the Allegheny Mountain section and the Ridge and Valley section (Stephenson 1993, Strausbaugh and Core 1964). The highest elevation zones within these two regions make up part of NatureServe's Central and Southern Appalachian Spruce-Fir Forest Ecological System and are the focal point for the distribution of red spruce in West Virginia (Byers et al. 2010, Comer et al. 2003). Within this ecological system, red spruce occurs primarily in the Allegheny Mountain section, and to a much lesser extent, the Ridge and Valley region section. This lower occurrence is due primarily to the climate of the Ridge and Valley section, which is much drier than its neighboring Allegheny Mountain section to the west. The boundary between the two sections is the Allegheny Front, and the eastern Ridge and Valley section lies in a rain-shadow in which a marked decline in precipitation occurs (Clarkson et al. 1980). Across the higher elevation areas of both physiographic regions where red spruce may be found, the 30-year average precipitation ranges from 1,220 to 1,680 mm per year with 30-year mean annual temperatures ranging from 6.7 °C to 9.4 °C (Byers et al. 2010).

To determine areas where red spruce was likely to occur, we used a preliminary red spruce habitat suitability map provided by the West Virginia Division of Natural Resources (WVDNR) (Byers et al. 2010). This map served as the basis for creating a maximum of random sample plot locations that we assumed could be sampled during the summers of 2008 and 2009. Because Maxent is a presence-only modeling approach, 250 random Universal Transverse Mercator (UTM) coordinates were then generated using a Geographic Information System (GIS) in areas modeled to possess a greater than 33 percent likelihood for red spruce habitat, as plots within these areas would more likely possess red spruce opposed to strictly random plots.

In the summers of 2008 and 2009, a total of 168 variable-radius plots, using a 10-BAF (i.e., basal area factor) prism, were established (Fig. 1). At each plot location, trees considered for tally (i.e., "in" trees determined by the 10-factor prism) were measured and recorded by diameter at breast height (d.b.h.) and species to assess overstory and understory tree composition at each plot location. Using relative basal area (BA) and relative trees per hectare (TPH), importance values (IVs) were calculated by averaging the sum of BA and TPH. Finally, geographic coordinates (WASS-enabled) were recorded for all plots created as replacement or supplemental plots for implementation into a GIS.

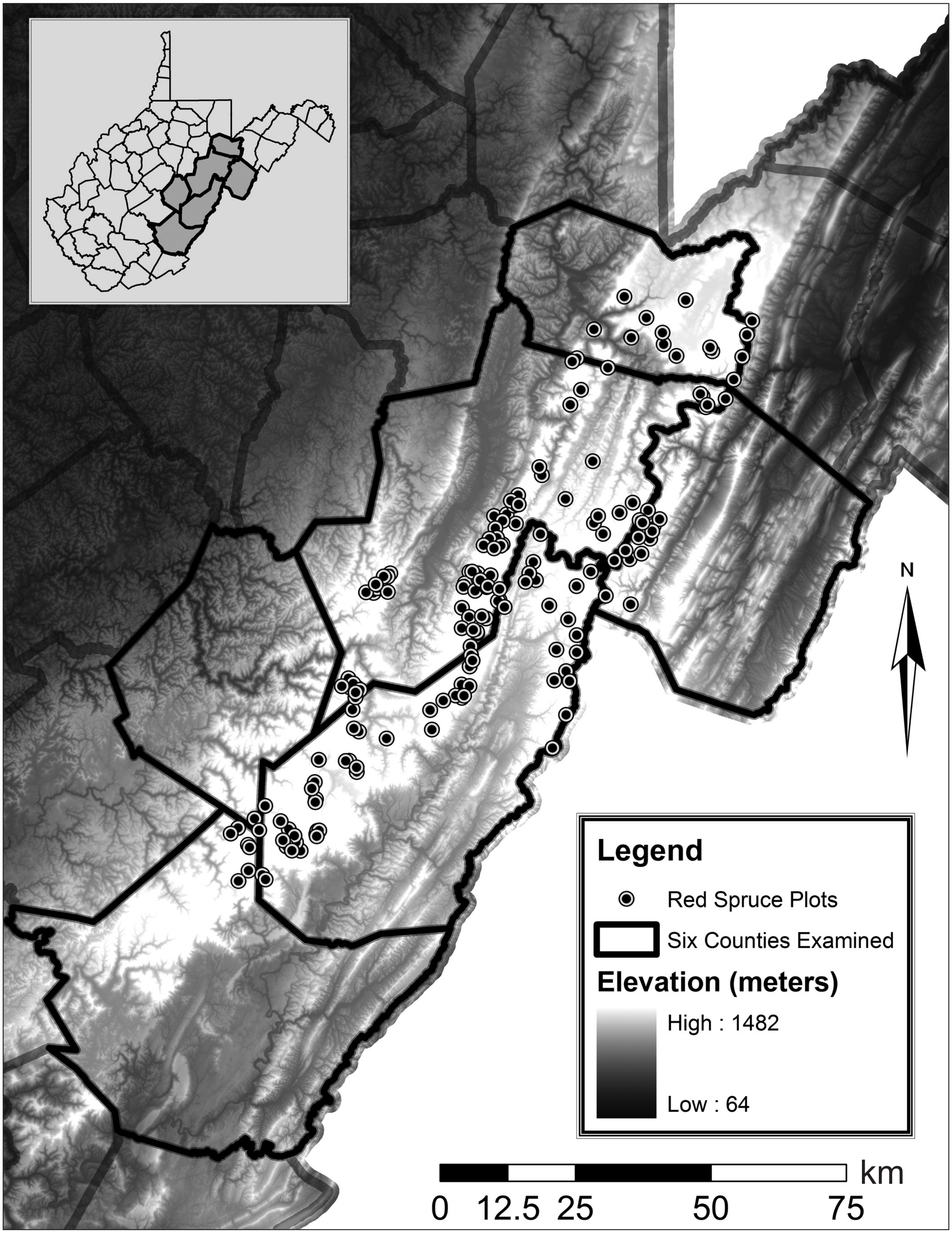

Figure 1.—Field data collected throughout the Appalachian Mountain Region (AMR) of West Virginia in the summers of 2008 and 2009.

A total of 32 environmental and site-specific variables were used as independent variables for the model and included climatic, topographic, and edaphic variables. Nineteen bioclimatic variables were calculated using original statewide climatic datasets (i.e., minimum, maximum, and average monthly temperature and average monthly precipitation) provided by WVDNR in 2009. The original climatic datasets were obtained at 400-m resolution and were resampled using bilinear interpolation within a GIS to a 30-m resolution to match other variables considered in the model.

