

Modeling the historical distribution of American chestnut (*Castanea dentata*) for potential restoration in western New York State, US

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ABSTRACT

American chestnut (*Castanea dentata*) once held great economic and ecological importance in eastern US forests before its demise due to an invasive blight fungus. Backcross breeding and genetic engineering methods are currently developing a blight-resistant tree with mostly American chestnut traits. With the potential re-introduction of chestnut, research has sought to understand the geographic distribution of chestnut to locate potential restoration sites, but less research has compared ideal restoration sites to underlying land ownership. This research models the historical distribution of chestnut in western New York State (NYS, approximately 27,617 km²), containing a portion of the original range of chestnut, in order to determine suitable areas for chestnut reintroduction. This study models chestnut distribution using original land survey record (OLSR) data (ca. 1797–1799 CE) and species distribution models (SDMs), then compares model predictions to current protected lands. Results indicate that depending upon modeling technique, predicted suitable habitat for chestnut ranges 27.9–49.7% of the study area, and that 8.0–11.5% of suitable area is within protected land parcels. SDMs suggest that within the study area, the two predictors most important to chestnut distribution are soil pH and terrain slope, with chestnut favoring acidic soils and steeper slopes. By identifying sites for potential re-introduction of chestnut, this study highlights that reintroduction will depend upon cooperation of private landowners along with governments and non-governmental agencies. This study offers a revision to the historical distribution of chestnut in western NYS, and provides insight into land ownership and management issues facing its restoration.

1. Introduction

American chestnut (*Castanea dentata*; hereafter “chestnut”) once held great economic and ecological importance in the eastern United States (US) before its functional extinction due to an invasive blight fungus (Wang et al., 2013). A tree with immense size potential (Collins et al., 2017), chestnut was found in virtually all US states east of the Mississippi River and into southern Ontario, Canada (Little and Viereck, 1971), achieving its highest abundance in the Appalachian Mountains (Braun, 1950). Chestnut was generally an upland tree species found in temperate climates on well-drained, acidic soils (Russell, 1987), limited in its northern distribution by frost sensitivity (Gurney et al., 2011). The tree species likely avoided calcium-rich soils throughout its geographical range (Russell, 1987). In the middle of its range, historical records suggest that chestnut was found on ridges (Nowacki and Abrams, 1992), and on sites with low moisture, high topographic roughness, and loam or sandy loam (Thomas-Van Gundy and Strager,

2012). In southern Ontario, chestnut is found today on acidic, sandy soils and gently sloping terrain (Tindall et al., 2004). Efforts led by The American Chestnut Foundation (TACF, 2020) have sought to develop blight-resistant chestnut through either backcross breeding with Chinese chestnut (*Castanea mollissima*) to retain mostly American chestnut traits (Griffin, 2000), or through the introduction of blight resistance via genetic engineering (Powell et al., 2019; Steiner et al., 2017). With the potential restoration of chestnut, research has sought to understand its potential impacts on ecosystems, such as with respect to biotic interactions (e.g. Goldspiel et al., 2019; Newhouse et al., 2018), carbon storage (e.g. Gustafson et al., 2018), and fire regimes (e.g. Kane et al., 2019).

Research has modeled the past or current geographic distribution of chestnut, contributing further knowledge on the factors shaping the tree's geographical range. Fei et al. (2007) modeled at 10 m resolution the current distribution of chestnut based on field observational data in Mammoth Cave National Park, US, finding that chestnut sprouts were

Abbreviations: FIA, Forest Inventory and Analysis; GIS, geographic information system; HLC, Holland Land Company; NYS, New York State; OLSR, original land survey record; SDM, species distribution model; TACF, The American Chestnut Foundation; US, United States

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generally found on steeper slopes and on mid-slopes or ridges. Chambers et al. (2013) modeled at 1 km resolution the relative abundance of 105 tree species in the eastern US using the Forest Inventory and Analysis (FIA) database; chestnut was one of the poorest-performing models out of all tree species in their study. Tulowiecki and Larsen (2015) created models at 100 m resolution using data from original land survey records (OLSRs; ca. 1800 CE) to predict the past distribution of chestnut in Chautauqua County, New York State, finding its distribution was correlated with distance to Native American settlement along with environmental predictors. Barnes and Delborne (2019) created models at 2.5 min resolution (≈ 4.5 km at the equator) using occurrence data from the Global Biodiversity Information Facility and the FIA database to predict the current distribution of chestnut across its entire range, finding that precipitation, temperature, and seasonality predictors were most predictive of its distribution. Other studies have used modeling or statistical methods to assess niche overlap among *Castanea* species (Fei et al., 2012) or to assess environmental correlates of blight resistance (Van Drunen et al., 2018).

Though fine-resolution modeling and mapping of chestnut's geographical range is likely to be important to successfully restore chestnut, previous research is limited in two ways. First, research (e.g. Barnes and Delborne, 2019; Chambers et al., 2013; Fei et al., 2007) has often used current data on chestnut distribution as training data for modeling, meaning that effects such as sampling bias and Euro-American land use may complicate the understanding of historical relationships between chestnut and environmental predictors. Second, with the exception of Zhang et al. (2019), studies have not sought to rigorously understand the underlying land management or ownership coinciding with potential chestnut restoration sites. This second limitation is noteworthy because management and administrative issues are crucial considerations in the successful reintroduction of chestnut to eastern US forests (Clark et al., 2014).

