Journal of Forestry
https://doi.org/10.1007/s44392-025-00042-z

PRACTICE OF FORESTRY

Mapping Oak (*Quercus* spp.) Regeneration Potential Within the Nantahala National Forest

Quentin Ikuta[1,2] · John Zobel[1] · Joseph Knight[1,3] · Jonathan Knott[4] · Brandon Stephens[2] · Nicholas J. Partington[1] · Marcella A. Windmuller-Campione[1]

Received: 17 October 2024 / Accepted: 8 May 2025

Abstract
Forest mesophication threatens the regeneration and potential future perpetuation of oak (*Quercus* spp.) forests throughout southern Appalachia and eastern United States (US). We explored methods to produce stand-scale oak site suitability maps, within the Nantahala National Forest in North Carolina, which can be used to prioritize site-specific treatments to allow for oak regeneration and recruitment using silvicultural strategies to reduce forest mesophication. To establish initial conditions, USDA Forest Service common stand exam quick plot protocol was followed, and plot data collected from June through August 2023 at 180 sample points within 15 stands totaling 500 acres. Collection of seedling height class data was important for showing a gap in regeneration, between the number of small seedlings (~1 ft) (1038 stems) and large seedlings (>4.5 ft) (301 stems). Two popular site suitability modeling techniques, Maximum Entropy (MaxEnt) and Random Forest, were run for five common oak species with seven predictor variables including available water capacity, elevation, eastness, ecozone, northness, soil acidity, and soil type. MaxEnt models consistently outperformed Random Forest models with the most important variables including ecozone, soil acidity, and soil type. The maps highlight locations that can be prioritized for silvicultural treatments that target regeneration and recruitment of oaks to combat or reverse forest mesophication.

Keywords Species distribution model · MaxEnt · Oak · Quercus · Southern appalachia · Nantahala national forest

✉ Marcella A. Windmuller-Campione
mwind@umn.edu

1 Department of Forest Resources, University of Minnesota, Saint Paul, MN 55108, USA

2 USDA Forest Service, Nantahala National Forest, Franklin, NC 28734, USA

3 Department of Forest Resources and Environmental Conservation, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA

4 USDA Forest Service, Northern Research Station, Saint Paul, MN 55108, USA

Introduction

Oak (*Quercus* spp.) forests have been stewarded across the United States of America (USA) for thousands of years (Davis 1983; Prentice et al. 1991). These forests are foundational for their economic, ecological, nutritional, and cultural services and values. For example, oak dominated forests can contribute as much as $13 billion USD and 50,000 jobs to the economy of a single US state, provide critical sources of timber, environmental regulation, habitat, shelter, food, and material for cultural resources such as Cherokee woven baskets (Cavender-Bares 2016; Patterson et al. 2022; Baumflek et al. 2022). Furthermore, pre-colonial settlement records indicate that oaks comprised 30–80% of forested cover across the southeast, suggesting that oaks were one of the most dominant genera since the last glacial maximum (Davis 1983; Prentice et al. 1991). Historically, ecosystems dominated by oak were high-light, open woodland-type environments with larger diameter overstory trees, open mid-stories, and highly diverse understories which included hickories (*Carya* spp.), American chestnut (*Castanea dentata*), and pines (*Pinus* spp.) as co-dominant species in the overstory (Hanberry and Nowacki 2016).

Fire, especially by the Indigenous Cherokee stewards, shaped the historical structure and composition of southeastern forests for thousands of years (Yarnell 1998; Stambaugh et al. 2015; Baumflek et al. 2022). These fires were implemented through thoughtful and intentional planning with the general goal of the fires being low-severity and high frequency (Jacobs et al. 2013). Fire was and still is an important disturbance in oak forests as the severity and frequency of forest fires historically influenced structural diversity and canopy openness (Yarnell 1998; Hanberry and Nowacki 2016). Currently, prescribed or controlled fire disturbances are increasingly used by western land managers to maintain oak systems in fire dependent forests (Brose and Hutchinson 2019); there are a diversity of forest ecosystems (e.g. mesic coves) where oak regeneration is not the goal. In stands prioritizing oak regeneration and recruitment, low-severity, frequent fire stewardship can suppress oak competitors (e.g. red maple (*Acer rubrum* L.)) in the seedling and sapling stage (Abrams 1992; Dey 2014). More specifically, surface fires distinctly impact the accumulation of oak advance reproduction as part of the regeneration process. Meanwhile, disturbances that create canopy gaps affect the recruitment of oaks. More so, in the absence of fire as a primary disturbance agent, oaks capture growing space through their competitive adaptations such as drought and pH tolerance (Dey 2014; Johnson 1992; Sander 1984).

During the past few centuries, and especially as of the mid-nineteenth through twentieth centuries, colonization, the introduction of non-native species, and the subsequent shifts in stewardship regimes have drastically influenced the current oak forests of the southeast (Baumflek et al. 2022; Nowacki and Abrams 2008; Baumflek et al. 2022). These changes to stewardship regimes culminated in the federal government of the USA forcefully removing the Indigenous Cherokee peoples from their homelands of the southeast throughout the mid-nineteenth century in a process known as the Trail of Tears via the Indian Removal Act (Finger 1991). As a result, oak woodlands of the past subsequently developed as late-successional ecosystems and were mistaken by Europeans as wilderness despite the intensive stewardship regimes applied by the Cherokee people (Delcourt and Delcourt 2004).

Despite the drastic cultural and ecological changes of the nineteenth and twentieth centuries, oaks have remained resilient and continue to show their adaptive abilities to accumulate advanced regeneration even among increased competition in the twenty-first century (Edge et al. 2023; but see Haavik et al. 2015; Rodríguez-Calcerrada et al. 2017; and Crocker et al. 2023 for impact on oak decline). Unfortunately, the American chestnut has been largely lost across the region due to the chestnut blight (Kuhlman 1978). Because of the extensive decline of American chestnut, oaks have largely infilled and play an increasingly critical role in supporting wildlife habitat, ecosystem services, and human cultural systems (Wang and Huifeng 2015).

Even where advance regeneration is present, recruiting oaks following regeneration harvests has remained problematic due to herbivory and competition by native and non-native plant species; this problem has been exacerbated by a lack of controlled burning, fire suppression efforts, and changes in temperature and precipitation patterns (McShea et al. 2007; Dey 2014; Alexander et al. 2021). However, the presence of large advance regeneration (> 1 in. diameter at breast height, dbh) serve as strong indicators of future recruitment and the maintenance of oak species in the midstory (5 to 15 in. dbh) and overstory (> 15 in. dbh) (Sander 1971, 1984; Sander and Clark 1971; Harris et al. 2022). Where abundant and large advance regeneration occurs of desirable species (defined as 249 trees per acre (tpa) of oak, hickory, and cherry species) (USDA Forest Service 2023), silviculturists can use intermediate treatments or regeneration harvests, considering the spatial distribution of oak regeneration (e.g. Keasberry et al. 2016), to promote recruitment into the midstory and overstory (Harris et al. 2022). Thus, oak forests in the southeastern USA are at an inflection point, where tools to identify and utilize regeneration data could help prioritize treatment areas, supporting oak recruitment both within and across ownerships.

Our overarching goal was to link commonly collected seedling and sapling data to available environmental variables to develop spatially explicit models of oak regeneration potential for prioritizing further tending for regenerating and recruiting oaks after a regeneration harvest. We accomplished this through a research-management partnership which included field data collection of regenerating and recruiting species, the use of species distribution models (SDMs) such as MaxEnt and Random Forest to link regeneration with environmental data derived from the USDA Soil Survey Geographic Database (SSURGO) and other sources, and finally, matching model results with each species' silvics. We presented both spatially via rasters (pixel-based map layers) and in tabular form for application during the silvicultural planning process. Results from this project are expected to be applicable to other locations across the US that are experiencing oak regenerating and recruitment failures.

Methods

Study Region

North Carolina, USA is a heavily forested state with approximately 18.8 million acres (7.6 million hectares) of forested land. The majority of these acres (11.3 million acres or 4.6 million hectares) are in family forest ownership. Public lands including federal, state, and local public lands total 2.6 million acres (1.1 million hectares) (North Carolina Forest Service).

Our study area covers approximately 100,000 acres (40,469 hectares) of the western portion of the Nantahala Ranger District's federal management boundary within the Nantahala National Forest in North Carolina. The study area is also known as the "Nantahala Mountains." The Nantahala National Forest was established in 1920 as a result of the passage of the 1911 Weeks Act.

Due to the long history of humans on the landscape, many small land holdings have fragmented the forest, constraining larger-scale forest management. These lands were colonized, opened to colonial settlement and subsequent federal control only after the ethnic cleansing and forced displacement of Indigenous peoples between 1830 and 1850 via the Indian Removal Act of 1830, which, in this area included the Eastern Band of Cherokee Indians (Finger 1991).

The Nantahala Mountains represent a temperate climate (Appendix A). Average seasonal climatic information for Franklin, North Carolina include winter temperatures (December, January, and February) of approximately 40 F (4.4 C) and summer (June, July, and August) temperatures of approximately 70 F (21.1 C). Precipitation varies among months but all months average over 3 inches (7.6 cm) with January, March, and December averaging over 5 inches (12.7 cm).

