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ScienceDirect
Forest Ecology and Management 252 (2007) 201–207
Forest Ecology and Management
www.elsevier.com/locate/foreco

Spatial habitat modeling of American chestnut at Mammoth Cave National Park

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Received 22 February 2007; received in revised form 15 June 2007; accepted 19 June 2007

Abstract

The American chestnut (*Castanea dentata*) was historically one of the most important trees in forests of the eastern U.S., but it was severely decimated by chestnut blight (*Cryphonectria parasitica*). Efforts are underway by The American Chestnut Foundation (TACF) and other organizations to develop blight-resistant chestnut trees for restoration. To ensure local adaptability, a variety of American chestnut trees with a broad genetic base is required in the breeding programs, but finding rare flowering American chestnut trees to incorporate into these breeding programs is often difficult. In this study, we used ecological niche factor analysis (ENFA) to determine the site affinities of surviving American chestnut trees and to produce a chestnut habitat suitability map for Mammoth Cave National Park (MCNP). Chestnut sprouts were found to be strongly associated with geological formation, slope steepness, elevation, and topographic position. Chestnuts were nearly absent on previously cultivated or pastured lands. The model provides information for efficiently locating chestnut trees, which could be used in breeding programs, and identifying potential restoration sites within the park and in other areas with similar site conditions.

Keywords: American chestnut; Chestnut blight; GIS; Ecological niche factor analysis (ENFA)

1. Introduction

American chestnut (*Castanea dentata*) was historically one of the most ecologically and economically important trees in the eastern U.S. (MacDonald, 1978). It was eliminated from the overstory by the chestnut blight fungus (*Cryphonectria parasitica*) during the early 20th century (McCormick and Platt, 1980). Although the trees often sprout repeatedly when the main stem dies from blight, most of the billions of pre-blight chestnut trees and their sprouts have died. Currently, few chestnut trees in Kentucky and Tennessee exceed a diameter of 10 cm and reach the canopy (Schibig et al., 2005). The loss of this historically dominant and important forest species is one of the most important events in the history of the eastern North American forest (McEwan et al., 2005).

Several approaches to developing blight-resistant American chestnut trees are underway. The most notable are The American Chestnut Foundation's (TACF) backcross breeding program (Burnham et al., 1986; Hebard, 2002, 2005), American Chestnut Cooperators' Foundation's (ACCF) intercrossing of pure American chestnut trees (Griffin et al., 2005), the transgenic approach (Powell et al., 2005), and inoculating native American chestnut trees with hypovirulent strains of *Cryphonectria parasitica* (MacDonald and Double, 2005). Throughout the eastern U.S., TACF volunteers have been searching for rare flowering American chestnut trees to be used in their backcross breeding program. To ensure local adaptability, using American chestnut trees with a broad genetic base is required (Alexander et al., 2004), but finding flowering American chestnut trees to be used in the breeding programs is difficult. Predictive models for probable American chestnut sites would greatly facilitate the location of new chestnut specimens. In recent years, predictive modeling of species distribution has become an increasingly important tool to address various issues in ecology, biogeography, evolution, conservation biology, and climate change (Guisan and Thuiller, 2005). Our primary objectives were to develop and test a spatial modeling approach for determining American chestnut site affinities in Mammoth Cave National Park (MCNP) which would allow us to efficiently locate new chestnut specimens,

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doi:10.1016/j.foreco.2007.06.036

Table 1
Variables used in spatial modeling of American chestnut habitat at Mammoth Cave National Park, Kentucky, USA

Variables	Resolution (m)	Description
Curvature	10	Convexity/concavity based on DEM
Elevation	10	Elevation from DEM
Topographic position index	10	Topographic position based on DEM (Jenness (2006))
Slope	10	Slope steepness (degree)
Topographic relative moisture index	10	Dryness–wetness index based on DEM (Parker (1982))
Land use history	–	Land use history (based on 1936 vegetation map)
Geology	–	General bedrock formation (1:24,000 scale)

and to identify suitable sites for chestnut restoration within the park and in other areas with similar site conditions.