Bioclimatic variables are important for ecological applications because they calculate the average climatic values during unique times where biological limitations are likely to or could occur (e.g., mean temperature of the driest quarter of the year). The use of bioclimatic variables also allowed for a drastic reduction in the number of climatic variables examined. All bioclimatic variables were calculated using the Arc Macro Language (AML)-script provided by the WorldClim database (see Hijmans et al. 2005). Additional variables considered in the model included elevation, slope, aspect, topographic relative moisture index (TRMI), TRMI-landform, geologic series, solar radiation, and soil derived variables including soil type (map unit name), soil pH, percent clay, percent organic matter, percent sand, and percent silt. These topographic and site-specific variables were used because they were presumed to be important in identifying red spruce habitat (Table 1).

When Maxent is used, features are incorporated as independent variables that the user believes are important drivers for a given species' occurrence on the landscape. Each feature serves as a constraint for the model, and the maximum entropy model selected is the one that best satisfies the constraints of each feature examined (Manning and Schutze 1999). Maxent performs similarly to logistic regression by weighting each feature (i.e., environmental or site-specific variable) by a constant, with the estimated probability distribution divided by a scaling constant to ensure the probabilities range from 0 to 1 and also sum to 1 (Hernandez et al. 2006).

Although methods employing presence/absence data are often prioritized, presence-only modeling approaches should be used when the objective is to identify suitable habitat of a given species, particularly when the current distribution of the species is unknown or has been dramatically altered (e.g., historical anthropogenic disturbances) (Brotons et al. 2004). Presence-only modeling methods are also preferred when ambiguous absences occur due to geographic barriers, local extinction, small patch sizes, species generalization, and biotic interactions (e.g., succession stage, competition) (Hirzel and LeLay 2008). Because Maxent does not use absence data, background points with their associated environmental variable values are used within the study area. These randomly selected background points serve as pseudo-absences for model assessment and are used to determine the logistic output, which ranges from 0 (low suitability) to 1 (high suitability) for habitat prediction.

Within the Maxent output, an area-under-curve (AUC) value is calculated from the receiver operating characteristic (ROC) plot. The AUC value may be interpreted as a single test statistic that assesses model performance with a range of 0 to 1, indicating the ability of the model to correctly classify the training data used. AUC values <0.5 indicate the model is no better than random, values >0.5 to 0.7 indicate a fair model, values 0.7 to 0.9 indicate a good model, and values >0.9 indicate excellent model performance (Baldwin 2009).

Using the results from our 10 jackknife simulations, we graphed the individual variable results of test gain, training gain, and AUC values for all variables examined (Fig. 2). Comparisons of the AUC and the gain from the test and training data allow us to assess how much unique information occurs for each variable in predicting red spruce habitat. Considering only variables with a test and/or training gain greater than one and an AUC statistic greater than 0.8, several additional variables were identified that were not considered important (i.e., ≤3 percent variable contribution) in our model results.

Table 1.—Average variable percent contribution for all 10 replicated Maxent analyses; see Worldclim (http://www.worldclim.org/bioclim) for further variable descriptions and calculations; "c_" before the variable code indicates a categorical variable

Variable description	Variable code	Percent contribution
Maximum temperature of warmest month	bio_5	40.6
Minimum temperature of coldest month	bio_6	13.7
Slope percent	slope30	6.9
Mean temperature of coldest quarter	bio_11	6.5
Mean annual temperature	bio_1	4.6
Soil type	c_soil	4.0
Elevation	ned30m	3.0
Topographic relative moisture index by landform	c_trmimlf	2.0
Mean temperature of warmest quarter	bio_10	1.6
Precipitation of wettest quarter	bio_16	1.6
Geologic series	c_geology	1.6
Total annual global solar radiation	sol	1.5
Temperature annual range	bio_7	1.3
Precipitation of driest month	bio_14	1.1
Precipitation of warmest quarter	bio_18	1.0
Mean diurnal temperature range	bio_2	1.0
Aspect	aspct30	0.9
Percent silt, weighted average, all horizons	silt	0.8
Precipitation seasonality (coefficient of variation)	bio_15	0.8
Annual precipitation	bio_12	0.8
Mean temperature of wettest quarter	bio_8	0.8
Topographic relative moisture index	trmim	0.7
Mean temperature of driest quarter	bio_9	0.6
Temperature seasonality (coefficient of variation)	bio_4	0.5
Isothermality ((bio_2/bio7)*100)	bio_3	0.5
Precipitation of wettest month	bio_13	0.4
Precipitation of coldest quarter	bio_19	0.4
Precipitation of driest quarter	bio_17	0.3
Percent organic matter, weighted average, all horizons	om	0.2
Percent clay, weighted average, all horizons	clay	0.1
Soil pH, weighted average, all horizons	sph	0.1
Percent sand, weighted average, all horizons	sand	0

When using background data within Maxent, it is important for the user to understand that this model makes no assumptions of where a particular species does not occur. Rather, the assumption is that a model based on occurrence and background data (i.e., pseudo-absences) will not focus on sampling bias. Therefore, the primary focus of a Maxent model is to distinguish the differences between the distribution of occurrences and that of the background points examined (Phillips et al. 2009, Yates et al. 2010).

The 5,000 background points used in our model were randomly generated using GIS and are believed to represent the diversity of environmental features occurring within our six-county study area. Much of the necessary data preparation required for this analysis was performed within a GIS using ESRI® ArcMap™ 9.3.1 under an ArcEditor license. Within ArcMap, a shapefile was created for the 168 red spruce presence localities as well as the 5,000 randomly generated background points, with UTM coordinates