Field Data Collection

Data were collected by a team of field technicians during the summer of 2023 in the Nantahala Mountains in areas that are planned for regeneration harvest treatments in 2024–2026 focusing on oak regeneration and recruitment. Sampling did not occur across all ecozones within the Nantahala Mountains. The stands were preselected by National Forest land managers based on being 90 years or older, fully stocked, and ready for harvest. The 15 stands, representing about 500 acres (202 hectares) within the 100,000-acre (40,469 hectares) study area (Fig. 1) were largely unmanaged for the last 80–100 years with the exception of two stands receiving controlled burning treatment for the purpose of fuels reductions within the last 10–15 years. USDA Forest Service (Forest Service) common stand exam quick plot protocol was followed for the collection at 180 sample points within 15 stands (an average of 1 sample point per 2–3 acres, about 1 per hectare) in the oak forest types (USDA 2014). Specifically, the stand exams focused on forest types which have the potential to be considered for regeneration of northern red oak (*Q. rubra*), white oak (*Q. alba*), chestnut oak (*Q. montana*), and other oak including black (*Q. velutina*) and scarlet (*Q. coccinea*) oaks.

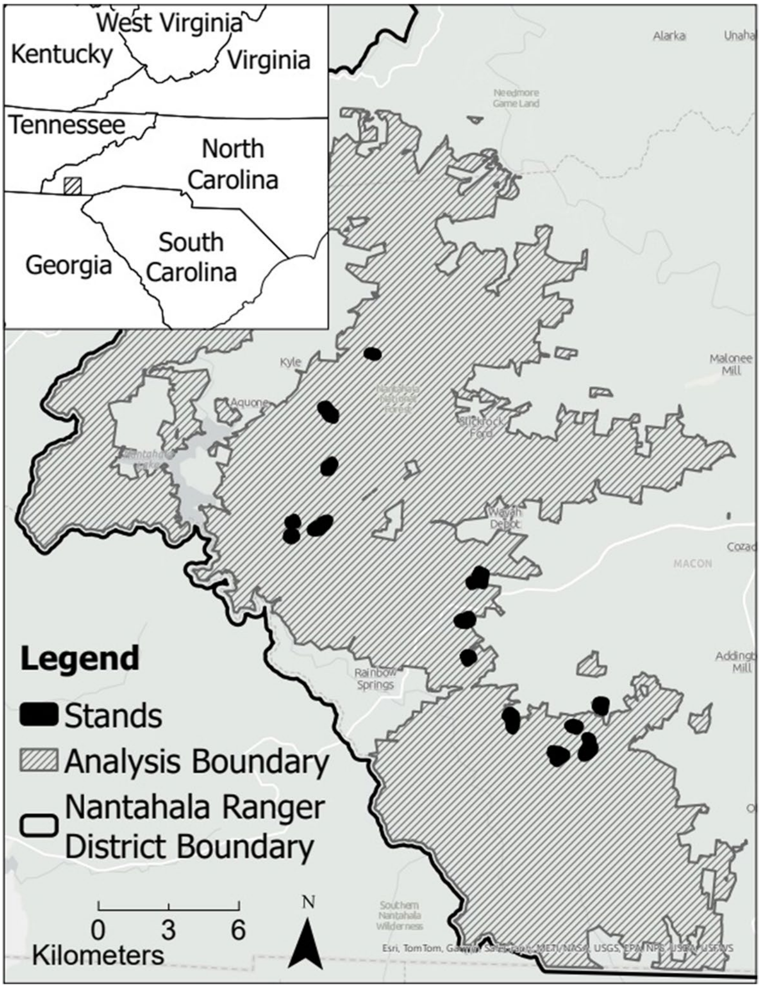

Fig. 1 Location of plots sampled during summer 2023 in stands that will receive treatments in 2024–2026 in the Nantahala National Forest. There were 180 sample points across 15 stands comprising about 500 acres. The study area's coordinates are 35.163764,−83.620084

We selected these oak species due to their abundance and presence in the study area. To ensure statistically significant sampling throughout the stands, we used ArcGIS Pro (ESRI 2023, version 3.1) to place the field data points randomly in the stands.

At each sample point, the overstory was measured by point sampling, while the midstory and regeneration layers were measured with nested fixed plots. The overstory, defined as trees greater than 15 in. dbh (38.1 cm), was sampled using a variable radius plot with a 20 basal area factor (BAF) angle gauge; the use of 15 in. dbh (38.1 cm) as a minimum for the overstory relates to sawtimber markets in the region. The midstory (defined as trees from 5–15-in dbh (12.7–38.1 cm)) and regeneration layers (defined as woody stems under 5 in. dbh (12.7 cm)) were sampled in circular 1/40 th acre (1/100 th ha) and 1/100 th acre (1/250 th ha) fixed-radius plots, respectively. Height was tallied for all regenerating individuals in the following height classes 0 −1, 1.1—2, 2.1—3, 3.1–4.5 and > 4.5 ft (0.30, 0.61, 0.91, 1.22, 1.37 + meter). The resulting dataset included density (trees per acre, TPA) for all size classes by species (regeneration, mid-, and overstory) and basal area (BA) for mid- and overstory. The complete dataset totaled 180 plots with 1398 mid- and overstory trees and 4817 understory stems.

Environmental Variables

Using environmental variables identified by Kabrick et al. (2014), soil acidity (pH), soil available water capacity (AWC), and aspect were sourced from the USDA SSURGO Database; additional variables (elevation, soil type) from this dataset were also included (USDA NRCS 2023). Detailed information can be found in Appendix B. Additionally, the Nantahala National Forest has an ecozones layer which captures eleven unique potential natural vegetation types across the study region with associated desired conditions (Simon 2011, appendix 1). These spatial variables (aspect, elevation, ecozones, soil type, soil pH, soil AWC, and soil type) were all resolutions of 98.4 ft (30 m) or less (USDA NRCS 2023).

Determining the Best Model to Predict Oak Site Suitability

We utilized the collected forest inventory data as inputs across two different species distribution modeling approaches: Maximum Entropy (MaxEnt) and Random Forest. MaxEnt is a presence-only, maximum entropy, supervised machine learning model that produces predicted probability of presence, which can also be interpreted as site suitability as determined by raster output based on presence points and covariate rasters. The main benefit of MaxEnt over other species distribution models is that it chooses an underlying probability distribution which maximizes agreement with that which is known while carefully avoiding assuming anything that is not known, holding to the principle of maximum information entropy (Jaynes 1991). Random Forest is an ensemble machine learning algorithm that uses many decision trees to generate a predictive model based on explanatory and response variables. Random forest is prized for its flexibility of application and ability to avoid overfitting (Qi 2012). Retaining comparability with the MaxEnt parameterization, the Random Forest models were also run as presence-only. The Random Forest model can produce a probability raster similar to the MaxEnt predicted presence raster output.

Area under the curve (AUC) of the receiver operating characteristic (ROC) curve is a metric for comparing the performance of the MaxEnt and Random Forest models. AUC values range from 0 to 1, and higher AUC indicates that the probability of a random positive (presence) instance and a random negative (non-presence) instance are correctly ordered by the classifier. Generally, an AUC of 0.7 or greater is indicative of a good model (Phillips et al. 2005). An AUC of 0.5 is considered random prediction while an AUC of 1 is rare and may indicate overfitting. In other words, a higher AUC indicates that MaxEnt or Random Forests are good at distinguishing between presence and absence of regeneration. Because the models were fit on presence-only data, positive instances are put ahead of negative in terms of predicted probability. Both MaxEnt and Random Forest models can produce predicted probability of site suitability outputs and thus ROCs with AUC scores. Additionally, both model types were trained on the same presence-only response data. Therefore, the AUC measures may be directly compared, the highest AUC generally indicates the best performing model to be used in predicted probability/site suitability raster creation.

Data Analysis

Summary statistics by species were calculated for each vegetative layer for TPA; basal area per acre (sq.ft/ac) was calculated for the mid-story and overstory. The overstory and midstory data were combined for summary statistics. To explore additional dynamics within the regeneration layer, we prepared an average TPA per species table including per-species percentages of TPA regeneration at both 1 and 4.5 + feet along with the difference between those two percentages for each species to understand how species are currently recruiting through initial height classes. Percentage difference of species recruitment between early height classes is of interest because larger seedlings/saplings can serve as better predictors of future regeneration potential (Sander et al. 1976; Loftis 2004; McWilliams et al. 2015; Harris et al. 2022).

We used the java-based desktop MaxEnt GUI (Phillips et al. 2005, version 3.4.4) to run the MaxEnt models. The inputs were pre-processed to ensure compliance with MaxEnt procedures (Phillips et al. 2005). Critical parameters that differed from the default settings included the following: Iterations: 1000, Resampling: bootstrap ×10; subsampling ×10, Regularization Multiplier: 2, and Training/Testing Split: 75/25%. We increased the number of iterations to 1000 to ensure that the model had time to fully converge before producing an average result. We ran two resampling schemes to compare the result – bootstrap and subsampling. We increased the regularization multiplier from 1 to 2, avoiding possible overfitting by penalizing model complexity, a common issue with MaxEnt (Phillips and Dudík 2008). Finally, the model was run with these parameters for each species group including red, white, chestnut, and the category "other oaks", which included black and scarlet oaks. The resulting ROC/AUC from the best model, variable response curves, and jackknife significance charts were saved for presentation and interpretation in the results section.