1.1. Study area

Mammoth Cave National Park was acquired in 1926 by the federal government and was fully established in 1941. The park has an area of 21,396 ha that is located on the eastern edge of the Shawnee section of the Interior Low Plateau Province (Fenneman, 1938) in west-central Kentucky. The Green River bisects the park into northern and southern portions. The ridges and upper slopes of the park are capped with sandstone which produces soils that are usually acidic, sandy, and rocky. Sandstone boulders commonly outcrop on the uppermost slopes. The lower slopes and ravines are usually capped with limestone, and many caves and sinkholes occur in this karstic landscape. The area has a continental climate characterized by mild winters and hot humid summers, and lacks a distinct dry season (McEwan et al., 2005). Average monthly temperature ranges from 1.3 °C in January to 24.8 °C in July and average monthly precipitation ranges from 8.8 cm in October to 13.3 cm in May (1971–2000 data; National Oceanic and Atmospheric Administration 2002).

American chestnut is known to have been a component of forests in and around MCNP based on the documents recorded by European explorers (Hussey, 1884) and witness tree data (McEwan et al., 2005). Chestnut blight severely decimated chestnut trees in MCNP during the 1930s and 1940s, and by the late 1940s nearly all the large chestnut trees were dead (Schibig et al., 2005).

2. Methods

2.1. Inventory

American chestnut sprouts were inventoried in MCNP from 2003 to 2006 over diverse landscapes during the summer when chestnut sprouts were more easily identifiable. The "Big Woods," a chestnut-rich old growth forest (120 ha) in the northeastern section of the park, was thoroughly sampled. Elsewhere, we searched for chestnut specimens in most sections of the park that were reasonably accessible (usually within a hiking distance of 2 km from a road). For each specimen, geographic coordinates were recorded with a global positioning system (GPS) unit. Stem diameter at 1.4 m above ground (dbh) was measured and height was visually estimated. Signs of blight and flowering status were also recorded. If stems were in a cluster (clone), only the largest stem was measured. Field notes on slope steepness and position were recorded. Slope steepness was recorded in three categories (very steep, moderately steep, and relatively gentle slope), and slope position was also recorded in three categories (upper, mid, and lower slope).

2.2. Spatial modeling

Seven variables were used in our spatial model (Table 1). Slope curvature, elevation, topographic position index (TPI), slope steepness, and topographic relative moisture index modified (TRMIM) were derived from a 10 m resolution digital elevation model (DEM). Slope curvature, elevation, and slope steepness were calculated using tools in ArcGIS 9.2 (ESRI, Redlands, CA, U.S.), TPI was calculated in ArcView 3.2 (ESRI, Redlands, CA, U.S.) using an extension developed by Jenness (2006), and TRMIM was calculated in Arc Grid (ESRI, Redlands, CA, U.S.) based on Parker's (1982) method.

To validate the above analytically derived information, two DEM-based variables (TPI and degree of slope; numerical) were compared with two field-observed variables (slope position and slope steepness; categorical). Average TPI for the three field recorded slope position categories were significantly different from each other (upper slope 13.13 ± 0.54, mid slope -0.26 ± 0.43, and lower slope -6.96 ± 0.30), and average degree of slope for the three slope steepness categories were also significantly different from each other (very steep 45.6 ± 0.7, moderate steep 36.8 ± 0.4, and relatively gentle slope 27.3 ± 0.3). Although the variables were not directly comparable (numerical versus categorical and local scale versus landscape scale), they generally agreed with each other.

Geological formation obtained from the Kentucky Geological Survey was also used in the model. Geological formations were classified into sandstone and limestone families, and Euclidean distance from the boundary of the sandstone and limestone formations was then calculated and used in the spatial model. Land use history was reconstructed based on the 1936 vegetation map provided by MCNP. Based upon the park's history, we classified the non-restocking and restocking categories as historical agricultural areas (previously cultivated fields and pastures) and the other forest types as non-agricultural areas. Because land use history is a human driven factor, we did not include it in the habitat modeling; however, it was incorporated as a mask to build a map to locate surviving American chestnut sprouts.