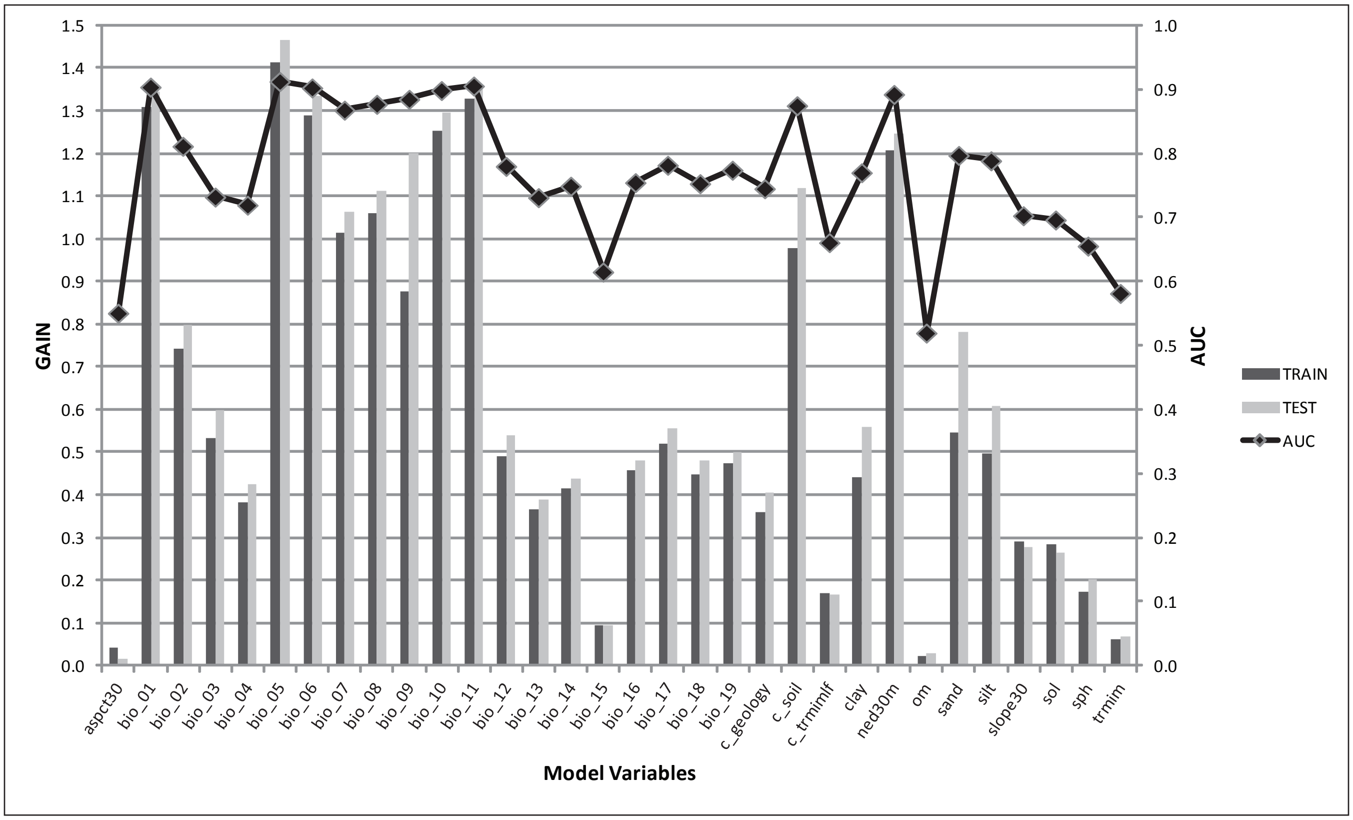

Figure 2.—Results of training gain, test gain, and area-under-curve (AUC) values using each variable by itself. This examination is useful when strong variable correlations exist (i.e., climatic data). Additionally, comparison of the training to test gain allows for the assessment of how well the model fits the test dataset. See Table 1 for variable code descriptions.

listed for each data point in the attribute table. Next, the 32 independent variables were added as raster grids (.img format) and used to construct attribute tables that identified each variable's value for all presence and background localities.

Using the samples with data (SWD) file format, a comma-separated values (CSV) file for the red spruce presence localities and the background points was incorporated into the Maxent model platform. The conversion of the red spruce presence and background points from database format (.dbf) to CSV format was performed using Microsoft Excel 2007. Additionally, all raster grids were converted to ASCII grid (.asc) format for implementation into Maxent. These ASCII grids are necessary to create the statewide red spruce habitat suitability map. All grid conversions were performed using the "Raster to ASCII" conversion tool within the ArcMap—ArcToolbox.

Once the data were added to the model, all categorical variables were specified accordingly so that they were not considered as a continuous variable. Within the settings window, a bootstrap replicate run (i.e., sampling with replacement) type was selected for 10 replicates (run time ~2 days) with a random test percentage of 25 percent (n=42) used. The option to use a random seed was chosen so that each replicate run would start with a random seed to ensure that a separate test/train dataset was used for each of the 10 replicate models. An independent dataset was not available for model assessment and we did not want to partition the dataset into test and training data, and lose valuable training data. As an alternative, bootstrap replication splits the dataset multiple times, and in each case, predictive performance is assessed against the test dataset. This allows for all occurrence data to be used with a random partition performed with each Maxent replicate run.

RESULTS

A total of 29 tree species were identified within the red spruce plots sampled during the field seasons of 2008 and 2009. The species most often encountered were red spruce (IV=40.2), red maple (*Acer rubrum* L.) (16.7), yellow birch (*Betula alleghaniensis* Britton) (11.4), eastern hemlock (*Tsuga canadensis* [L.] Carr.) (10.6), and black cherry (*Prunus serotina* Ehrh.) (9.2) (Table 2). The average stand BA was 44.6 m^2/ha with 405 TPH. The average DBH for all species or species groups examined was 34.2 cm, with the largest average diameter occurring for eastern white pine (*Pinus strobus* L.) and yellow-poplar (*Liriodendron tulipifera* L.) (80 cm and 55 cm, respectively). An examination of the BA and TPH for these two species reveals they were abnormally large trees occurring in only a few of the sampling plots. Regarding "*Quercus* spp.," the most common species sampled was northern red oak (*Quercus rubra* L.), with white oak (*Q. alba* L.) and chestnut oak (*Q. prinus* L.) identified only at a few ridgetop sites.