R (version 4.2.2) was used to assemble the code for the Random Forest model for each species group. Before running the models, predictor variables that exhibited collinearity to the response variable were removed from the dataset. The predictor variable dataset included non-highly correlated understory variables in addition to mid- and overstory variables and site characteristics.

Finally, the AUC of each model type run was collected and plotted on a dot plot to easily visualize and understand which model performed the best for each species. The models with the highest AUC were then selected for creation of site suitability rasters for the entire study area. The resulting rasters were imported into ArcGIS Pro and assigned a coordinate reference system of NAD 1983 (2011) State Plane North Carolina FIPS 3200 (US Feet). Additional information including ROC charts, variable response curves, and jackknife significance charts were explored to identify the most important variables and how species respond to individual variables. Importantly, the MaxEnt variable response curves have been linked with the published silvics for each species.

Results

Existing Conditions

There were 29 tree species present, five of which were oaks; the five oak species included white, northern red, chestnut, black, and scarlett. Average midstory and overstory densities and BA were 155 TPA (± 5.5 TPA) and 157 ft^2/ac (± 4.1 ft^2/ac), respectively. Oaks represented 13% of TPA (21 ± 2.3 TPA) and 21% of BA (33 ± 3.1 ft^2/ac) and, on average, were not the dominant species in the overstory and midstory. Yellow poplar and red maple were the dominant species in the mid and overstories. Yellow poplar averaged 44 TPA (± 3.8 TPA) or 29% of TPA and 64 ft^2/ac (± 4.5 ft^2/ac) or 41% of BA, while red maple averaged 29 TPA (± 3.1 TPA) or 19% of TPA and a BA of 19 ft^2/ac (± 1.9 ft^2/ac) or 12% of BA. Total average regeneration was 1978 TPA (± 32.2 TPA) across all species and height classes, 284 TPA (± 5.6 TPA) across all non-oak hardwood species at 4.5 + feet, and 17 TPA (± 1.6 TPA) for oaks at 4.5 + feet (Table 1).

The diameter distribution (4-inch classes) indicated a reverse-J shaped diameter distribution (Fig. 2). The smaller DBH classes from 6–14 inches (15.2–35.6 cm) included a greater number of species present (with 24 out of 29 species present across the study area) and were primarily dominated by red maple (22%) and yellow poplar (21%) followed by hickory (8%) and American basswood (8%). The middle diameter classes from 15 to 30 inches (35.7–76.2 cm) included 24 species and were primarily dominated by yellow poplar (47%). The larger diameter classes from 31–42 inches (76.3–106.7 cm) included eleven species and were primarily dominated by yellow poplar (39%) and northern red oak (26%). The largest diameter classes greater than 42 inches (106.8 cm) only contain northern red oak. The number of unique species present on this site decreased as diameter class size increased. In the larger size classes, the proportion of yellow poplar increased.

Oak regeneration was abundant, but a lack of seedlings in the largest size class suggests a regeneration gap (Table 1). Total TPA for oak advance regeneration seedlings range from 4 to 356 with an average among all oak species of 165 TPA (± 72 TPA). Regeneration TPA of oak species across the site is highly variable with northern red oak and chestnut oak showing the greatest stem density with total average TPA of 356 (± 44) and 298 (± 54), respectively. However, there were only an average of 18 TPA (± 1.6) in the 4.5 + feet category. Oaks comprise approximately 60% of the proportion of 1-foot seedlings, but only 5.9% of the 4.5 + foot seedlings.

Table 1 Average trees per acre (TPA) of desirable timber species' advanced regeneration with red maple as of August 2023

Categories	SPECIES	HEIGHT (feet)					Total TPA (species)	Proportion at 1 Foot	Proportion > 4.5 feet	Proportion difference in stem count between 1 and 4.5 + feet tall
		1	2	3	4	4.5 +				
		TPA								
Oaks	Oak (Black)	23	3	2	0	1	30	2.2%	0%	−2%
	Oak (Chestnut)	273	15	5	2	3	298	26.3%	1%	−25%
	Oak (Northern Red)	241	66	27	14	9	356	23.2%	3%	−20%
	Oak (Scarlet)	0	1	2	1	0	4	0.0%	0%	0%
	Oak (White)	84	23	16	8	4	135	8.1%	1%	−7%
Main Competitors	Maple (Red)	154	47	31	23	52	307	14.8%	17%	2%
	Yellow-Poplar	25	11	18	10	46	110	2.4%	15%	13%
Other Hardwoods	American Basswood	9	14	5	3	46	78	0.9%	15%	14%
	American Beech	2	5	6	9	23	45	0.2%	8%	7%
	Ash (White)	94	80	30	14	14	233	9.1%	5%	−4%
	Birch (Yellow)	1	3	3	1	4	12	0.1%	1%	1%
	Cherry (Black)	5	6	4	5	3	23	0.5%	1%	1%
	Hickory	102	55	10	8	45	221	9.8%	15%	5%
	Maple (Sugar)	25	25	18	8	50	126	2.4%	17%	14%
	Total TPA	**1038**	**354**	**177**	**106**	**300**	**1978**	**100.0%**	**100%**	

*The last column, "Difference between 1 foot and 4.5 + feet proportions" highlights the increase or decrease of each species'

TPA proportion across all species and their respective recruitment to 4.5 + feet. This column helps explain the general trends of species recruitment across height classes. For example, oak advance regeneration exhibits a total 54% proportional decline in TPA at 1 foot compared to 4.5 + feet. In other words, oak advance regeneration TPA decreases as height increases

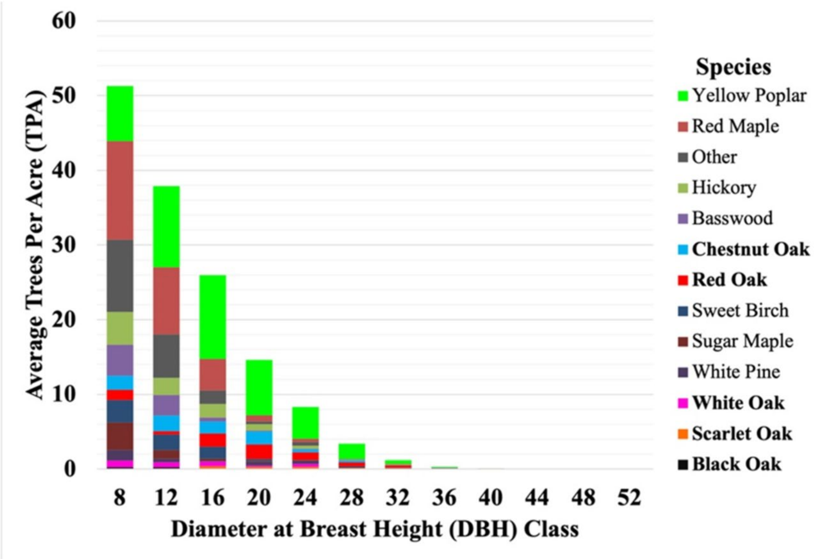

Fig. 2 Diameter distribution graph (4-inch class) representing the mid- and overstories as of August 2023. This figure shows the top 10 species by average total TPA plus the additional oak species outside of the top 10. The other category includes 17 species common to the area but not dominant in the overstory

Model Comparisons and Relationship to Environmental Variables

MaxEnt (bootstrap), MaxEnt (subsample), and Random Forest were run for each of the species and compared using the area under the curve (AUC). The best models for every species were the bootstrapped MaxEnt models. These models exhibited higher AUC measures than the MaxEnt subsampled and Random Forest models (Fig. 3). The model with the highest overall AUC is the white oak MaxEnt (bootstrap) model with an AUC of 0.915. In general, the MaxEnt models, bootstrap and subsample, performed better than the random forest models; all MaxEnt models had an AUC score greater than 0.7 except for MaxEnt (subsample) for the other oak category.

In general, across the different MaxEnt models and species, ecozones, soil type, or soil acidity (pH) were considered important variables (Table 2). The chestnut oak MaxEnt bootstrap model substituted ecozones for aspect (northness).

The test of variable importance (Fig. 4) included three iterations of the models to determine significance: one with all variables, one with a single variable, and one with all but one variable. For northern red oak, chestnut oak, and the category "other oak," ecozone was the most important variable; while for white oak soil type was the most important.