This study models the historical geographic distribution of chestnut to determine suitable chestnut habitat in western New York State (NYS), and assesses how much suitable habitat is within private versus public lands. Modeling suitable habitat is performed using species distribution models (SDMs) that correlate historical observations of chestnut with environmental conditions. To the author's knowledge, no study has yet compared the distribution of suitable habitat for chestnut with underlying land ownership and management using historical observations of chestnut distribution. This study advances research into chestnut distribution and management considerations for its restoration.

2. Study area

The study area is western NYS (approximately 27,617 km²), bounded by Lake Ontario on the north, the State of Pennsylvania on the south, Lake Erie and the Niagara River on the west, and by Seneca Lake on the east (Fig. 1). It contains portions or the entirety of 15 modern-day counties. It is comprised of the warmer-drier Erie-Ontario Lowland in the north and west with generally flat terrain, and the cooler-moister Allegheny Plateau in the south and east with gently to steeply sloping terrain (Fenneman, 1938). Across the study area, mean annual precipitation ranges from 80 to 131 cm and mean annual temperature ranges from 6° to 10° C (PRISM Climate Group, 2013). Generally speaking, the two physiographic provinces dictate soil characteristics, with more acidic and shallow Inceptisols on the Allegheny Plateau, and less acidic and deeper Alfisols on the Erie-Ontario Lowland (Natural Resources Conservation Service, 2014).

Historically, chestnut was found throughout the study area but likely at low relative abundance (Fig. 1). When compared to Little and Viereck's range map for chestnut (1971), 13 out of 15 counties in the study area are partially or completely within chestnut's range, and 6 out of 8 counties with OLSR data used in this study (Fig. 2) are partially or completely within its range (Fig. 1a). Paciorek et al. (2016) and OLSRs

used in this study (see also Seischab, 1992) suggest localized presence of chestnut even in areas where Little and Viereck (1971) suggest its absence. A compilation of older range maps by Russell (1987) suggests that chestnut was continuously present throughout the study area. Wang (2007) estimated from witness-tree data within OLSRs that chestnut had a relative abundance of 1.2% in the western portion of the study area. Paciorek et al.'s (2016) 8-km resolution interpolation of historical relative abundance for chestnut based on OLSRs estimated local peaks as high as 17.2% (Fig. 1b). Researchers at The State University of New York College of Environmental Science and Forestry are developing a transgenic chestnut (State University of New York, 2019), and NYS hosts numerous backcross-breeding orchards (TACF, 2020), further making the study area a potentially important release site for chestnut.

3. Materials and methods

This study was performed in two main steps. This study first developed SDMs to predict the historical distribution of chestnut (interpreted as suitable habitat), and then compared predictions to underlying land ownership and management. Tasks requiring geographic information systems (GIS) software were performed using Esri ArcGIS (Esri, 2017), and SDM development was performed using R statistical computing (R Core Team, 2018).

3.1. Developing SDMs

SDMs were developed to predict the historical distribution of chestnut and therefore environmentally-suitable habitat for chestnut restoration, by relating chestnut presence/absence (dependent variable) to environmental predictors (independent variables). SDMs are quantitative techniques for predicting geographic distributions of species, often using species presence/absence records as training data (Franklin and Miller, 2009).

To derive a sample of historical chestnut distribution, surveyor "field notes" from OLSRs were used. OLSRs are records of the first land surveys in the US, which delineated land into townships and lots for sale and settlement (Wang, 2005; Whitney, 1996). OLSRs contain timber descriptions along survey lines, and records of trees marked along survey lines or at township or lot corners (witness-trees or bearing-trees). Though they can contain uncertainty (e.g. Mladenoff et al., 2002) and bias (e.g. Kronenfeld and Wang, 2007), OLSRs are one of the most valuable and utilized datasets for mapping the historical distribution of tree species in the US. Previous work has used OLSRs to understand historical distribution and abundance of chestnut throughout its range (Nowacki and Abrams, 1992; Paciorek et al., 2016; Rentch and Hicks, 2005; Thomas-Van Gundy and Strager, 2012; Tulowiecki and Larsen, 2015; Wang, 2007).

This study used timber descriptions from OLSRs of the Holland Land Company (HLC) township survey (1797–1799 CE) from the western portion of the study area (Fig. 2), which were previously transcribed and mapped as a GIS data layer (Tulowiecki et al., 2015; Wang, 2007). The HLC surveyed townships from 1797 to 1799 CE typically along a 9.7×9.7 km (6×6 mi) grid. Positional error for these OLSRs is estimated at approximately 10 m (Tulowiecki et al., 2015). The layer depicted 2,668 line segments containing timber descriptions (e.g. "chestnut, hemlock, white oak, black oak, and white pine") with up to 14 tree taxa per description, and ranging from 20 m to 12,946 m (median = 626 m) in length. Each timber description in the HLC township survey was believed to correspond to relatively consistent environmental conditions (e.g. a slope with "2nd quality soil", a "swamp", a "bottomland"), and timber descriptions are believed to describe species found evenly along the entire length of the segment corresponding to the description. OLSRs were not obtained for the eastern portion of the study area, but this portion was determined to contain similar environmental conditions by creating multivariate