We ran the Maxent model using 168 overstory red spruce plots, 5,000 background points, and 32 independent variables. Model setup included 10 bootstrapped replicate runs (i.e., sampling with replacement) using a random test percentage of 25 percent (n=42) to assess model performance without excluding a portion of the dataset to be used exclusively for model testing. The mean AUC for all 10 model runs was 0.97 (sd=0.009), a value considered to indicate excellent model performance. The variables

Table 2.—Importance value (IV), basal area (BA), trees per hectare (TPH), and DBH for all species or species groups examined (values in parentheses are standard deviations)

Species	IV (%)	BA (m^2/ha)	TPH	DBH (cm)
Picea rubens Sarg.	40.21	16.77 (0.08)	170.99 (0.87)	35.32 (10.92)
Acer rubrum L.	16.75	7.38 (0.05)	66.60 (0.42)	37.44 (13.38)
Betula alleghaniensis Britton	11.41	4.43 (0.04)	50.58 (0.32)	29.44 (9.21)
Tsuga canadensis (L.) Carr.	10.59	4.98 (0.06)	40.58 (0.44)	36.65 (13.63)
Prunus serotina Ehrh.	9.25	5.18 (0.09)	27.93 (0.44)	45.61 (14.20)
Quercus spp. [a]	3.27	1.98 (0.22)	8.53 (0.47)	43.87 (17.18)
Fagus grandifolia Ehrh.	3.02	1.17 (0.02)	13.82 (0.18)	30.91 (15.03)
Betula lenta L.	1.00	0.41 (0.03)	4.41 (0.34)	31.19 (8.58)
Acer saccharum Marsh.	0.87	0.40 (0.03)	3.38 (0.23)	36.98 (18.30)
Pinus resinosa Aiton	0.62	0.30 (0)	2.35 (0)	39.85 (0)
Magnolia acuminata (L.) L.	0.45	0.22 (0.01)	1.62 (0)	38.49 (16.34)
Acer pensylvanicum L.	0.40	0.07 (0.01)	2.65 (0.12)	17.65 (8.46)
Liriodendron tulipifera L.	0.35	0.22 (0.05)	0.88 (0.25)	57.64 (7.52)
Amelanchier arborea (Michx. f.) Fernald	0.33	0.06 (0.01)	2.06 (0.06)	19.41 (5.84)
Magnolia fraseri Walter	0.33	0.12 (0.02)	1.62 (0.24)	27.71 (8.87)
Fraxinus americana L.	0.31	0.14 (0.02)	1.18 (0.08)	37.04 (20.62)
Pinus strobus L.	0.20	0.15 (0)	0.29 (0)	80.01 (0)
Sorbus americana Marsh.	0.15	0.05 (0.02)	0.74 (0.07)	22.19 (13.06)
Other [b]	0.48	0.17 (0.02)	2.35 (0.14)	26.12 (11.78)
TOTAL	100.00	44.46 (23.41)	404.96 (118.98)	34.21 (8.03) [c]

[a] *Quercus* spp. include northern red oak (*Q. rubra* L.), white oak (*Q. alba* L.), and chestnut oak (*Q. prinus* L.).

[b] Other species include pin cherry (*Prunus pensylvanica* L.), American basswood (*Tilia americana* L.), hawthorn species (*Crataegus* sp. L.), yellow buckeye (*Aesculus flava* Aiton), black locust (*Robinia pseudoacacia* L.), sweet cherry (*Prunus avium* [L.] L.), shagbark hickory (*Carya ovata* [Mill.] K. Koch), mockernut hickory (*Carya tomentosa* [Lam.] Nutt.), and bigtooth aspen (*Populus grandidentata* Michx.).

[c] This is the average diameter across all sites.

that provided the most information (i.e., gave the largest percent contribution) across all 10 replicate model runs were (1) maximum temperature of warmest month (40.6%), (2) minimum temperature of coldest month (13.7%), (3) slope percent (6.9%), (4) mean temperature of coldest quarter (6.5%), (5) mean annual temperature (4.6%), (6) soil type (4%), and (7) elevation (3%) (Table 1). We should note that due to multicollinearity among variables considered in our analysis, variable importance should be carefully considered due to the nature of how variable importance is calculated within Maxent. Specifically, once Maxent identifies a variable of high importance, it is selected and no further evaluation is performed. Therefore, another highly correlated variable (e.g., elevation) may be as important as maximum temperature of the warmest month, but was not selected because of the processing order within Maxent. To alleviate this concern in our analysis, we considered the average values across all 10 bootstrapped model runs (using random partitioning of test versus training data) to determine overall variable importance. Although variable selection across all model runs was stable, it is still necessary that the variable importance calculations are considered in the context of all 32 variables.

To identify the threshold values of variables considered important to the overall model, we examined each variable independently by creating a Maxent model using only the corresponding variable. Maximum temperature of warmest month was the most important variable in the model (i.e., variable contribution of 40.6%) and possessed a temperature threshold of 25.0 °C. All areas that possessed a maximum temperature less than 25.0 °C during the warmest month of the year resulted in an increased probability of possessing suitable red spruce habitat. Minimum temperature of coldest month possessed a threshold value of approximately -8.5 °C. All values less than -8.5 °C resulted in an increased probability of possessing suitable habitat for red spruce to a peak of approximately -10.5 °C.

Slope percentage was also considered important for the model with a 6.9 percent variable contribution and was an important variable because it decreased the regularized training gain the most when omitted. Therefore, slope percentage appears to offer the most information that is not present in the other variables. The range of slope percentages where suitable red spruce habitat was predicted most likely to occur was 0 to 35 percent.

Mean temperature of coldest quarter was also considered important for the model and possessed a threshold value of approximately -1.8 °C. Any values lower than -1.8 °C indicated an increased likelihood of red spruce presence. Mean annual temperature was also important and possessed a threshold value of approximately 8.5 °C. Mean annual temperatures less than 8.5 °C resulted in an increased likelihood of suitable habitat for red spruce.

The last two variables considered important in the analysis were soil type, a categorical variable, and elevation. Soil type contributed 4 percent to model performance and possessed 136 soil-type categories for West Virginia. In our red spruce plots sampled, only 12 soil categories were identified, with three categories occurring in more than 75 percent of the red spruce plots sampled. These three soil types, in order of importance, were Trussel-Simoda-Mandy-Gauley (soil category 92, frigid soil series), Shouns-Cateache-Belmont (soil category 63, mesic soil series), and Dekalb-Buchanan (soil category value 109, mesic soil series). The final variable that had a variable contribution ≥ 3 percent was elevation. A threshold for elevation was identified at 900 m, at which any values greater than 900 m resulted in increased probability of possessing red spruce habitat.

After analyzing variables important in the model, the next step was to create suitability maps that indicated areas suitable for red spruce habitat in West Virginia. When a replicated Maxent model is created using a training and test dataset, a table of cumulative and logistic threshold values is provided in the output. The threshold values given in this table are determined by calculating binomial probabilities with associated one-sided p-values for the null hypothesis. When test samples exceed 25, a normal approximation to the binomial is used. The null hypothesis tested for here is that the test points are not predicted with any more certainty than a random prediction within the same area.