Variable response curves show how each environmental variable affects the MaxEnt prediction along the gradient or category of the individual variable (Table 2, appendix 2). All species exhibited greater suitability in higher pH but still acidic (pH <7) and well drained, loamy soils. The pH range within the study area was from 4.5—6.2 meaning the soils were generally acidic yet all oak species of interest

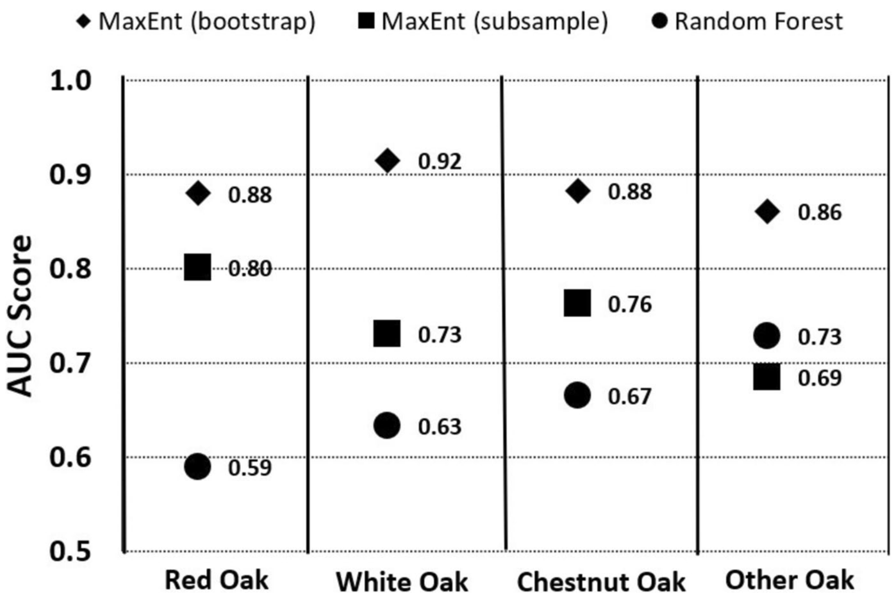

Fig. 3 Area under the curve (AUC) scores for the three compared models. The MaxEnt Bootstrap models exhibited the highest AUC across each species group while the Random Forest typically exhibited the lowest AUC across each species group. The exception is in the Other Oak species group where the Random Forest exhibited slightly improved AUC versus the MaxEnt Subsample replication model

show greater suitability as acidity approached the 5.3–5.4 pH level. Individual species suitability was variable among ecozones and soil types. For example, northern red oak has greater suitability in ecozone types which include northern hardwood, rich cove, and high elevation red oak (HERO), with any other ecozones providing lower suitability. Northern red oak tolerates soils of low pH although soils with higher pH are also suitable. Preferred soil types include Edneyville-Chestnut complex, basin, 15 to 30 percent slopes, stony (EdD), Cecil Sandy Loam, Thin Solum, 25 to 60 percent slopes (CuF), and Tunbridge-Woodstock fine sandy loams, very rocky, 3 to 8 percent slopes (TwB).

Discussion

We used data from the Nantahala National Forest to assess current oak regeneration and MaxEnt and Random Forest models to predict locations with high suitability for oak regeneration. This is important because securing advance regeneration is critical to the success of the regeneration process (Sander et al. 1984). Our results showed that oak advance regeneration exhibited decreasing TPA with increasing height across the study area. Similar results have been observed in other oak ecosystems (e.g. Beck 1970; McGee and Hooper 1970; Johnson 1992; Van Lear and Watt 1993; Aldrich et al. 2005; Dey 2014; Vickers et al. 2023 and citations within). Likewise, we predicted and mapped high-potential oak

Table 2 Top 3 variables for each species with percentage contributions toward model prediction and subsequent response curve interpretations for each species

Species	Top 3 Variables & Responses
N. Red Oak	- Ecozone (33%): Northern Hardwood, Rich Cove, High Elevation
	Red Oak (HERO)
	- pH (31%): 5.3 +
	- Soil type* (13%): EdD, CuF, TwB
White Oak	- Soil type* (48%): EdC, SrE, TrF
	- Ecozone (23%): Dry-Mesic Oak, HERO, Northern Hardwood
	- pH (15%): 5.4 +
Chestnut Oak	- Soil type* (42%): EvF, EdE, EdD
	- pH (26%): 5.4 +
	- Northness (13%): Northerly
Other Oak (Scarlet and Black)	- Ecozone (36%): Rich Cove, Dry-Mesic Oak, HERO
	- Soil type* (32%): EvE, EdE, EvD
	- pH (26%): 5.3 +

*Soil Types Include

CuF Cullasaja-Tuckasegee complex, 50 to 95 percent slopes, stony; EdC Edneyville-Chestnut complex, 8 to 15 percent slopes, stony; EdD Edneyville-Chestnut complex, high precipitation, 15 to 30 percent slopes, stony; EdE Edneyville-Chestnut complex, high precipitation, 30 to 50 percent slopes, stony; EvD Evard-Cowee complex, 15 to 30 percent slopes; EvE Evard-Cowee complex, 30 to 50 percent slopes; EvF Evard-Cowee complex, 50 to 95 percent slopes, stony; SrE Spivey-Santeetlah complex, 30 to 50 percent slopes, stony; TrF Trimont gravelly loam, 50 to 95 percent slopes, stony; TwB Tuckasegee-Whiteside complex, 2 to 8 percent slopes

regeneration locations with MaxEnt models that were validated and are robust with respect to their underlying assumptions. In general, the areas of priority for each species exhibit similar but different trends and generally align with the known silvics (Table 3) (Burns and Honkala 1990; Fei and Steiner 2008). This has implications for oak silviculture and stewardship which are currently facing the challenge of forest mesophication (Alexander et al. 2021).

Oak regeneration failures and limitations have been well documented (e.g. Vickers et al. 2023). The success of oak regeneration is highly dependent upon the abundance, size, and distribution of oak advance reproduction (Sander et al. 1984). As a result, scientists and natural resource managers are noting the importance of collecting height-class regeneration data to inform both regeneration and recruitment (Vickers et al. 2019). We observed 621 TPA of oak regeneration in the seedling class (1-foot seedlings) of northern red and chestnut oaks; greater numbers of regeneration was linked to the availability of suitable sites, allowing greater opportunities for advance regeneration to occur and accumulate (Larsen and Johnson 1998). Other studies have noted greater numbers of northern red oak regeneration

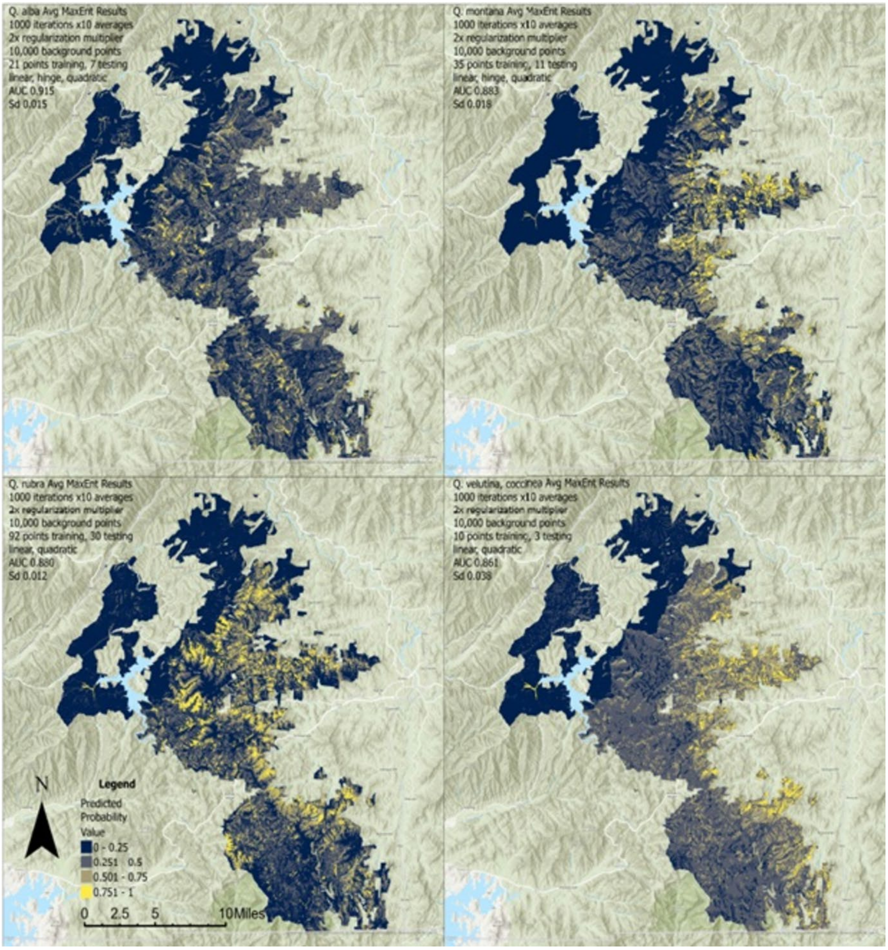

Fig. 4 MaxEnt (bootstrap replication) site suitability maps for each species group in the study area. Predicted probability of site suitability is symbolized in quarter sections from blue (low suitability) to yellow (high suitability)

and the link to mast years; northern red oak density was fivefold greater during a mast year in eastern New York compared to the previous year (Abrams and Johnson 2013). However, this will require conducting mast surveys as there is low potential for many oaks to use dendrochronology to infer masting records (Patterson et al. 2023). However, recent germinants or small oak seedlings have a very low probability of recruiting (Sander et al. 1984; Vickers et al. 2023). We also observed limited number of saplings (> 4.5 ft) which is likely due to high competition with mesophytic species (e.g. maples and yellow poplar) on richer sites (Larsen and Johnson 1998).