In this study, only locations that had American chestnut were recorded. As summarized by Hirzel et al. (2006), two main approaches have been developed in modeling taxonomic distributions across landscapes with presence-only data. The first approach is to generate pseudo-absences and then apply the standard presence/absence techniques, and the second approach is to assess how much the model predictions differ from random expectation [ecological niche factor analysis (ENFA)]. ENFA considers the density of points within subenvelopes of data and is, therefore, an improvement on presence-only approaches (Pearce and Boyce, 2005). In this study, ENFA was used to compute the habitat suitability map for American chestnut in Biomapper 3.1 (Hirzel et al., 2004). ENFA is designed to compute the factors (like the Principal Components Analysis) that explain the major part of the ecological distribution of the species. The extracted factors are uncorrelated but have biological signification: the first factor is the marginality factor, which describes how far the species optimum is from the mean habitat in the study area. The specialisation factors are sorted by decreasing amount of explained variance; they describe how specialised the species is by reference to the available range of habitat in the study area (Hirzel et al., 2004).

Data partitioning was applied to all the 2156 located American chestnut sprouts as a validation technique (Fielding and Bell, 1997). Two thirds of the specimens (1437) were used in Biomapper to build the spatial model, and one third (719) were used to validate the model. Distributions of the variables that were recognized by ENFA to have strong association with chestnut were further compared between chestnut locations and random locations (1437 spatially random points generated in GIS) in the study area. Biomapper only provides a range of habitat suitability (0–100) and does not provide a threshold of favorable habitat. We used the maximum cumulative frequencies difference method (Browning et al., 2005, Thompson et al., 2006) to estimate the threshold. We first obtained habitat suitability values for both the 1437 chestnut locations and 1437 random locations, calculated the cumulative frequencies of locations by habitat suitability, and then located the maximum difference between the two cumulative frequencies to define the threshold.

The chestnut habitat suitability model derived from ENFA was then evaluated using two approaches. The first approach was a cross-validation conducted in Biomapper 3.1. The study area was partitioned into 10 sub-regions to validate the model. To minimize the spatial-autocorrelation among the partitions, locations of the partitions were randomly assigned. In the second approach, we used the 719 trees that were not included in the habitat modeling process to test the robustness of the model derived from ENFA. Percentages of trees located in each of the probability zones in the habitat model were then calculated.

3. Results

3.1. Chestnut population characteristics

Of the chestnut specimens recorded at MCNP, 86.9% had a dbh less than 2.5 cm; 9.0% had a dbh of 2.5–5.0 cm; 3.4% had a dbh of 5.0–10.0 cm; only 0.7% had a dbh greater than 10 cm. The maximum diameter recorded for a chestnut tree in the park was 17.8 cm. In terms of height, 90.6% of the chestnut trees were less than 3 m, 7.3% were 3–6 m, and only 2.1% were taller than 6 m. The tallest chestnut tree had a height of 18.3 m. Of the 2156 chestnut specimens observed at MCNP, only 1 was flowering, and only 2% of the stems were blighted.

3.2. Site affinity

Land use history had a strong influence on the current distribution of chestnut sprouts. Based on the 1936 vegetation map, about 41% of the area (8057 ha) was classified as abandoned agricultural land. A total of 89% of the chestnut sprouts at MCNP were located within areas that were classified as non-agricultural land. The remaining 11% of the chestnuts were located within a 10 m buffer around non-agricultural land. Thus, all surviving chestnuts were located in or close to the edge of historically non-agricultural land.

Based on ENFA, chestnut distribution was strongly associated with elevation, geological formation, slope steepness, and TPI (Table 2). The three factors derived from ENFA explained 98.3% of the total variance and 96.6% of specialisation. Factor 1 which explained most of the variance (78.8%) was mainly due to the Euclidean distance from the edge of sandstone and limestone formations. Factor 2 was mainly due to slope steepness and elevation, while Factor 3 was mainly contributed by elevation and TPI. Geological formation, as expressed as the Euclidean distance, had a much stronger association with the distribution of chestnut than the other variables.