For our study, the logistic threshold value for the minimum training presence (MTP), derived from all 10 Maxent model runs, was selected to determine areas of suitable and unsuitable red spruce habitat. Our assurance of data accuracy was the driver for this threshold level selection, as the MTP threshold value indicated the habitat suitability threshold value of a training point (i.e., a red spruce presence point) that was used in the model. This MTP value is the lowest threshold at which a plot is used for training that possesses red spruce. Therefore, all pixels with threshold values greater than or equal to the MTP logistic threshold served as areas that possessed red spruce habitat. Using average MTP across all 10 bootstrapped replicate Maxent model analyses (MTP=0.074, sd=0.039), we identified the total area of suitable red spruce habitat at 282,939 ha.

We further distinguished red spruce habitat quality by identifying areas of low, medium, and high habitat suitability. The suitability index thresholds incorporated were unsuitable (0 to <0.074), low (0.074 to 0.36), medium (>0.36 to <0.65), and high (0.65 to 1). These MTP threshold values were classified in ArcMap using equal-interval splits for all areas identified as possessing suitable red spruce habitat (i.e., MTP ≥0.074). The areas identified with high suitability were identified for approximately 7,800 ha in West Virginia. Mapped areas of medium suitability were estimated to occupy 83,000 ha, while areas of low suitability were identified on approximately 192,000 ha. Figure 3 displays the modeled red spruce habitat in West Virginia by suitability class.

The next step in our analysis was to examine the distribution of red spruce forest habitat in counties identified to possess suitable habitat. Eighteen counties were identified with suitable red spruce habitat; however, five counties possessed more than 85 percent of the total area identified as red spruce habitat: Randolph (33%), Pocahontas (31%), Tucker (12%), Grant (8%), and Greenbrier (6%). In addition, nine counties possessed high suitability, with Randolph, Pocahontas, Pendleton, Grant, and Tucker Counties accounting for more than 99 percent of these areas. Furthermore, four of the ten counties identified as possessing medium suitability accounted for more than 90 percent of these areas: Randolph, Pocahontas, Grant, and Tucker. Lastly, of the 18 counties identified with low red spruce habitat, only half possessed areas that exceeded 1,000 ha. These counties were Pocahontas (59,096 ha), Randolph (56,118), Tucker (25,809 ha), Greenbrier (14,091 ha), Pendleton (10,843 ha), Grant (10,480 ha), Webster (7,556 ha), Preston (5,379 ha), and Mineral (1,388 ha) (Table 3).

DISCUSSION

The Maxent analyses performed well (i.e., AUC ≥0.9) in identifying red spruce forest habitat in West Virginia. Specifically, the model was able to correctly classify the training data with a 0.97 probability. It is important to note that the maps created from this modeling effort do not indicate the occurrence of red spruce. Rather, they indicate areas on the landscape most likely to possess red spruce habitat because they share similarities with respect to the environmental and site-specific variables identified in the red spruce presence localities used as inputs for the model. However, these suitability maps for red spruce habitat greatly surpass the range and habitat maps that have been created at this scale for West Virginia.

The variables considered to contribute substantially to model performance were important to identify because they explain the particular habitat preferences where red spruce forests now occur. Identifying these variables and the thresholds at which they define the occurrence of red spruce is an excellent

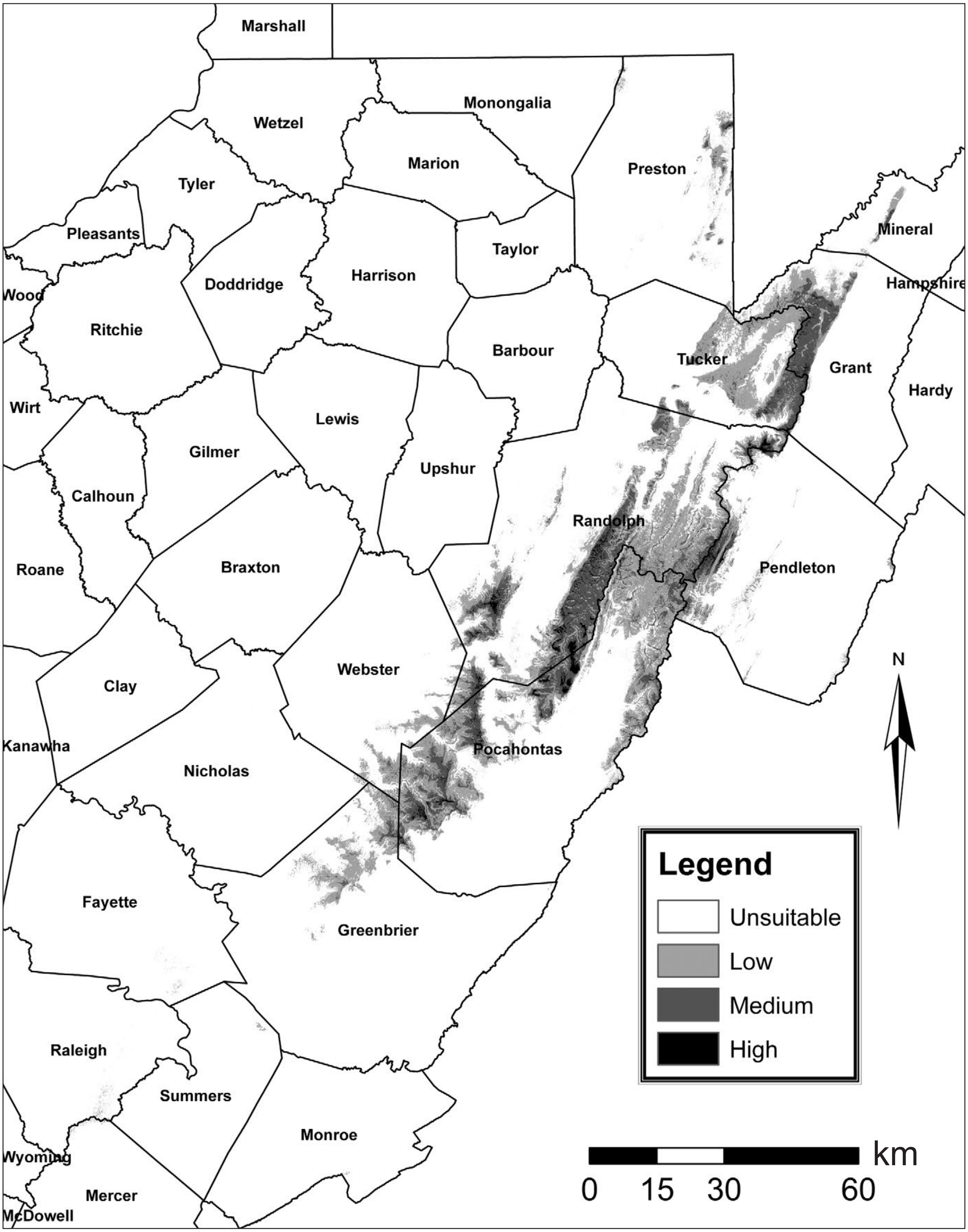

Figure 3.—Current model results identifying counties in West Virginia with low, medium, and high suitability for red spruce habitat.