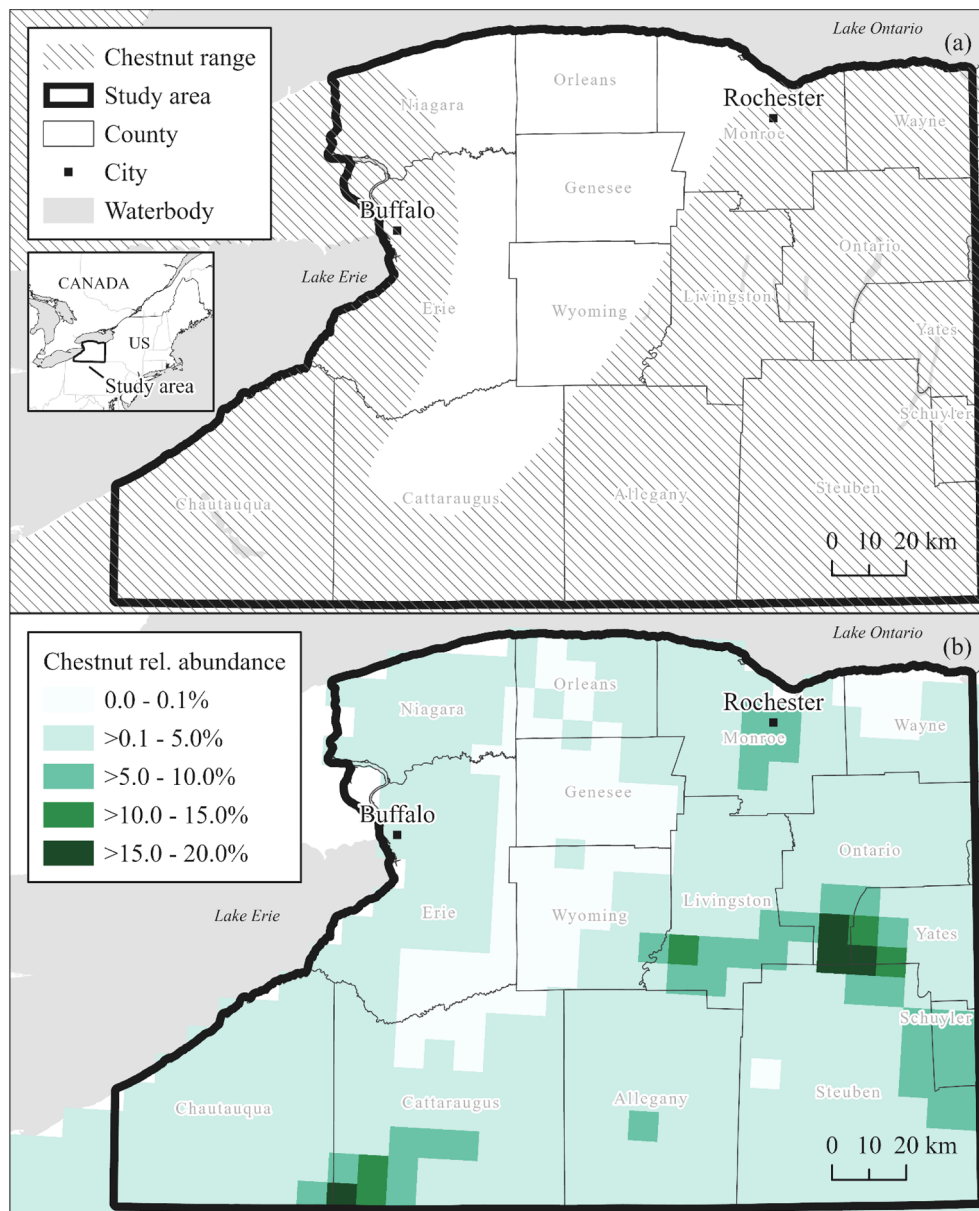


Fig. 1. (a) Study area, along with Little and Viereck's map of American chestnut (*Castanea dentata*) range (1971). (b) Paciorek et al.'s interpolated historical relative abundance data for chestnut based on original land survey records (2016); this interpolation was based on aggregated witness-tree counts including those from Holland Land Company (HLC) surveys.

environmental similarity surfaces using MaxEnt software, version 3.4.1 (Phillips et al., 2017).

To create a sample of chestnut presence/absence, a GIS-format point layer was superimposed with points at 2-km spacing along the GIS-format lines representing timber descriptions. If a timber description at a point mentioned chestnut then the point was assigned a value of "1" (present); otherwise, the point was assigned a value of "0" (absent). This procedure yielded 1,239 points with complete environmental data (see next paragraph), of which 211 were chestnut presences (Fig. 2). The 2-km spacing was chosen to ensure an adequate number of chestnut presences for training and testing SDMs ($n > 100$), and to minimize spatial autocorrelation that might result from close spacing. A random 25% of points ($n = 310$), stratified to maintain the same prevalence rate, were reserved as common test data to evaluate all final SDMs, and the remaining 75% ($n = 929$) were used as training and validation data. Timber descriptions were similarly used to develop a sample of presence/absence locations in one study (Tulowiecki, 2014); that study also suggested that timber descriptions led to more accurate SDMs than

those trained with presence/absence points developed from witness-tree data.