White oak regeneration, recruitment, and production for timber is increasingly being prioritized (e.g. Dhungel et al. 2024). Within our study, we observed that

Table 3 Summarized silvics for each oak species including findings from the variable response analysis. Silvics are summarized according to the Forest Service Silvics Manual (Burns and Honkala 1990). Variable interpretations from the MaxEnt Bootstrap model are prefixed with "MaxEnt"

Species	Silvics—Tolerance	Silvics—Soil Preference	MaxEnt—Soil Preference	MaxEnt—Soil Types*	MaxEnt—Soil pH	Silvics—Slope Position	Silvics—Elevation	Silvics—Aspect(s)	MaxEnt—Aspect(s)	MaxEnt—Ecozones	Peters et al. 2020—Adaptability and Infilling Potential
Q. *rubra* *(Red Oak)*	Mid -tolerant	Loam to silt–clay loam	Loamy-skeletal, Fine-loamy, Coarse-loamy	EdD, CuF, TwB	5.3 +	All—best on lower, middle	Up to 5,500 feet	All—best on northerly, easterly	All—best on northerly, easterly	Northern Hardwood, Rich Cove, High Elevation Red Oak (HERO)	High
Q. *alba* *(White Oak)*	Mid -tolerant	Ranges from gravely to loamy	Loamy-skeletal, Fine-loamy, Coarse-loamy	EdC, SrE, TrF	5.4 +	Lower, coves, ridges	All—usually below 4,500 feet	All—best on southerly, westerly	All—best on southerly, westerly	Dry-Mesic Oak, HERO, Northern Hardwood	High
Q. *montana* *(Chestnut Oak)*	Mid -tolerant	Sandy-loam, rocky, silt-loam	Fine-loamy, Coarse-loamy	EvF, EdE, EdD	5.4 +	Ridges, upper	1475 to 4600 feet	All—best on southerly, westerly	All—best on northerly, easterly	Rich Cove, Mesic Oak, Northern Hardwood	High
Q. *coccinea* *(Scarlet/Other Oak)*	Mid -tolerant/Intolerant	Many—Best on sand-gravely	Fine-loamy, Coarse-loamy	EvE, EdE, EvD	5.3 +	All—best on ridges, upper	Up to 5000 feet, common below 3000 feet	All—best on southerly	All—best on southerly	Rich Cove, Dry-Mesic Oak, HERO	Moderate

Table 3 (continued)

Species	Silvics—Tolerance	Silvics—Soil Preference	MaxEnt—Soil Preference	MaxEnt—Soil Types*	MaxEnt—Soil pH	Silvics—Slope Position	Silvics—Elevation	Silvics—Aspect(s)	MaxEnt—Aspect(s)	MaxEnt—Ecozones	Peters et al. 2020—Adaptability and Infilling Potential
Q. *velutina (Black/ Other Oak)*	Mid -tolerant	Silty-clay, loam also sandy	Fine-loamy, Coarse-loamy	EvE, EdE, EvD	5.3 +	All—best on lower, middle	Up to 4000 feet	All—best on northerly, easterly	All—best on easterly	Rich Cove, Dry-Mesic Oak, HERO	Moderate

* Soil Types Include

CuF Cullasaja-Tuckasegee complex, 50 to 95 percent slopes, stony; EdC Edneyville-Chestnut complex, 8 to 15 percent slopes, stony; EdD Edneyville-Chestnut complex, high precipitation, 15 to 30 percent slopes, stony; EdE Edneyville-Chestnut complex, high precipitation, 30 to 50 percent slopes, stony; EvD Evard-Cowee complex, 15 to 30 percent slopes; EvE Evard-Cowee complex, 30 to 50 percent slopes; EvF Evard-Cowee complex, 50 to 95 percent slopes, stony; SrE Spivey-Santeetlah complex, 30 to 50 percent slopes, stony; TrF Trimont gravelly loam, 50 to 95 percent slopes, stony; TwB Tuckasegee-Whiteside complex, 2 to 8 percent slopes white oaks are likely accumulating advance regeneration in the short term slightly better than the other oaks because they are more shade tolerant and are typically found among drier, less rich sites that allow less restricted accumulation due to fewer impacts of forest mesophication (Larsen and Johnson 1998). Additionally, on the drier sites, there are typically fewer competing species meaning oaks can occupy more growing space. Black and scarlet oaks are not effectively accumulating advance regeneration due to their relative shade intolerance and scarcity and lack of adequate canopy disturbance (Nowacki and Abrams 2008). Even if large advance reproduction is present, forest mesophication may severely limit its recruitment (Nowacki and Abrams 2008; Alexander et al. 2021).

This regeneration issue has many other co-drivers in addition to forest mesophication including stand age, herbivory, forest health threats (e.g. spongy moth (*Lymantria dispar)*, general oak decline due to invasive species (Potter and Conklin 2023) and the compounding impacts of climate change (Nowacki and Abrams 2008; Vickers et al. 2023). Though ungulate grazing (herbivory) heavily impacts some sites, the stands examined within this study were not heavily impacted by ungulate grazing (Author personal observation 2023).

MaxEnt was successful in modeling species-specific priority areas based on site suitability (Fig. 4). These highly suitable areas have been modeled from the presence of oak at any size class and not just regeneration. Thus, the resulting maps represent realized niche with probability for presence of oak in any stratum and/or environmental characteristics conducive for oak. This suggests that these areas of higher probability either already contain or are well suited for oak regeneration and/or generally for oak silvicultural treatments. Those areas with high suitability would have a higher likelihood of regenerating oaks using oak-focused silvicultural systems. Furthermore, most of the high suitability areas across all species are accessible upon the existing network of Forest Service roads with some exceptions in particularly remote or steep areas. Additionally, the most important site exploratory variables from the models included ecozones, soil pH, and soil type which align with the generalized silvics of oak seedling; they are moderately shade tolerant and slower growing, and rely upon their tolerances to drought and acidity to capture growing space in absence of disturbance.

Oak tolerance to acidity was captured in the models as soil pH was an important variable in modeling oak advance regeneration sites in both this study and Kabrick et al. (2014). However, a difference is that the relative training gain provided by soil available water capacity (AWC), as found to be a critical variable in the Kabrick et al. 2014 study, was not as important in these models. One reason why AWC was less important may be explained by the regional soil characteristics. These soils, on average, do not face water deficit, meaning that precipitation always exceeds evapotranspiration plus water stored in soil. Thus, drought tolerance is not as important when modeling for regeneration potential within the study area. Additional descriptive, categorical inputs such as soil type and ecozones which were used in this study but not by Kabrick et al. (2014) can be important variables to consider depending on the ecosystem.

Climate change is another factor that was considered in the potential impacts on site suitability across species. To address this consideration, the range of each species was checked for potential impacts under each emissions scenario in the USDA Climate Change Atlas (Table 3) (Peters et al. 2020). According to the Atlas, the range and resilience of each species will not be heavily impacted, if at all, under projected emissions scenarios based on an average of three global climate models (GCMs) under both moderate (RCP 4.5) and high (RCP 8.5) emissions scenarios (Peters et al. 2020). Peters et al. (2020) noted the species of interest are unlikely to be heavily impacted throughout the study area as their range limits extend far beyond the area. However, Novick et al. (2022) using a meta-analysis did observe differences among oak species and their range of growth and mortality under drought conditions with white oak growth least sensitive to drought conditions which is also supported through our modeling. There exist additional opportunities for science management partnerships to explore and test future projected changes in the seasonal water balance and how longer dry periods may result in greater water deficits and the potential for the accumulation of oak advanced regeneration.

These results help link the MaxEnt output to the published silvics and offer additional variables to consider when selecting species-specific suitable sites such as soil types and ecozones (Table 3). Currently, because ecozones are used as the primary ecological stewardship unit on the Nantahala National Forest, understanding possible site characteristic-species relationships is important for effective stewardship. While ecozones are valuable for landscape-scale understanding of expected forest cover-type, they do not consider soils as a covariate when determining ecozone sub-types (Simon 2011). Additionally, ecozone and other classification methods like habitat typing are assumed to be “stable” or “static” which may not be a valid assumption with climate change and invasive species (Cook 1995; Matthews et al. 2018) Thus, a main importance of this study is that the MaxEnt models utilize both ecozones and soil characteristics to model oak-species-specific site suitability which builds on the ecozones as an input and primary contributing variable in modeling landscape-level expected conditions.

Some limitations of our study are related to the models used. Maxent tends to be biased towards areas of site selection (generally, suitability tends to correlate with sampling intensity/spatial correlation of sampling sites) (Veloz 2009). This is because of the way Maxent selects a random set of points as background pseudo-absences (mismatch between randomly selected background points and nonrandomly sampled sites). Additionally, training and testing of the models included low sample sizes for the “other oak” category. A total of 12 sample plot points where seedlings were present, 9 for training and 3 for testing, despite MaxEnt being designed to handle low sample sizes, may produce misleading results due to the small number of training and testing points (Wisz et al. 2008). Subsequently, lower sample sizes increase the amount of area considered “low suitability,” whereas in reality these areas of low suitability simply were not sampled. In other words, if the field data collection points do not sample all possible environmental variable types, then these areas will be incorrectly classified as unsuitable when in reality many of the sites may or may not actually be suitable. For example, the northwest section of the study area for each species appears to be highly unsuitable. However, this was due to a lack of sample points within that section, and the associated unique soil types which were not represented in the field data sampling and data are needed to model suitability within the northwest section. Finally, independently-collected data for map validation could be used at a local scale (Smith et al. 2012; Gogol-Prokurat 2011), with the goal of these maps being iterative and updated with additional data to continue to inform and refine management on the Nantahala National Forest.