Table 3.—West Virginia area (ha) by county for low, medium, and high suitability for presence of red spruce habitat

	Suitability			
Counties	Low	Medium	High	Total
Barbour	7.2	-	-	7.2
Fayette	134.5	-	-	134.5
Grant	10,479.9	10,257.1	396.0	21,133.0
Greenbrier	14,090.8	1,414.3	18.3	15 ,23.4
Mercer	181.1	-	-	181.1
Mineral	1,387.5	316.3	5.8	1,709.7
Monongalia	96.6	7.0	-	103.6
Monroe	31.1	-	-	31.1
Nicholas	257.9	-	-	257.9
Pendleton	10,843.3	4,216.9	681.7	15,741.9
Pocahontas	59,095.7	25,526.3	2,554.9	87,176.9
Preston	5,379.2	763.6	49.2	6,192.1
Raleigh	405.6	-	-	405.6
Randolph	56,117.9	32,450.8	3, 973.9	92,542.6
Summers	129.7	-	-	129.7
Tucker	25,809.0	7,683.0	157.2	33,649.2
Webster	7,556.0	417.0	-	7,973.0
Wyoming	35.5	-	-	35.5
TOTAL	192,038.6	83,052.5	7,837.1	282,928.2

tool for ecologists. The strong association of climate with the detection of red spruce habitat, particularly when assessing the bioclimatic variables individually (Fig. 2), is evident from our model. Although several variables contributed to model performance, maximum temperature of warmest month and minimum temperature of coldest month were most important, together contributing more than 50 percent to overall variable contribution (Table 1). These findings indicated that temperature rather than precipitation may be considered the most important driver with respect to habitat preference for red spruce in West Virginia. Other studies (e.g., Cogbill and White 1991, Cook and Johnson 1989, Johnson et al. 1988, McLaughlin et al. 1987) have also identified red spruce to be primarily temperature rather than precipitation sensitive, with the historic distributions of red spruce in the Appalachian Mountain Region driven primarily by small changes in temperature (Vann et al. 1994).

The threshold values or range of values identified from the Maxent analyses are useful in identifying the parameters where red spruce habitat exists. The findings of this study suggest that in West Virginia, red spruce habitat is predominantly found at elevations exceeding 900 m where maximum summer temperature is ≤ 25 °C, minimum winter temperature ≤ -10.5 °C, and mean annual temperature < 8.5 °C.

Furthermore, the bioclimatic variable maximum temperature of warmest month was considered the most important variable in the Maxent model. Other research work has also indicated July temperature (i.e., warmest month) to be an important determining factor for identifying red spruce presence and/or the ecotone between spruce-fir and hardwood ecosystems (e.g., Cogbill and White 1991, Pielke 1981, Wolfe 1979). Wolfe (1979) proposed 20 °C in the warmest month for the boundary between coniferous and broad-leaved vegetation in the Northern Hemisphere and

Australasia; however, in North America the regions with temperatures below the 20 °C isotherm were also identified to possess the spruce transition forest where red spruce occurs within areas dominated by northern hardwood species. In addition, Vann et al. (1994) reported a lower elevation limit in New York coinciding with the approximate 27.7 °C isotherm for average July daily maximum temperature. Looking at three regions in the Northeast U.S., Federer et al. (1989) also identified temperature in the latter part of the previous growing season and temperature in the winter as important.

In West Virginia, Pielke (1981) also identified a 20 °C isotherm that included areas that exhibited only a minor red spruce component. This finding coincides well with our assessment and indicates the importance of summer temperatures in identifying red spruce habitat. Pielke (1981) attributed the 20 °C isotherm as a critical temperature during the hot summer months as a temperature threshold at which red spruce seedlings were likely to be permanently damaged by heat. Although the growing conditions of red spruce have been well documented, it is not been well established what constraints these temperatures have on growth rates and survival of red spruce (e.g., Blum 1990, Korstian 1937, Oosting and Billings 1951). Federer et al. (1989) suggested that high respiration in summer reduces carbohydrates available for storage over the winter, and thus, diameter growth and vigor in the next year. Vann et al. (1994) found a temperature compensation point of 30 to 35 °C for red spruce, and they also noted visible needle chlorosis, indicating severe cellular injury, when temperatures exceeded 32 °C. We agree with Pielke (1981) that red spruce seedlings are vulnerable to high summer temperatures, and coupled with increased competition from northern hardwood species in areas with these warmer temperatures, it seems logical that red spruce does not possess optimal habitat in such areas.

Minimum temperatures during the coldest months of the year have recently been addressed as an important consideration when determining the drivers of vegetation and ecosystem functioning (e.g., Kreyling 2010). Although uncertain, it seems the minimum temperature threshold during the coldest month of the year identified in our model may prevent many competitive northern hardwood species from dominating such areas because of their relatively lower resistance to frost damage. This ability of red spruce to endure extreme cold temperatures therefore emphasizes the importance of temperature-based climatic conditions in identifying suitable red spruce habitat.

Elevation has often been used in the description of red spruce habitat in the central and southern Appalachian Mountain Region, and it provided the impetus for our inclusion of this variable in the model analysis (Nowacki and Wendt 2010). Elevation is also considered important in the delineation of boundaries between species and community assemblages. The elevation threshold for red spruce presence, when examined solely, occurred at approximately 900 m in West Virginia. When used exclusively in a Maxent model, the AUC value for this variable is 0.9 and compares similarly in model importance when examined against other important bioclimatic variables (Fig. 2). This 900-m threshold identified in our study affirms historical and current descriptions of the elevational transition into red spruce forest habitats identified in West Virginia (e.g., Egleston 1884, Nowacki and Wendt 2010, Pielke 1981, Stephenson 1993).