A total of 19 predictors representing climate, soil, and topographic characteristics were initially considered for inclusion in SDMs, and were acquired in and/or transformed into GIS-format raster data (Table 1). All predictors were aggregated or resampled to a resolution of 100 m. Soil predictors were originally converted from vector to raster format at a resolution of 10 m, and then mean-aggregated to 100 m. Terrain predictors, along with compound topographic index (CTI), were originally created at a resolution of 10 m and then mean-aggregated to 100 m. Climate predictors were downsampled from an initial resolution of approximately 800 m using cubic convolution resampling. Of the 19 predictors originally considered, 6 were omitted due to collinearity with other predictors (Pearson's $r > |0.70|$). While this study used current climate data, previous research in the study area has suggested that these data capture the same general patterns in climate as the ca. 19th century, and differ only modestly in actual temperature or precipitation amounts (Tulowiecki et al., 2020, Supplemental Content).

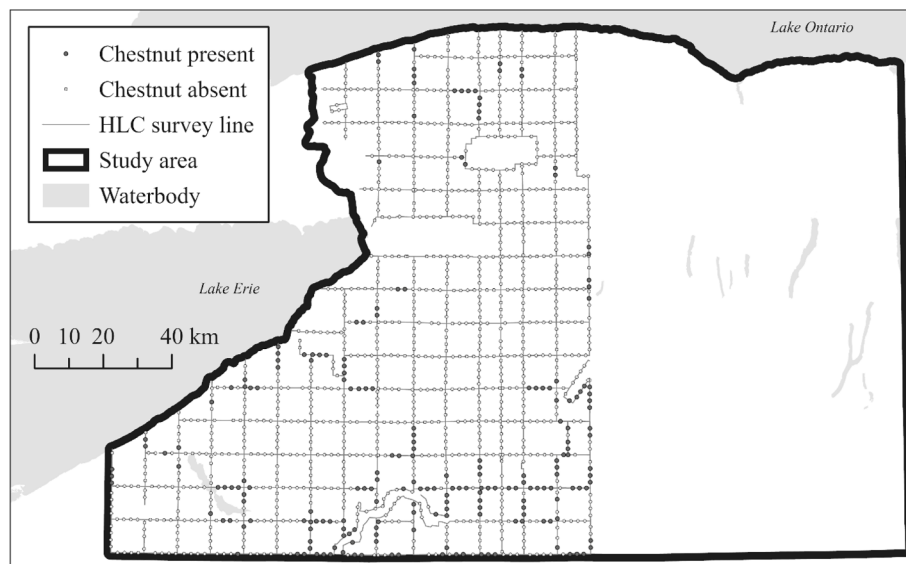


Fig. 2. Locations of Holland Land Company (HLC) township survey lines ca. 1797–1799 CE, and chestnut presence/absence points derived from timber descriptions along survey lines (used for training species distribution models in this study).

Though chestnut is sensitive to frost damage (Gurney et al., 2011), this study did not include winter (e.g. January) temperature as a predictor since all monthly temperature variables are highly correlated with annual temperature in the study area (Pearson's $r > 0.9$).

Nine SDM techniques (summarized in Franklin and Miller, 2009) were used to model chestnut distribution: artificial neural networks (ANN), classification tree analysis (CTA), flexible discriminant analysis (FDA), generalized additive models (GAM), gradient boosting models (GBM), generalized linear models (GLM), multiple adaptive regression splines (MARS), maximum entropy modeling (MaxEnt), and random forests (RF). These SDM techniques encompass different approaches to modeling species distributions. SDM techniques varied by whether they were based on statistical or machine-learning methods, whether they could model linear and/or non-linear relationships between dependent

and independent variables, and whether they could model variable interactions.

Sample points on chestnut presence/absence and raster layers of predictors were imported into R statistical computing platform (R Core Team, 2018) for SDM development. All SDMs were trained using the “biomod2” package (Thuiller et al., 2013, 2009). For each of the nine SDMs created (i.e. one per technique), the same procedure was followed. Presence/absence data ($n = 929$) not reserved for model testing were first randomly partitioned into training (80%; $n = 743$) and validation (20%; $n = 186$) data. The model was then developed using the training data, and applied to predict chestnut presence/absence in the validation data. This procedure was repeated 25 times, and the model that best predicted presence/absence in the validation data was chosen as the final model. Technique-specific modeling parameters were tuned

Table 1

Predictors initially considered in species distribution models (SDMs). “Predictor codes” are abbreviations for predictors elsewhere in this study. The final column indicates whether predictors were retained after checking for collinearity among predictors. NRCS = Natural Resources Conservation Service SSURGO database (2014), USGS = United States Geological Survey (2013).