A few unanswered questions include why exactly the MaxEnt subsample and Random Forest models did not perform as well as the MaxEnt bootstrap models. One possible explanation for why the subsampled model did not perform as well is that subsampling reduces the number of presence-points used to train/test which may explain the drop in performance over the bootstrap model which does not reduce the number of presence-points used. Furthermore, this decrease in AUC may be attributed to potential spatial autocorrelation of the field sampled data points which is effectively captured in the bootstrapped model. In the subsampled model, the data points are effectively thinned potentially reducing the performance. One possible explanation for why the Random Forest model did not perform as well as the bootstrap model is that predicted site suitability for oak in the study area was not well approximated by sets of decision trees.

Management Implications

The maps developed in our study can be used to inform management decisions. Oak silviculture area priority could be given to map areas that exhibit high suitability for oak, followed by moderate suitability (Fig. 5). Areas of high or moderate suitability had either preexisting advance regeneration or a lack of advance regeneration but highly suitable site characteristics (e.g., soil type, acidity, etc.). Areas with the highest probability of presence/site suitability for a given species might be overlaid with other critical layers such as stand boundaries, wildlife refuges, management matrices, exclusion zones, forest roads, riparian corridors, land cover, topography, etc. to further improve maps of potential oak stewardship opportunity (i.e., by excluding areas where access and/or management activities are challenging or prohibited). These results are based on our data and, caution should be taken when extrapolating the relative importance of predictor variables to oak regeneration outside of our study area where environmental conditions may be different. Both the methods and the partnership approach could be replicated in different regions and with different species.

Silvicultural systems and early-intermediate treatments that benefit oak can influence species composition and recruitment, helping to target and favor oaks and alleviate the regeneration issue (Sander 1984). As demonstrated by Brose (2010), oak may persist, but its relative abundance compared to more competitive, mesophytic species often remains low. Beasley et al. (2022) further emphasize the complexity of interpreting oak regeneration success, highlighting that site productivity and treatment history greatly influence outcomes. Additionally, Schweitzer et al. (2019) provide relevant insights from thinning and repeated burning treatments. The burn shelterwood sequence (burning before for site preparation, then again after advance regeneration is established) can control fire sensitive species, while oaks can resprout from their robust rootstock, allowing oaks to regenerate with less competition (Vander Yacht et al. 2019). In other words, once adequate oak advance regeneration is

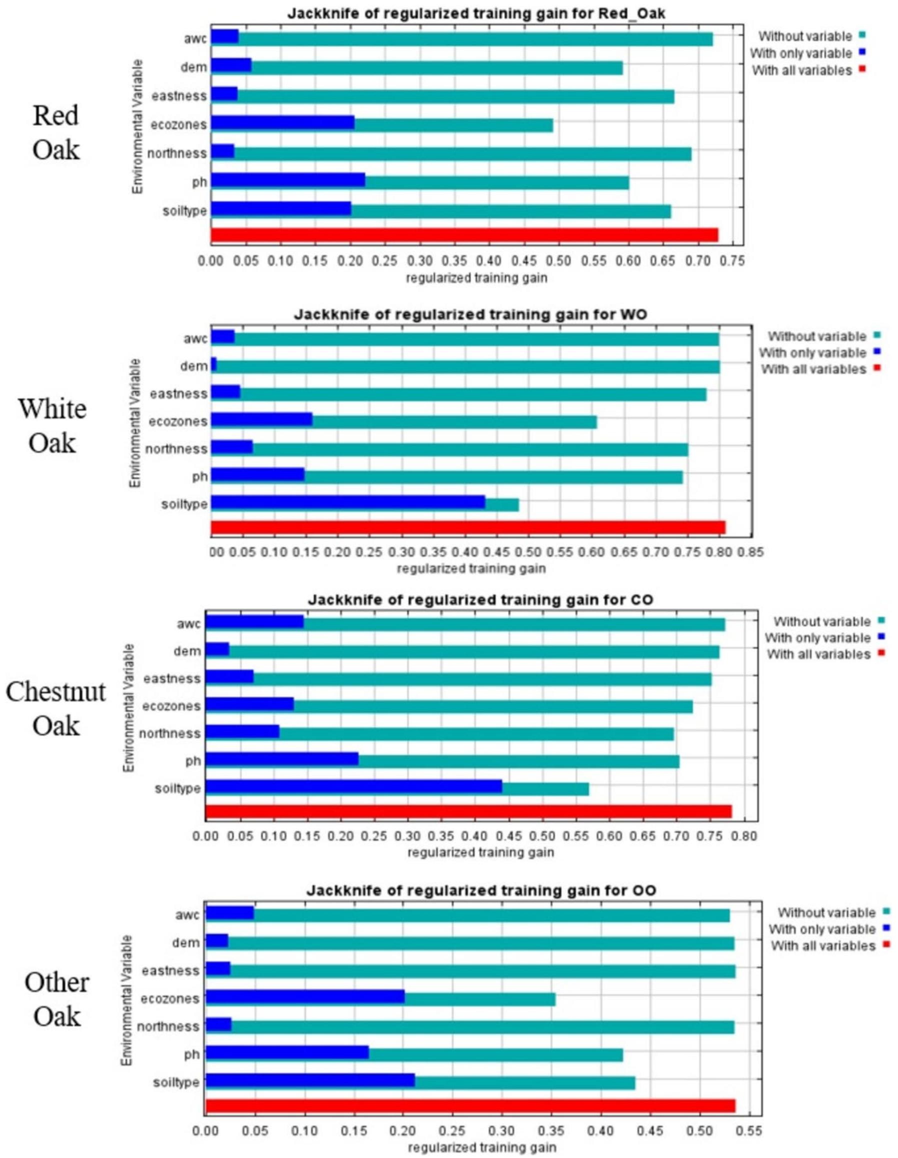

Fig. 5 Jackknife tests of variable importance for each species. The shorter blue bars for each variable indicate the model run with only that variable, while the longer teal bars indicate the model run excluding that variable. Longer blue bars with shorter teal bars indicate unique or important variables to the models

secured, canopy removals can be performed to allow recruitment. However, this burn, or series of burns, is usually coupled with intermediate mechanical or chemical control of non-desirable species, since intolerant species like yellow poplar and red maple grow quickly and can outcompete oak even with prescribed fire early in stand development (especially after many years of fire exclusion) (Nowacki and Abrams 2008; Alexander et al. 2021). Importantly, fire is not universally effective at reducing fire-sensitive oak competitors (Arthur et al. 1998, 2012). As such, there is a growing body of oak regeneration research that continues to communicate the nuance and variability associated with treatment effects across different forest types.

Intermediate treatments may prove most useful from the stand initiation through the stem exclusion phases (Edge et al. 2023). Adaptive methods such as variations on the shelterwood-burn system or other intermediate treatments such as herbicide stump/sprouting treatments for mesophytic species may also be effective (Dey et al. 2012, 2017). Thus, a more intensive approach could be considered to maximize potential success with limited resources. This intensive approach aligns well with the silvicultural definition provided by Achim et al. (2022), "a holistic scientific discipline that relies on many data points or dimensions of measurements throughout the forest lifecycle, allowing it to be highly dynamic and adaptive to rapidly changing social, financial and climatic constraints." Expanding on the heavy-removal, two-aged shelterwood cuts—typically applied uniformly across a stand, which has been implemented on the Nantahala National Forest for many years—to include shelterwood removals that contain variable density retentions for increasing diversity in light/shading conditions may prove to be initially challenging. Despite the potential challenges of adapting to more intensive stewardship regimes, site-prioritized stewardship can be a first step toward successfully reconnecting with effective regimes of the past, such as fire, while maintaining and restoring oak ecosystems.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s44392-025-00042-z.

Acknowledgements The findings and conclusions in this publication are those of the authors and should not be construed to represent any official U.S. Department of Agriculture or U.S. Government determination or policy.

Author Contributions This work represents Quentin Ikuta's thesis work at the University of Minnesota. Quentin was involved in all parts of the manuscript development. Marcella Windmuller-Campione served as Q. Ikuta's primary advisor and provided feedback throughout the process. Drs. John Zobel, Joe Knight, Jonathan Knight provided expertise on methods, data analysis, and review of manuscript development. Brandon Stephens was a core partner on the data collection methods and data collection and provided expertise on local knowledge and management opportunities and constraints. Nick Parrington provided review and critique throughout the data collection, analysis, and manuscript development.

Funding We appreciate the Department of Forest Resources and the College of Food, Agriculture, and Natural Resource Science at the University of Minnesota and Minnesota Agricultural Experiment Station (MAES Project MIN-42–108).

Data Availability The resulting raster layers that support the findings of this study are available from the corresponding author upon reasonable request. Please contact the corresponding author with your request. Additionally, the raster layers are openly available via an ArcGIS Online StoryMap at https://arcg.is/1iSvaL1.

Declarations

Competing interests The authors declare no competing interests.