The identification of 282,939 ha of suitable red spruce habitat in West Virginia provides a baseline for determining areas on the landscape where red spruce forests exist today or could potentially inhabit and persist under current climatic conditions. This research effort has great utility for the active red spruce restoration activities being implemented to establish connectivity between stands and to connect red spruce at higher elevations with the red spruce occurring in the high-elevation valleys, specifically Canaan Valley (Tucker County). Many red spruce plantings have been conducted in West Virginia in recent years by many federal, state, and local parties to re-establish connectivity of the red spruce ecosystem.

Regarding restoration, this Maxent analysis using statistically downscaled bioclimatic data will also allow users of these output maps to examine the local potential for spruce restoration at a 30-m resolution, and would be highly beneficial when used in combination with high-resolution aerial photographs to identify areas that possess suitable habitat but lack the presence of red spruce. Identifying areas that possess the highest probability of supporting red spruce habitat (i.e., high suitability) and implementing these findings into the current restoration and conservation management strategies being used would be wise so that the labor and money are spent in these actions with the greatest potential for success. Planting and managing for red spruce in such areas would greatly increase the likelihood of survival and establishment of a red spruce forest community in the future.

CONCLUSION

Maxent provided a powerful utility to mapping and prioritizing red spruce forest habitat in West Virginia. The importance of temperature on red spruce habitat confirms historical accounts and affirms the climatic envelope at which this species occurs. This modeling effort illustrates an efficient and powerful approach to identify suitable red spruce forest habitat, and the creation of suitability maps provides a guide for identifying areas most likely to possess the highest suitability and therefore the best combination of environmental and site-specific conditions for current and future conservation and restoration management activities. In the face of climatic uncertainty, ensuring that the areas identified possess a high suitability for red spruce habitat should be of primary concern.

These modeled areas represent core areas with respect to habitat and likely possess the unique habitat required by complex red spruce communities. Once these areas have been prioritized for future restoration efforts, then areas that possess medium or low suitability may be examined. The restoration of red spruce will not only increase the habitat required by the numerous species that thrive in this unique forest ecosystem, but will also give red spruce the greatest resilience to future climatic conditions by establishing connectivity and increasing genetic diversity. Future research efforts should focus on potential impacts of climate change to red spruce habitat in West Virginia. Defining climatic windows for red spruce, as opposed to using physical parameters such as elevation and aspect, will facilitate the use of climate models for predicting suitable red spruce distributions in the future.

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LITERATURE CITED

Acciavatti, R.E.; Allen, T.J.; Miller, A.R. [et al.]. 1993. **Insects and spiders of the upland forests.** In: Stephenson, S.L., ed. Upland forests of West Virginia. Parsons, WV: McClain Printing: 143-178.

Audley, D.E.; Skelly, J.M.; McCormick, L.H.; Jackson, W.A. 1998. **Crown condition and nutrient status of red spruce (*Picea rubens* Sarg.) in West Virginia.** Water, Air, and Soil Pollution. 102: 177-199.

Baldwin, R.A. 2009. **Use of maximum entropy modeling in wildlife research.** Entropy. 11: 854-866.

Blum, B.M. 1990. **Red spruce, *Picea rubens* Sarg.** In: Burns, R.M.; Honkala, B.H., tech. coords. Silvics of North America. Conifers. Agric. Handb. 654. Vol. 1. Washington, DC: U.S. Department of Agriculture, Forest Service: 250-259.

Bollinger, J.; Kienest, F.; Zimmerman, N.E. 2000. **Risks of global warming on montane and subalpine forests in Switzerland- a modeling study.** Regional Environmental Change. 1: 99-111.

Brooks, A.B. 1910. **Forestry and wood industries.** Morgantown, WV: Acme Publishing Company. 481 p.

Brotons, L.; Thuiller, W.; Araujo, M.B.; Hirzel, A.H. 2004. **Presence-absence versus presence-only modeling methods for predicting bird habitat suitability.** Ecography. 27: 437-448.

Byers, E.A.; Vanderhorst, J.P.; Streets, B.P. 2010. **Classification and conservation assessment of upland red spruce communities in West Virginia.** Elkins, WV: WV Natural Heritage Program, West Virginia Department of Natural Resources. 68 p.

Clarkson, R.B. 1964. **Tumult on the mountains.** Parsons, WV: McCain Printing Co. 410 p.

Clarkson, R.B.; Duppstadt, W.H.; Guthrie, R.L. 1980. **Forest wildlife plants of the Monongahela National Forest.** Pacific Grove, CA: Boxwood Press. 283 p.

Cogbill, C.V.; White, P.S. 1991. **The latitude-elevation relationship for spruce-fir forest and treeline along the Appalachian mountain chain.** Vegetatio. 94: 153-175.

Comer, P.; Faber-Langendoen, D.; Evans, R. [et al.]. 2003. **Ecological systems of the United States: a working classification of U.S. terrestrial systems.** Arlington, VA: NatureServe. 83 p.

Cook, E.R.; Johnson, A.H. 1989. **Climate change and forest decline: a review of the red spruce case.** Water, Air, and Soil Pollution. 48: 127-140.

Davis, M.B. 1981. **Quaternary history and the stability of forest communities.** In: West, D.C.; Botkin, D.B.; Shugart, H.H., eds. Forest succession. New York, NY: Springer-Verlag: 132-153.

Delcourt, P.A.; Delcourt, H.R. 1987. **Long-term forest dynamics of the temperate zone.** New York, NY: Springer-Verlag. 439 p.

Egleston, N.H. 1884. **Report on forestry.** Washington, DC: Government Printing Office. Vol. 40. 421 p.

Elith, J.; Phillips, S.J.; Hastie, T. [et al.]. 2011. **A statistical explanation of MaxEnt for ecologists.** Diversity and Distribution. 17: 43-57.

Federer, C.A.; Tritton, L.M.; Hornbeck, J.W.; Smith, R.B. 1989. **Physiologically based dendroclimate models for effects of weather on red spruce basal-area growth.** Agricultural and Forest Meteorology. 46: 159-172.

Hernandez, P.A.; Graham, C.H.; Master, L.L.; Albert, D.L. 2006. **The effect of sample size and species characteristics on performance of different species distribution modeling methods.** Ecography. 29: 773-785.

Hijmans, R.J.; Cameron, S.E.; Parra, J.L. [et al.]. 2005. **Very high resolution interpolated climate surfaces for global land areas.** International Journal of Climatology. 25: 1965-1978.

Hijmans, R.J.; Graham, C.H. 2006. **The ability of climate envelope models to predict the effect of climate change on species distributions.** Global Change Biology. 12: 2272-2281.