Type	Predictor (unit)	Value range within study area	Predictor code	Source	Considered in final SDMs?
Climate	Mean precipitation, May–September	37–61 cm	climate_precip0509	PRISM Climate Group	Yes
	Mean annual temperature	6.2–9.8° C	climate_tempann	PRISM Climate Group	No
Soil	Available water supply, 0 to 100 cm	2.1–40.0 cm	soil_aws100cm	NRCS	Yes
	Available water supply, 0 to 150 cm	2.7–40.0 cm	soil_aws150cm	NRCS	No
	Bulk density	0.2–1.7 g/cm	soil_bulkdensity	NRCS	Yes
	Compound topographic index (unitless; lower = drier)	1.9–33.1	soil_cti	USGS	Yes
	Depth to restrictive layer	30.0–201.0 cm	soil_depthrestrictive	NRCS	No
	Ranked drainage class (unitless; 1 = driest, 7 = wettest)	1–7	soil_drainageclass	NRCS	Yes
	Erodibility factor (unitless; higher = more erodable)	< 0.1–0.5	soil_kffact	NRCS	No
	Saturated hydraulic conductivity (permeability rate)	< 0.1–139.0 mm/hr	soil_ksat	NRCS	Yes
	Organic matter	0.1–87.0% (by weight)	soil_organicmatter	NRCS	Yes
	Clay	0.5–48.7% (by weight)	soil_percentclay	NRCS	No
	Sand	0.0–94.5% (by weight)	soil_percentsand	NRCS	Yes
	Degree of acidity or alkalinity (pH)	4.4–8.0	soil_ph	NRCS	Yes
	Passing sieve no. 10 (coarse) (% by weight)	25.6–100.0% (by weight)	soil_sieve10	NRCS	No
	Passing sieve no. 200 (fine) (% by weight)	0.0–100.0% (by weight)	soil_sieve200	NRCS	Yes
Topography	Eastness of aspect (unitless; –1 = west, 1 = east)	–1.0–1.0	topography_eastness	USGS	Yes
	Northness of aspect (unitless; –1 = south, 1 = north)	–1.0–1.0	topography_northness	USGS	Yes
	Mean terrain slope angle	0.0–75.2°	topography_slope	USGS	Yes

Table 2

Performance of species distribution models (SDMs) as judged against each model's unique validation data, and against the common test data. AUC = area under the curve, TSS = true skill statistic. Refer to Section 3.1 for SDM technique abbreviations.

Technique	AUC		TSS	
	Validation data	Test data	Validation data	Test data
ANN	0.749	0.682	0.497	0.265
CTA	0.783	0.660	0.529	0.291
FDA	0.721	0.680	0.484	0.295
GAM	0.745	0.717	0.477	0.351
GBM	0.799	0.741	0.490	0.380
GLM	0.762	0.743	0.490	0.328
MARS	0.774	0.674	0.484	0.255
MaxEnt	0.744	0.668	0.400	0.257
RF	0.751	0.726	0.490	0.258

and variable selection procedures were performed using the “BIO_MOD_tuning” function (Thuiller et al., 2013, 2009).

SDMs outputted two types of predictions of historical chestnut distribution, which were also interpreted as suitability measures: predicted probabilities of chestnut presence, and binary presence/absence predictions. To create binary predictions, a threshold value in predicted probabilities was chosen that maximized the true skill statistic (TSS); TSS = sensitivity + specificity – 1 (Allouche et al., 2006). TSS ranges from –1 to 1, with 0 being a model that is no better than a random guess. SDM predictions of chestnut distribution were then visually compared with existing published maps on historical chestnut distribution. These comparisons were made with Little and Viereck's range map (1971; Fig. 1a) and Paciorek et al.'s interpolation of relative abundance (2016; Fig. 1b). These comparisons were made to assess the strength of the SDM predictions, but also to critically examine these two previous chestnut range reconstructions.

Various SDM diagnostics and predictive performance measures were examined. Partial dependence plots characterized the relationship between each predictor and chestnut distribution, by plotting the predicted probability across the range of a predictor's values while holding all other predictors at their median value (Elith et al., 2005; Thuiller et al., 2013, 2009). Variable importance was calculated using the permutation importance measure (Liaw and Wiener, 2002; Thuiller et al., 2013, 2009). Permutation importance is calculated by first applying the model to predict probabilities at the sample point locations with the values of a single predictor randomly shuffled, then calculating the correlation (Pearson's *r*) between the original predictions and the predictions using the shuffled dataset; permutation importance = 1 – Pearson's *r*. TSS and the area under the receiver operating characteristic curve (AUC) measure were used to assess predictive performance. AUC ranges from 0 to 1, and the measure equals the probability of assigning a predicted probability value at a random presence point that is higher than assigning a predicted probability value at a random absence point (Fawcett, 2006). To offer different estimates of predictive performance, TSS and AUC were calculated using each SDM's unique validation data and the common test data.

3.2. Comparing SDM predictions to land ownership and management

To understand how predicted suitable habitat for chestnut coincides with private and currently protected lands, SDM predictions were compared to protected land parcels in the Protected Areas Database of the United States (USGS Gap Analysis Project, 2018) using GIS software. This database contains the locations of protected public lands and private lands protected under conservation easements. This analysis also served to assess if and where permanently protected areas existed that possessed suitable habitat for chestnut. Other studies have similarly assessed potential overlap between protected lands and the

geographic range of candidate species for de-extinction (Peers et al., 2016).