Different distribution patterns by variables derived from chestnut locations and random locations further confirmed the strong site affinities of chestnut sprouts (Fig. 1). American chestnut sprouts were more frequently located near the borderline of sandstone and limestone formations, with a buffer zone of 40 m on each side of the boundary (Fig. 1a). Chestnut sprouts were distributed in a relative narrow elevation range of 200–240 m (Fig. 1b). Chestnut sprouts were also more frequently located on steeper slopes between 25° and 40° (Fig. 1c). The distribution patterns between chestnut locations

Table 2
Score matrix of the first three factors derived from ecological niche factor analysis (ENFA) and the percentage of variance explained by each factor

Variables	Factors		
	1	2	3
Curvature	0.008	0.010	−0.012
Elevation	0.024	0.614	−0.596
EucDist[a]	0.997	−0.056	−0.255
Slope	0.056	0.776	−0.251
TPI	−0.041	0.092	−0.513
TRMIM	−0.015	−0.093	0.063
Variance explained (%)	78.8	14.2	3.6

[a] EucDist, Euclidean distance from the boundary of sandstone and limestone formations.

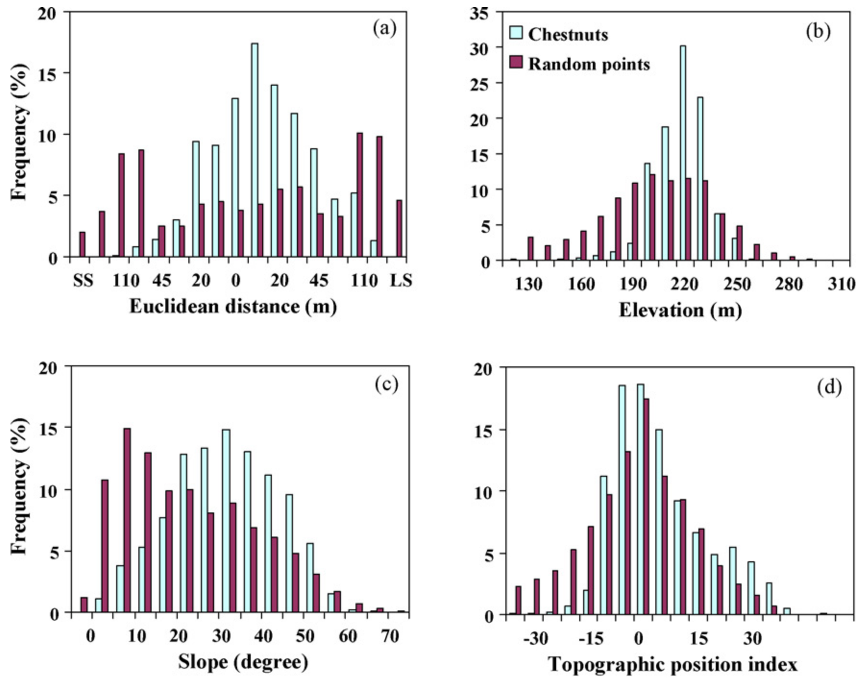

Fig. 1. Distribution pattern of variables from known American chestnut locations and from random points in MCNP for (a) Euclidean distance from the borderline of sandstone (SS) and limestone (LS) formation, (b) elevation, (c) slope steepness (degree), and (d) Topographic position index (negative value represents trend toward valley, zero represents flat areas if slope is shallow or mid-slope if significant slope, and positive value represents trend toward ridge top).

and random points of TPI do not have an apparent difference compared to the other three variables. However, relatively low chestnut presence on ravine and ridge sites compared to higher presence on steep mid-slopes and upper slopes was observed (Fig. 1d). A comprehensive view of chestnut distribution on a topographic relief geological map further confirms the association between chestnut sprouts and environmental variables (Fig. 2).

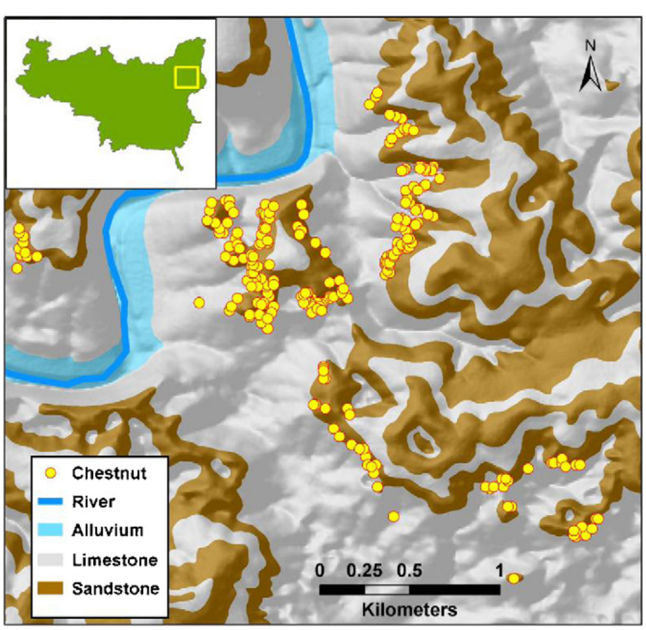

Fig. 2. Example of American chestnut spatial distribution in the northeastern section of MCNP on a topographic relief geological map.