Hirzel, A.H.; Le Lay, G. 2008. **Habitat suitability modeling and niche theory.** Journal of Applied Ecology. 45: 1372-1381.

Hopkins, A.D. 1891. **Black spruce: preliminary report.** West Virginia Agricultural Experiment Station Bull. 17: 93-102.

Johnson, A.H.; Cook, E.R.; Siccama, T.G. 1988. **Climate and red spruce growth and decline in the northern Appalachians.** Proceedings, National Academy of Sciences of the United States of America. 85(15): 5369-5373.

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

Kreyling, J. 2010. **Winter climate change: a critical factor for temperate vegetation performance.** Ecology. 91(7): 1939-1948.

Lewis, R.L. 1998. **Transforming the Appalachian countryside: railroads, deforestation, and social change in West Virginia, 1880-1920.** Chapel Hill, NC: University of North Carolina Press. 348 p.

Manning, C.; Schutze, H. 1999. **Foundations of statistical natural language processing.** Cambridge, MA: MIT. 680 p.

McLaughlin, S.B.; Downing, D.J.; Blasing, T.J. [et al.]. 1987. **An analysis of climate and competition as contributors to decline of red spruce in high elevation Appalachian forests of the eastern United States.** Oecologia. 72: 487-501.

Menzel, J.M.; Ford, W.M.; Edwards, J.W.; Ceperly, L.J. 2006a. **A habitat model for the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the Central Appalachian Mountains.** Res. Pap. NE-729. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 10 p.

Menzel, J.M.; Ford, W.M.; Edwards, J.W.; Terry, T.M. 2006b. **Home range and habitat use of the vulnerable Virginia northern flying squirrel *Glaucomys sabrinus fuscus* in the Central Appalachian Mountains, USA.** Oryx. 40(2): 204-210.

Millspaugh, C.F. 1891. **Forest and shade tree insects. Part II. Black spruce (*Picea mariana* (Mill.)).** West Virginia University. Agricultural Experiment Station Rep. 3: 171-180.

Nowacki, G.; Wendt, D. 2010. **The current distribution, predictive modeling, and restoration potential of red spruce in West Virginia.** In: Rentch, J.S.; Schuler, T.M., eds. Proceedings, conference on the ecology and management of high-elevation forests in the central and southern Appalachian Mountains. Gen. Tech. Rep. NRS-P-64. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station: 163-178.

Odom, R.H.; Ford, W.M.; Edwards, J.W. [et al.]. 2001. **Developing a habitat model for the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the Allegheny Mountains of West Virginia.** Biological Conservation. 99: 245-252.

Oosting, H.J.; Billings, W.D. 1951. **A comparison of virgin spruce-fir forest in northern and southern Appalachian system.** Ecology. 32(1): 84-103.

Pearson, R.G. 2007. **Species' distribution modeling for conservation educators and practitioners.** Synthesis. American Museum of Natural History. Available at http://ncep.amnh.org. (Accessed February 2, 2009).

Phillips, S.J.; Anderson, R.P.; Schapire, R.E. 2006. **Maximum entropy modeling of species geographic distributions.** Ecological Modelling. 190: 231-259.

Phillips, S.J.; Dudik, M.; Elith, J. [et al.]. 2009. **Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data.** Ecological Applications. 19(1): 181-197.

Phillips, S.J.; Dudik, M.; Schapire, R.E. 2004. **A maximum entropy approach to species distribution modeling.** In: Proceedings, 21st international conference on machine learning. New York, NY: 655-662.

Pielke, R.A. 1981. **The distribution of spruce in west-central Virginia before lumbering.** Castanea. 46(3): 201-216.

Raxworthy, C.J.; Martinez-Meyer, E.; Horning, N. [et al.]. 2003. **Predicting distributions of known and unknown reptile species in Madagascar.** Nature. 426: 837-841.

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(2): 88-98.

Stephenson, S.L. 1993. **Upland forest vegetation.** In: Stephenson, S.L., ed. Upland forests of West Virginia. Parsons, WV: McClain Printing Co.: 11-34.

Stephenson, S.L.; Clovis, J.F. 1983. **Spruce forests of the Allegheny Mountains in Central West Virginia.** Castanea. 48(1): 1-12.

Strausbaugh, P.D.; Core, E.L. 1964. **Flora of West Virginia.** Introductory section. West Virginia University Bull. Series 65. No. 3-1.

Vann, D.R.; Johnson, A.H.; Casper, B.B. 1994. **Effect of elevated temperatures on carbon dioxide exchange in *Picea rubens*.** Tree Physiology. 14: 1339-1349.

Wiegl, P.D. 2007. **The northern flying squirrel (*Glaucomys sabrinus*): a conservation challenge.** Journal of Mammology. 88: 897-907.

Wolfe, J.A. 1979. **Temperature parameters of humid mesic forests of eastern Asia and relation to forests of other regions of the Northern Hemisphere and Australasia.** Prof. Paper 1106. U.S. Geological Survey.

Yates, C.J.; McNeill, A.; Elith, J.; Midgley, G.G. 2010. **Assessing the impacts of climate change and land transformation on Banksia in the South West Australian Floristic Region.** Diversity and Distributions. 16: 187-201.

Beane, Nathan R.; Rentch, James S.; Schuler, Thomas M. 2013. **Using maximum entropy modeling to identify and prioritize red spruce forest habitat in West Virginia.** Research Paper NRS-23. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 16 p.

Red spruce forests in West Virginia are found in island-like distributions at high elevations and provide essential habitat for the endangered Cheat Mountain salamander and the recently delisted Virginia northern flying squirrel. Therefore, it is important to identify restoration priorities of red spruce forests. Maximum entropy modeling was used to identify areas of suitable red spruce habitat, with a total of 32 variables analyzed. Maximum temperature of the warmest month and minimum temperature of the coldest month were identified as variables explaining the most information about red spruce forest habitat. In addition, habitat maps identifying areas of high, medium, and low suitability were created and quantified at the county level. These results will benefit current and future conservation and restoration management activities as they identify core areas that possess the necessary environmental conditions for supporting future complex red spruce communities. Restoration efforts focused in areas possessing high suitability ensure peak potential of success and will ultimately give red spruce forests in West Virginia the greatest resilience to future climatic conditions by establishing connectivity between red spruce forests and increasing genetic diversity.

KEY WORDS: red spruce, habitat suitability, maximum entropy, distribution modeling, forest ecology

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