Three main analyses were performed. First, SDM predictions were compared to protected land parcels to quantify how much predicted suitable habitat is found on protected lands versus unprotected private lands. Second, mean committee average was calculated within each protected land parcel to understand which parcels would be most suitable for chestnut reintroduction. Committee average (Thuiller et al., 2013; 2009) is the number of SDMs that predicted suitable habitat for chestnut at a location (based on binary predictions; Section 3.1). Mean committee average, therefore, is the mean number of SDMs that predicted the presence of chestnut across all locations within a parcel (e.g. if a parcel's mean committee average is 8, locations throughout the parcel have, on average, 8 of 9 SDMs predicting suitable habitat for chestnut). Smaller parcels were omitted from this analysis; mean committee average was calculated for all parcels ≥ 1 km². Third, this study mapped contiguous patches with high SDM consensus regarding suitability for chestnut to identify large high-quality areas. “High-consensus” was defined as locations where 7+ out of 9 SDMs predicted suitable habitat.

4. Results

4.1. SDM performance and diagnostics

SDMs of historical chestnut distribution showed fair to good ability to predict chestnut presence/absence (Table 2). When SDMs were applied to predict presence/absence in their unique validation datasets, AUC ranged from 0.721 to 0.799 and TSS ranged from 0.400 to 0.529. When SDMs were applied to predict chestnut presence/absence in the common test data, SDMs demonstrated slightly lower predictive performance: 0.660–0.743 for AUC, and 0.255–0.380 for TSS. Note that some have interpreted AUC values of 0.6–0.7 as “fair” models and 0.7–0.8 as “good” models (Swets, 1988). GBM, GLM, and GAM emerged as the most predictive SDMs based on their predictive measures when calculated using the common test data.

SDMs suggest that chestnut distribution was most influenced by soil and topographic conditions. Soil pH and terrain slope angle were the most important predictors of chestnut distribution as judged by permutation importance measures (Table 3), and their modeled relationships with chestnut distribution were the most consistent across modeling techniques as determined from partial dependence plots (Table 4). Soil pH (median importance rank = 1) was the most or second-most important variable in 8 out of 9 models, was chosen by every SDM, and demonstrated a negative relationship with chestnut distribution across all SDMs (more acidic = more probable). One model (i.e. FDA) chose only soil pH as a predictor of chestnut distribution. Terrain slope angle was the first- to fourth-most important predictor among SDMs that chose the predictor (median importance rank = 2), was chosen by 7 out of 9 SDMs, and demonstrated a positive relationship with chestnut distribution across SDMs (steeper = more probable). No other predictors aside from soil pH and terrain slope angle demonstrated consistent modeled relationships with chestnut distribution across all modeling techniques. Soil percent sand, soil organic matter, and growing-season (May–September) precipitation were the next most important predictors as judged from permutation importance measures across all modeling techniques, although SDMs did not agree on the nature of their relationships with chestnut. Soil bulk density (median rank = 6) displayed a positive relationship with chestnut distribution (denser = more probable) for nearly every SDM that chose this predictor; soils low in bulk density within the study area are associated with swamplands rich in organic matter, suggesting that chestnut does not grow in swampy locations.

Table 3

A summary of variable importance measures for species distribution models of American chestnut (*Castanea dentata*). Shown are permutation importance measures, ranging from 0.00 (least important or not selected by model) to 1.00 (most important). Refer to [Section 3.1](#) for SDM technique abbreviations, and to [Table 1](#) for predictor codes.

Predictor	Modeling technique								
	ANN	CTA	FDA	GAM	GBM	GLM	MARS	MaxEnt	RF
climate_precip_0509	0.12	0.00	0.00	0.22	0.03	0.14	0.00	0.04	0.02
soil_aws100cm	0.23	0.00	0.00	0.01	0.05	0.00	0.00	0.04	0.03
soil_bulkdensity	0.00	0.00	0.00	0.08	0.03	0.07	0.00	0.05	0.04
soil_cti	0.06	0.00	0.00	0.02	0.01	0.00	0.00	0.05	0.02
soil_drainageclass	0.06	0.00	0.00	0.09	0.01	0.00	0.00	0.09	0.01
soil_ksat	0.43	0.00	0.00	0.02	0.01	0.00	0.00	0.04	0.02
soil_organicmatter	0.05	0.33	0.00	0.01	0.09	0.00	0.00	0.16	0.04
soil_percentsand	0.34	0.00	0.00	0.18	0.06	0.00	0.09	0.20	0.04
soil_ph	0.03	0.64	0.98	0.25	0.18	0.86	0.34	0.30	0.09
soil_sieve200	0.21	0.00	0.00	0.04	0.02	0.00	0.09	0.10	0.02
topography_eastness	0.03	0.00	0.00	0.01	0.02	0.00	0.00	0.08	0.03
topography_northness	0.12	0.28	0.00	0.00	0.03	0.00	0.00	0.04	0.02
topography_slope	0.37	0.00	0.00	0.18	0.21	0.22	0.36	0.27	0.08