3.3. Habitat map

Two habitat maps were generated for American chestnut (Fig. 3). Biomapper 3.1 provided a continuous habitat suitability map with a range of 0–100, but it did not provide a threshold of favorable chestnut habitats. Based on the maximum cumulative frequencies difference method (Browning et al., 2005, Thompson et al., 2006), the threshold of favorable chestnut habitats was around a habitat suitability of 16 (Fig. 4). To make a conservative prediction, we defined areas as favorable chestnut habitats when habitat suitability was greater than 20. Fig. 3a is the overall habitat suitability map for American chestnut in MCNP. About 28% of the areas were predicted as favorable chestnut habitats. Nearly 10% of the areas were predicted to have a habitat suitability greater than 50, and 4% of the areas had a suitability greater than 75. Suitable habitat for American chestnut was more concentrated in the north-central and northeastern part of MCNP. Fig. 3a provides a spatial reference for future chestnut restoration.

On the second map, a mask of land use history was added (Fig. 3b). Land use history was superimposed on Fig. 3a, and areas classified as historical agricultural lands were masked, because most chestnut sprouts were located on non-agricultural land. With the land use history mask, about 19% of the areas were predicted as favorable chestnut habitat, 8% of the areas had a habitat suitability greater than 50, and 3% of the areas had a suitability greater than 75. Figure 3b provides a spatial reference for locating more chestnut specimens in the future. Based on the map, there would be a low chance of finding American chestnut sprouts in the western and southeastern portion of MCNP.