References

Achim, A., G. Moreau, N. C. Coops, J. N. Axelson, J. Barrette, S. Bédard, K. E. Byrne, J. Caspersen, A. R. Dick, L. D'Orangeville, G. Drolet, B. N. I. Eskelson, C. N. Filipescu, M. Flamand-Hubert, T. R. H. Goodbody, V. C. Griess, S. H. Hagerman, K. Keys, B. Lafleur, M. M. Girona, D. M. Morris, C. A. Nock, B. D. Pinno, P. Raymond, P. Roy, R. Schneider, M. Soucy, B. Stewart, J. D. Sylvain, A. R. Taylor, E. Thiffault, N. Thiffault, U. Vepakomma, and J. C. White. 2022. The changing culture of silviculture. *Forestry: an International Journal of Forest Research* 95 (2): 143–152. https://doi.org/10.1093/forestry/cpab047.

Abrams, M. D. 1992. Fire and the Development of Oak Forests. *BioScience* 42 (5): 346–353. https://doi.org/10.2307/1311781.

Abrams, M. D., and S. E. Johnson. 2013. The impacts of mast year and prescribed fires on tree regeneration in oak forests at the Mohonk Preserve, southeastern New York, USA. *Natural Areas Journal* 33 (4): 427–434.

Aldrich, P. R., G. R. Parker, J. Romero-Severson, and C. H. Michler. 2005. Confirmation of oak recruitment failure in Indiana old-growth forest: 75 years of data. *Forest Science* 51 (5): 406–416.

Alexander, H. D., C. Siegert, J. S. Brewer, J. Kreye, M. A. Lashley, J. K. McDaniel, A. K. Paulson, H. J. Renninger, and J. M. Varner. 2021. Mesophication of oak landscapes: Evidence, knowledge gaps, and future research. *BioScience* 71 (5): 531–542. https://doi.org/10.1093/biosci/biaa169.

Arthur, M. A., R. D. Paratley, and B. A. Blankenship. 1998. Single and repeated fires affect survival and regeneration of woody and herbaceous species in an oak–pine forest. *Journal of the Torrey Botanical Society* 125 (3): 225–236. https://doi.org/10.2307/2997223.

Arthur, M. A., Alexander, H. D., Dey, D. C., Schweitzer, C. J., & Loftis, D. L. (2012). Fire in the forest: A synthesis of fire ecology and fire effects research in the southern Appalachian region. USDA Forest Service General Technical Report SRS-173. Asheville, NC: Southern Research Station. https://doi.org/10.2737/SRS-GTR-173

Baumflek, M., T. Cabe, J. Schelhas, and M. Dunlavey. 2022. Managing forests for culturally significant plants in traditional Cherokee homelands: Emerging platforms. *International Forestry Review* 24 (3): 298–314. https://doi.org/10.1505/146554822835941841.

Beasley, R. R., D. C. Dey, C. J. Schweitzer, and D. L. Loftis. 2022. Oak regeneration in the Central and Southern U.S.: A regional synthesis. *Forest Ecology and Management* 503:119781. https://doi.org/10.1016/j.foreco.2021.119781.

Beck, D. E. 1970. *Effect of competition on survival and height growth of red oak seedlings*. USDA Forest Service Research Paper SE-56. Asheville, NC: Southeastern Forest Experiment Station.

Brose, P. H. 2010. Long-term effects of single prescribed fires on hardwood regeneration in oak-dominated forests of eastern North America. *Forest Ecology and Management* 260 (5): 703–711. https://doi.org/10.1016/j.foreco.2010.05.037.

Brose, P. H., and T. F. Hutchinson. 2019. *The fundamentals of release burning in mixed oak forests with emphasis on the shelterwood-burn technique.* Vol. 237, 79–88. e-Gen. Tech. Rep. SRS-237. Asheville: USDA Forest Service, Southern Research Station.

Burns, R., and B. Honkala. 1990. Silvics of North America: 1. Conifers; 2. Hardwoods. *Agriculture Handbook* 654 (2): 877. Washington: USDA Forest Service. https://www.srs.fs.usda.gov/pubs/misc/ag_654/table_of_contents.htm. Accessed June 2023.

Cavender-Bares, J. 2016. Diversity, Distribution and Ecosystem Services of the North American Oaks. *International Oaks* 27:37–48.

Cook, R. R. 1995. The relationship between nested subsets, habitat subdivision, and species diversity. *Oecologia* 101:204–210.

Crocker, E., K. Gurung, J. Calvert, C. D. Nelson, and J. Yang. 2023. Integrating GIS, remote sensing, and citizen science to map oak decline risk across the Daniel Boone National Forest. *Remote Sensing* 15 (9): 2250.

Davis, M. 1983. Quaternary History of Deciduous Forests of Eastern North America and Europe. *Annals of the Missouri Botanical Garden* 70 (3): 550–563. https://doi.org/10.2307/2992086.

Delcourt, P. A., and H. R. Delcourt. 2004. *Prehistoric Native Americans and Ecological Change: Human Ecosystems in Eastern North America since the Pleistocene*. Cambridge: Cambridge University Press.

Dey, D. C. 2014. Sustaining Oak Forests in Eastern North America: Regeneration and Recruitment, the Pillars of Sustainability. *Forest Science* 60 (5): 926–942. https://doi.org/10.5849/forsci.13-114.

Dey, D. C., E. S. Gardiner, C. J. Schweitzer, et al. 2012. Underplanting to sustain future stocking of oak (Quercus) in temperate deciduous forests. *New Forests* 43:955–978. https://doi.org/10.1007/s11056-012-9330-z.

Dey, D. C., John M. Kabrick, and Callie J. Schweitzer. 2017. Silviculture to Restore Oak Savannas and Woodlands. *Journal of Forestry* 115 (3): 202–211. https://doi.org/10.5849/jof.15-152.

Dhungel, G., T. O. Ochuodho, J. M. Lhotka, J. W. Stringer, and K. Poudel. 2024. Sustainability of white oak (Quercus alba) timber supply in Kentucky. *Journal of Forestry* 122 (1): 79–90.

Edge, G., Hutnik, B. (Hosts), Stringer, J. W. (Guest). 2023. White oak, whiskey, and wildlife (No. 410) [Audio podcast episode]. In *Silvicast*. University of Wisconsin - Stevens Point. https://www3.uwsp.edu/cnr-ap/WFC/Pages/Research-Development/white-oak-initiative.aspx. Accessed May 2023.

ESRI. 2023. ArcGIS pro (Version 3.1). Redlands: Environmental Systems Research Institute.

Fei, S., and K. C. Steiner. 2008. Relationships between advance oak regeneration and biotic and abiotic factors. *Tree Physiology* 28 (7): 1111–1119.

Finger, J. R. 1991. The impact of removal on the North Carolina Cherokees. In *Cherokee removal: Before and after*, ed. W. L. Anderson, 96–111. Athens, GA: University of Georgia Press.

Gogol-Prokurat, M. 2011. Predicting habitat suitability for rare plants at local spatial scales using a species distribution model. *Ecological Applications* 21 (1): 33–47.

Haavik, L. J., K. J. Dodds, and J. D. Allison. 2015. Do native insects and associated fungi limit non-native woodwasp, Sirex noctilio, survival in a newly invaded environment? *PLoS One* 10 (10): e0138516.

Hanberry, B. B., and G. J. Nowacki. 2016. Oaks were the historical foundation genus of the east-central United States. *Quaternary Science Reviews* 145:94–103. https://doi.org/10.1016/j.quascirev.2016.05.037.

Harris, L. B., C. W. Woodall, and A. W. D'Amato. 2022. Increasing the utility of tree regeneration inventories: Linking seedling abundance to sapling recruitment. *Ecological Indicators* 145:109654. https://doi.org/10.1016/j.ecolind.2022.109654.

Jacobs, D. F., H. J. Dalgleish, and C. D. Nelson. 2013. A conceptual framework for restoration of threatened plants: The effective model of American chestnut (Castanea dentata) reintroduction. *New Phytologist* 197 (2): 378–393. https://doi.org/10.1111/nph.12020.

Jaynes, E. T. 1991. Notes on present status and future prospects. In *Maximum entropy and bayesian methods, 1990*. 1–13. Laramie.

Johnson, P. S. 1992. *Perspectives on the ecology and silviculture of oak-dominated forests in the central and eastern states*. USDA Forest Service General Technical Report NC-153.

Kabrick, J. M., J. L. Villwock, D. C. Dey, T. L. Keyser, and D. R. Larsen. 2014. Modeling and Mapping Oak Advance Reproduction Density Using Soil and Site Variables. *Forest Science* 60 (6): 1107–1117. https://doi.org/10.5849/forsci.13-006.

Keasberry, A. M., J. L. Hart, D. C. Dey, and C. J. Schweitzer. 2016. Spatial patterns of irradiance and advanced reproduction along a canopy disturbance severity gradient in an upland hardwood stand. *Forests* 7 (4): 73.

Kuhlman, G. E. 1978. The devastation of American Chestnut by Blight. In *American Chestnut Proceedings*. USDA Forest Service, Southeastern Forest Experiment Station. https://rngr.net/publications/chestnut/1978/the-devastation-of-american-chestnut-by-blight. Accessed June 2023.

Larsen, D. R., and P. S. Johnson. 1998. Linking the ecology of natural oak regeneration to silviculture. *Forest Ecology and Management* 106 (1): 1–7. https://doi.org/10.1016/S0378-1127(97)00233-8.

Loftis, D. L. 2004. *Upland oak regeneration and management. Upland oak ecology symposium: history, current conditions, and sustainability*. Gen. Tech. Rep. SRS–73. Asheville: U.S. Department of Agriculture, Forest Service, Southern Research Station.