4.2. Chestnut distribution, and comparisons with land ownership and management

SDMs generally agreed on the distribution of chestnut across the study area: chestnut habitat is most notably predicted in upland conditions of the Allegheny Plateau, and along an upland region spanning southern Erie County and northwestern Chautauqua County ([Fig. 3](#)). Depending upon modeling technique, predicted suitable habitat (historical chestnut distribution) ranges from approximately 7,502–13,391 km² (27.9–49.7%) of the study area ([Table 5](#)), based on binary predictions ([Section 3.1](#)). GBM, GLM, and GAM were the top SDMs as judged by their predictive performance, and they predicted 8,194 km² (30.4%), 8,172 km² (30.4%), and 9,234 km² (34.3%) of the study area to contain suitable habitat, respectively. SDM predictions showed only a vague correspondence with previously-published maps of historical chestnut distribution ([Fig. 1a](#)) and relative abundance ([Fig. 1b](#)) in the study area.

[Fig. 3b](#) shows the amount of agreement among SDMs in designating areas of potential suitable habitat. All 9 SDMs were in agreement about the suitability of 3,002 km² and the unsuitability of 8,957 km². Areas with high consensus among modeling techniques (i.e. where 7 + out of 9 modeling techniques predicted suitable habitat) total 5,553 km² of the study area (20.6%), of which 690 km² is located on protected land parcels. Areas where the top three models (i.e. GAM, GBM, and GLM) all predicted suitable habitat totaled 4,822 km² (17.9%), of which 596 km² is located on protected lands. All estimates in this section

exclude waterbodies and areas missing soil data, such as the urban areas of the City of Buffalo and the City of Rochester.

8.0–11.5% of total suitable area falls within protected land parcels, whereas the remainder of suitable area is located on unprotected private lands ([Table 5](#)). Generally speaking, larger and more suitable protected land parcels are found in the southern portion of the study area, typically on state lands ([Fig. 4](#)). Parcels managed by NYS emerge as the protected areas with the highest potential to restore chestnut to its historical range. Land parcels protected by NYS contain 89.9% (620 km²) of total high-consensus predicted suitable habitat on protected lands, and 96.6% of the total when considering only contiguous patches of high-consensus predicted suitable habitat ≥ 1 km² ([Table 6](#)). These numbers represent a disproportionate share of total protected lands within the study area. NYS lands also possess the largest contiguous patches of high-consensus predicted suitable habitat on protected lands: the top 30 largest patches, and 45 of the top 50 largest patches, are on NYS lands. Allegany State Park emerges as an especially large protected land that possesses by far the largest contiguous patch of high-consensus suitable habitat (250 km², compared to the second-largest patch of 16 km²), and locations within the park on average have at least 8 out of 9 SDMs predicting suitability for chestnut.

5. Discussion

This study provides insight at a fine spatial resolution into the historical distribution of chestnut and where chestnut could be potentially

Table 4

A summary of partial dependence plots describing the relationship between predictors and the probability of observing American chestnut (*Castanea dentata*). “pos” = generally positive relationship, “neg” = generally negative relationship, “?” = relationship was difficult to generalize, and “(O)” = predictor was not included in the model. Refer to [Section 3.1](#) for SDM technique abbreviations.

Predictor	Modeling technique								
	ANN	CTA	FDA	GAM	GBM	GLM	MARS	MaxEnt	RF
climate_precip_0509	pos	(O)	(O)	?	neg	neg	(O)	?	?
soil_aws100cm	neg	(O)	(O)	pos	neg	(O)	(O)	neg	?
soil_bulkdensity	(O)	(O)	(O)	pos	pos	pos	(O)	pos	?
soil_cti	pos	(O)	(O)	neg	?	(O)	(O)	pos	?
soil_drainageclass	(O)	(O)	(O)	?	neg	(O)	(O)	neg	?
soil_ksat	pos	(O)	(O)	neg	?	(O)	(O)	?	neg
soil_organicmatter	?	?	(O)	neg	?	(O)	(O)	?	?
soil_percentsand	neg	(O)	(O)	?	neg	(O)	pos	?	neg
soil_ph	(O)	neg	neg	neg	neg	neg	neg	neg	neg
soil_sieve200	neg	(O)	(O)	?	pos	(O)	pos	?	pos
topography_eastness	(O)	(O)	(O)	neg	?	(O)	(O)	?	?
topography_northness	(O)	?	(O)	pos	?	(O)	(O)	?	?
topography_slope	pos	(O)	(O)	pos	pos	pos	pos	pos	pos