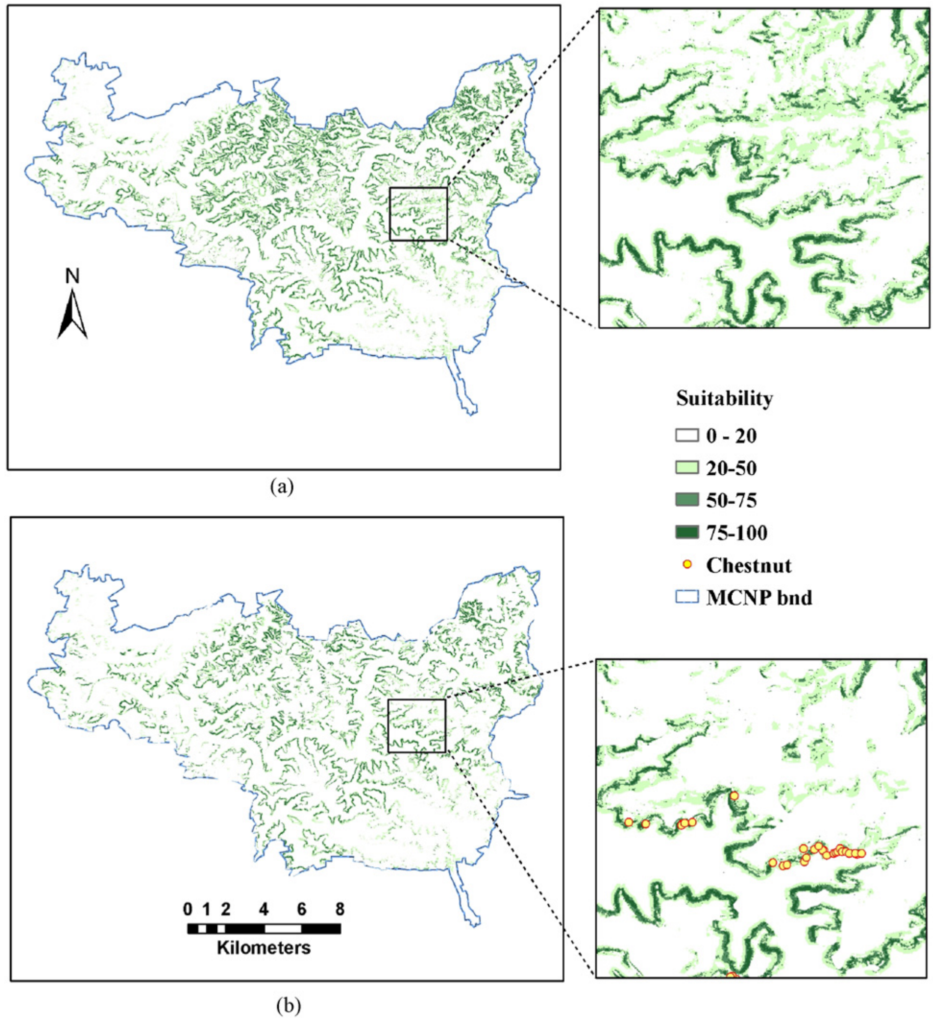

Fig. 3. American chestnut habitat suitability map for Mammoth Cave National Park: (a) suitability map for the entire park and (b) suitability map on the historically non-agricultural lands. Areas with habitat suitability greater than 20 are defined as favorable chestnut habitats.

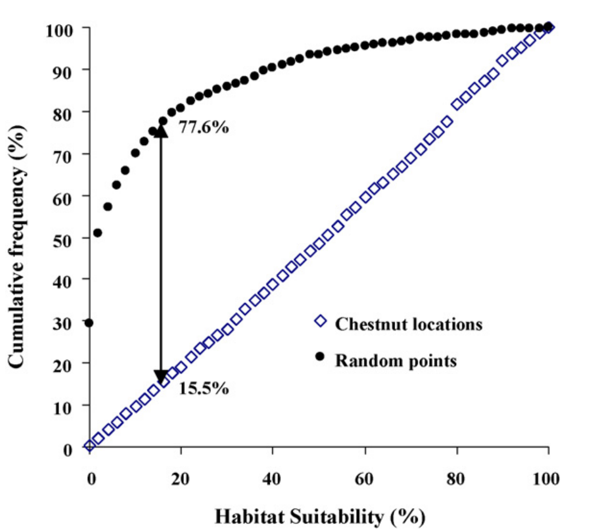

Fig. 4. Cumulative frequency distribution of habitat suitability for the 1437 American chestnut locations used in the habitat modeling process and the 1437 random locations. Difference between the cumulative frequencies maximized when habitat suitability is around 16%.

3.4. Model validation

Cross-validation was first applied to validate the chestnut habitat model. The Continuous Boyce Index (CBI, Boyce et al., 2002) was 0.97 ± 0.03 for the cross-validation on the 10 sub-regions random partition. The CBI indicated that our chestnut habitat suitability model was very robust (CBI equal to one indicates a perfect model). In addition, the relationship between the F-ratio (predicted/expected ratio) and probability of habitat suitability derived from the cross-validation also indicated that the chestnut habitat suitability model was robust (Fig. 5) because the F-ratio was low when habitat suitability was low, F-ratio was high when habitat suitability was high, and F-ratio was nearly monotonically increasing (Boyce et al., 2002).

We also used partitioning (Fielding and Bell, 1997) to validate the model based on locations of the 719 chestnuts that were not included in the habitat suitability model. Over 87% of the chestnuts were located in the areas that were classified as favorable chestnut habitats (Fig. 3b), and nearly 90% of the chestnuts were located in the favorable habitats if the habitat

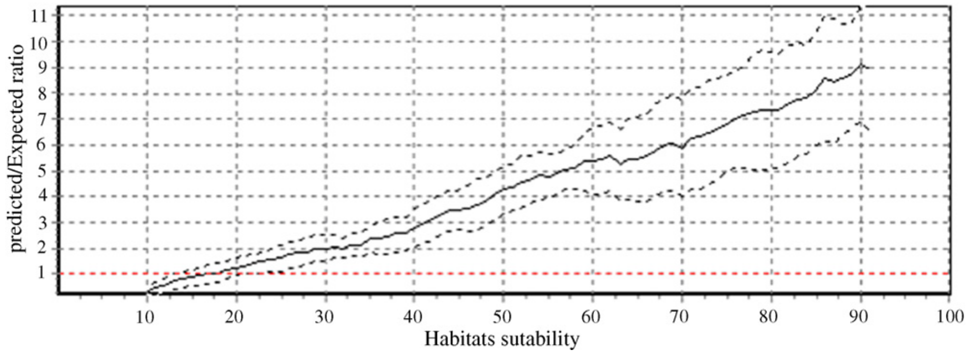

Fig. 5. Relationship between *F*-ratio (predicted chestnut presence/expected chestnut presence) and habitat suitability.