Matthews, S. N., L. R. Iverson, M. P. Peters, and A. M. Prasad. 2018. *Assessing potential climate change pressures across the conterminous United States: Mapping plant hardiness zones, heat zones, growing degree days, and cumulative drought severity throughout this century.* 31 (9): 1–31. RMAP-NRS-9. Newtown Square: US Department of Agriculture, Forest Service, Northern Research Station.

McGee, C. E., and R. M. Hooper. 1970. *Regeneration after clearcutting in the southern Appalachians*. USDA Forest Service Research Paper SE-80. Asheville: Southeastern Forest Experiment Station.

Mcshea, W. J., W. M. Healy, P. Devers, T. Fearer, F. H. Koch, D. Stauffer, and J. Waldon. 2007. Forestry Matters: Decline of Oaks Will Impact Wildlife in Hardwood Forests. *The Journal of Wildlife Management* 71 (5): 1717–1728. https://doi.org/10.2193/2006-169.

McWilliams, W. H., J. A. Westfall, P. H. Brose, D. C. Dey, M. Hatfield, K. Johnson, K. M. Laustsen, S. L. Lehman, R. S. Morin, M. D. Nelson, and T. E. Ristau. 2015. *A regeneration indicator for forest inventory and analysis: History, sampling, estimation, analytics, and potential use in the Midwest and Northeast United States*. Vol. 148, 1–74. Gen. Tech. Rep. NRS-148. Newtown Square: US Department of Agriculture, Forest Service, Northern Research Station.

Novick, K., I. Jo, L. D'Orangeville, M. Benson, T. F. Au, M. Barnes, S. Denham, S. Fei, K. Heilman, T. Hwang, T. Keyser, J. Maxwell, C. Miniat, J. McLachlan, N. Pederson, L. Wang, J. D. Wood, and R. P. Phillips. 2022. The Drought Response of Eastern US Oaks in the Context of Their Declining Abundance. *BioScience* 72 (4): 333–346. https://doi.org/10.1093/biosci/biab135.

Nowacki, G. J., and M. D. Abrams. 2008. The Demise of Fire and "Mesophication" of Forests in the Eastern United States. *BioScience* 58 (2): 123–138. https://doi.org/10.1641/B580207.

Patterson, C. P., Z. J. Hackworth, J. M. Lhotka, and J. W. Stringer. 2022. Light and regeneration patterns following silvicultural gap establishment in Quercus dominated stands of the northern Cumberland Plateau, USA. *Forest Ecology and Management* 505:119871.

Patterson, T. W., C. H. Greenberg, and A. Hacket-Pain. 2023. Acorn production, climate, and tree-ring growth of five oak species in southern Appalachian forests. *Forest Ecology and Management* 546:121310.

Peters, M. P., A. M. Prasad, S. N. Matthews, and L. R. Iverson. 2020. *Climate change tree atlas, version 4*. Delaware: U.S. Forest Service, Northern Research Station and Northern Institute of Applied Climate Science. https://www.nrs.fs.fed.us/atlas.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2005. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190 (3–4): 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026.

Phillips, S. J., and M. Dudík. 2008. Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography* 31 (2): 161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x.

Potter, K. M., and B. L. Conkling. 2023. Rapid white oak mortality: Patterns, potential causes, and management implications. *Forest Ecology and Management* 540:121073. https://doi.org/10.1016/j.foreco.2023.121073.

Prentice, I. C., P. J. Bartlein, and T. Webb. 1991. Vegetation and Climate Change in Eastern North America Since the Last Glacial Maximum. *Ecology* 72 (6): 2038–2056. https://doi.org/10.2307/1941558.

Qi, Y. 2012. Random Forest for Bioinformatics. In *Ensemble Machine Learning*, ed. C. Zhang and Y. Ma. New York, NY: Springer. https://doi.org/10.1007/978-1-4419-9326-7_11.

Rodríguez-Calcerrada, J., M. Li, R. López, F. J. Cano, and L. Gil. 2017. The role of stomatal control in preventing xylem embolism in oaks during drought is modulated by stomatal sensitivity to vapour pressure deficit and soil water availability. *Tree Physiology* 37 (4): 515–527. https://doi.org/10.1093/treephys/tpw124.

Sander, I. L. 1971. Height growth of new oak sprouts depends on size of advance reproduction. *Journal of Forestry* 69:809–811.

Sander, I. L. 1984. *Evaluating oak advance reproduction in the Missouri Ozarks*. Vol. 251. US Department of Agriculture, Forest Service, North Central Forest Experiment Station.

Sander, I. L., and F. B. Clark. 1971. *Reproduction of upland hardwood forests in the Central States*, Agric. Handb. 405. [Place of publication unknown]: USDA Forest Service.

Sander, I. L., P. S. Johnson, and R. F. Watt. 1976. *A guide for evaluating the adequacy of oak advance reproduction* (No. 23). US Department of Agriculture.

Sander, I. L., Johnson, P. S., and R. Rogers. 1984. Evaluating oak advance reproduction in the Missouri Ozarks. Res. Pap. NC 251. St. Paul: USDA Forest Service, North Central Forest Experiment Station.

Schweitzer, C. J., Dey, D. C., & Iverson, L. R. (2019). Impacts of repeated prescribed fire and thinning on composition, structure, and oak regeneration in upland hardwood forests. In Proceedings of the 20th Central Hardwood Forest Conference. USDA Forest Service, Northern Research Station, GTR-NRS-P-193, pp. 183–199. https://doi.org/10.2737/NRS-GTR-P-193-paper22

Simon, S. A. 2011. *Ecological Zones in the Southern Blue Ridge: 3rd Approximation*. Asheville, North Carolina: Ecological Modeling and Fire Ecology Inc.

Smith, A., B. Page, K. Duffy, and R. Slotow. 2012. Using Maximum Entropy modeling to predict the potential distributions of large trees for conservation planning. *Ecosphere* 3 (6): 1–21.

Stambaugh, M. C., J. M. Varner, R. F. Noss, D. C. Dey, N. L. Christensen, R. F. Baldwin, R. P. Guyette, B. B. Hanberry, C. A. Harper, S. G. Lindblom, and T. A. Waldrop. 2015. Clarifying the role of fire in the deciduous forests of eastern North America: Reply to Matlack: Fire in Deciduous Forests. *Conservation Biology* 29 (3): 942–946. https://doi.org/10.1111/cobi.12473.

USDA Forest Service. 2023. Nantahala and Pisgah national forests final land management plan. Southern Region, National Forests in North Carolina. https://www.fs.usda.gov/detail/nfsnc/landmanagement/planning/?cid=fseprd972970. Accessed Aug 2023.

USDA Forest Service. 2014. Region 8 common stand exam field guide. USDA Forest Service R8FG-1.

USDA NRCS. 2023. Natural resources conservation service, United States department of agriculture. Soil Survey Geographic (SSURGO) Database. https://sdmdataaccess.sc.egov.usda.gov. Accessed Aug 2023.

Van Lear, D. H., and J. M. Watt. 1993. The role of fire in oak regeneration. In *Oak regeneration: Serious problems, practical recommendations*, eds. D. L. Loftis, and C. E. McGee, 66–70. USDA Forest Service General Technical Report SE-84.

Vander Yacht, A. L., P. D. Keyser, S. A. Barrioz, C. Kwit, M. C. Stambaugh, W. K. Clatterbuck, and D. M. Simon. 2019. Reversing Mesophication Effects on Understory Woody Vegetation in Mid-Southern Oak Forests. *Forest Science* 65 (3): 289–303. https://doi.org/10.1093/forsci/fxy053.

Veloz, S. D. 2009. Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *Journal of Biogeography* 36 (12): 2290–2299.

Vickers, L. A., W. H. McWilliams, B. O. Knapp, A. W. D'Amato, D. C. Dey, Y. L. Dickinson, J. M. Kabrick, L. S. Kenefic, C. C. Kern, D. R. Larsen, and A. A. Royo. 2019. Are current seedling demographics poised to regenerate northern US forests? *Journal of Forestry* 117 (6): 592–612.

Vickers, L. A., B. O. Knapp, D. C. Dey, and L. S. Pile Knapp. 2023. Do forest health threats affect upland oak regeneration and recruitment? Advance reproduction is a key co-morbidity. *Forest Ecosystems* 10:100152. https://doi.org/10.1016/j.fecs.2023.100152.

Wang, G., and H. Huifeng. 2015. The replacements of American chestnut. In *Proceedings of the 17th biennial Southern silvicultural research conference*, e–Gen. Tech. Rep. SRS–203. Asheville: USDA Forest Service, Southern Research Station. https://www.srs.fs.usda.gov/pubs/gtr/gtr_srs203/gtr_srs203-103.pdf. Accessed July 2023.

Wisz, M. S., R. J. Hijmans, J. Li, A. T. Peterson, C. H. Graham, and A. Guisan. 2008. Effects of sample size on the performance of species distribution models. *Diversity and Distributions* 14 (5): 763–773. https://doi.org/10.1111/j.1472-4642.2008.00482.x.

Yarnell, S. 1998. The Southern Appalachians: A history of the landscape, Gen. Tech. Rep. SRS-18, p. 52. Asheville: USDA Forest Service, Southern Research Station. https://doi.org/10.2737/SRS-GTR-18.