suitability map was smoothed by a 3×3 filter with a mean value algorithm. This further indicates that our chestnut suitability model was robust.

4. Discussion

Our results indicate that the ENFA was effective in determining both the chestnut site affinities and habitat suitability map in MCNP. American chestnut sprouts have a relatively narrow niche in MCNP. Only 19% of the area in the park is classified as favorable chestnut habitat where a chestnut sprout would likely be located. Not surprisingly, previous land use had a strong influence on the current chestnut distribution in MCNP. Only a few chestnut sprouts were found on abandoned agricultural land. Chestnut sprouts were more often in less disturbed non-agricultural areas.

American chestnut has specific site affinities for steep slopes near the boundary of limestone and sandstone formations and an average elevation of 223 m. This confirms our field observations that chestnut sprouts were often on sites close to the crest of slopes in the vicinity of chunky sandstone rock outcrops. Historically, chestnuts were also more abundant in upland slope forests than on ravine flats and ravine slopes in MCNP (Braun, 1950). Pre-blight distribution of American chestnut ranged from Mississippi to Maine mostly on the spine of mountainous uplands (Little, 1977). Within its geographical range, it grew well on well-drained soil which was not too rich in lime, and was found with high abundance on sloping lands with acid, sandy-loam soils (Braun, 1950; Russell, 1987). Soil played an important role in chestnut distribution. Unfortunately, we do not have detailed, consistent soil maps for our study area which would be ideal for chestnut habitat modeling. Nevertheless, the fine scale geology map provides relevant soil information because of the direct link between soil formation and bedrock geology. Due to slope and gravity, sandy-loam soils formed from sandstone bedrock can drift down on top of the limestone bedrock for some distance. This may partially explain the observed chestnut distribution pattern near the boundary of sandstone and limestone formations, where the soil is sandy, acidic, and well drained.

Because American chestnut had a broad distribution range before the arrival of the chestnut blight, it probably also had a much broader ecological niche than surviving sprouts which are now struggling in a blight environment. Therefore, the chestnut site affinity and habitat suitability discussed in this study are primarily applicable to surviving American chestnut sprouts. This habitat model based on field data obtained at MCNP may be applied in regions which have similar habitat conditions. We believe this model can be a valuable tool for locating surviving American chestnuts for use in chestnut breeding programs. Another potential use of this model is to identify restoration sites where planted chestnut seedlings may have a good chance to survive. Because the current distribution of chestnut sprouts is mostly a combined result of landuse history and interaction between blight and chestnut growth, the potential suitable restoration sites may be wider than predicted by our model. The potential restoration sites predicted by the model may be areas where blight-susceptible American chestnut seedlings will have a good chance to survive but may not be the best sites for future blight-resistant American chestnut seedlings to thrive.

5. Conclusion

Strong site affinities were found for American chestnut sprouts in MCNP. They have a very low presence in relatively young forests on abandoned agricultural lands, but most often occur in less disturbed forests on relatively steep mid to upper slopes near the boundary of limestone and sandstone formations, but with greater preference for the sandstone soils. Our chestnut habitat model provides spatial information for efficiently locating additional surviving American chestnut sprouts in MCNP and regions with similar site conditions.

Acknowledgements

M. DePoy, Chief of Science and Resources Management at MCNP, was very supportive of this research. M. Lacki provided helpful comments on the manuscript. J. Tinsley, L. Fly, A. Osborn, and M. Skaggs helped with inventorying. L. Scoggins (GIS expert at MCNP) assisted with mapping. MCNP personnel staff participated in the fieldwork. The National Park Service and TACF in conjunction with the National Forest Foundation funded this project.

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