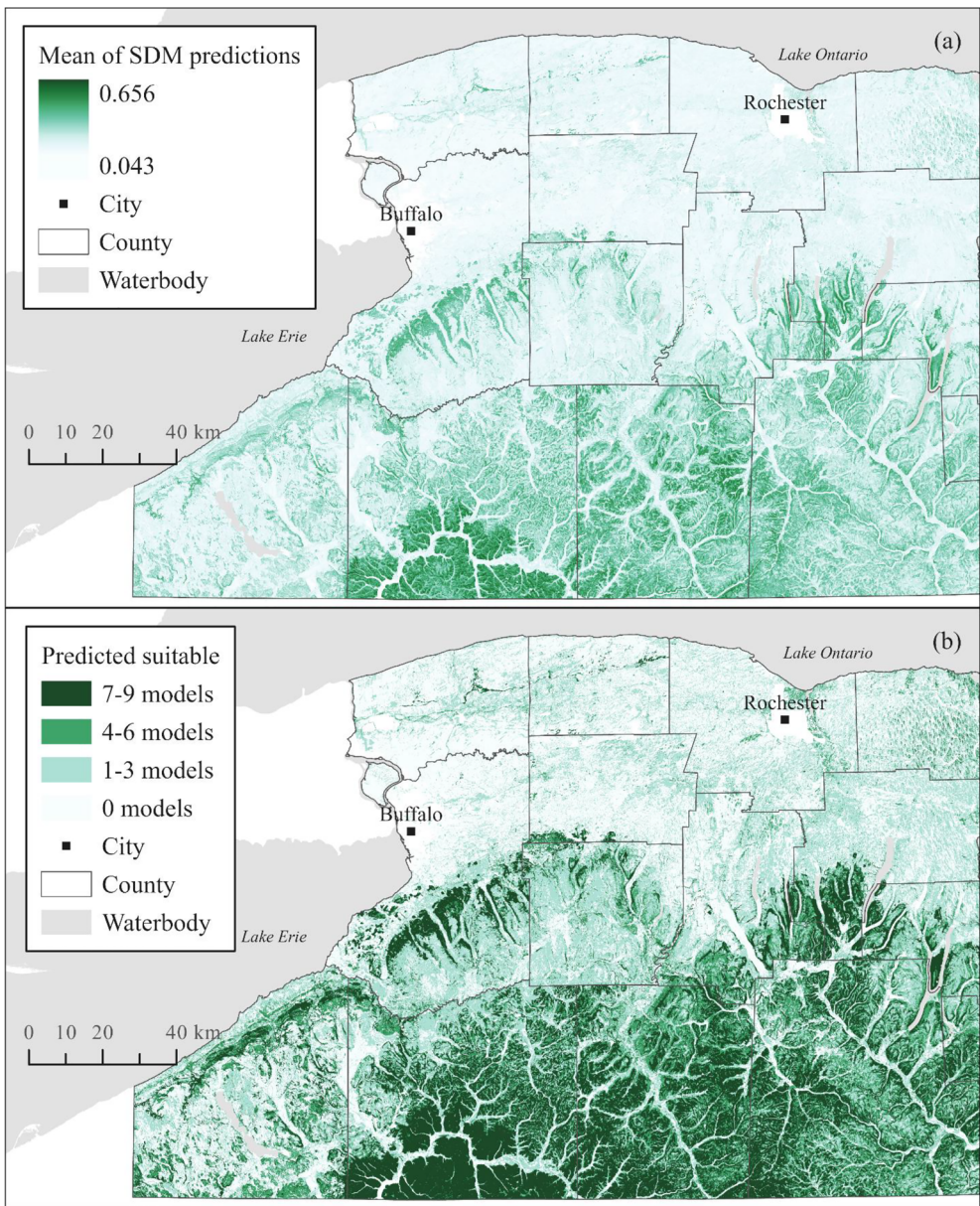


Fig. 3. Spatial predictions of American chestnut distribution made by species distribution models (SDMs). (a) Mean SDM predictions weighted by area under the curve (AUC) measures when SDMs were applied to each technique's unique validation data. (b) Committee average of SDM predictions (i.e. number of SDMs predicting the historical presence of chestnut).

Table 5
Total area for predicted suitable habitat within the study area, and within protected land parcels. Refer to Section 3.1 for SDM technique abbreviations.

Technique	Predicted suitable area		Predicted suitable area, within protected land parcels	
	km ²	% of study area	km ²	% of predicted suitable area
ANN	10,255	38.1%	913	8.9%
CTA	7622	28.3%	803	10.5%
FDA	7502	27.9%	797	10.6%
GAM	9234	34.3%	880	9.5%
GBM	8194	30.4%	837	10.2%
GLM	8172	30.4%	799	9.8%
MARS	6177	22.9%	710	11.5%
MaxEnt	10,570	39.3%	912	8.6%
RF	13,391	49.7%	1072	8.0%

reintroduced to its historical range in western NYS (Figs. 3 and 4). This study provides more detailed depictions of historical chestnut distribution within the study area than previous studies. SDM performance was fair to good, meaning that the SDM predictions should be interpreted as providing general guidance on historical chestnut distribution using OLSR data.

This study's results suggest that chestnut was predominantly found in the southern portion of the study area, and more sporadically elsewhere (Fig. 3); previous literature furthermore suggests that it was present at generally low relative abundance where present (Paciorek et al., 2016). SDM predictions of chestnut's historical distribution differed noticeably from both a commonly-utilized source on tree species ranges (Fig. 1a; Little and Viereck, 1971) and coarse-resolution historical interpolations from OLSR data (Fig. 1b; Paciorek et al., 2016). Three points are warranted pertaining to differences with Little and Viereck's map. First, generalization in their map may have introduced error, since their work produced continental-extent range maps for hundreds of species. Second, their work acknowledged the possibility of

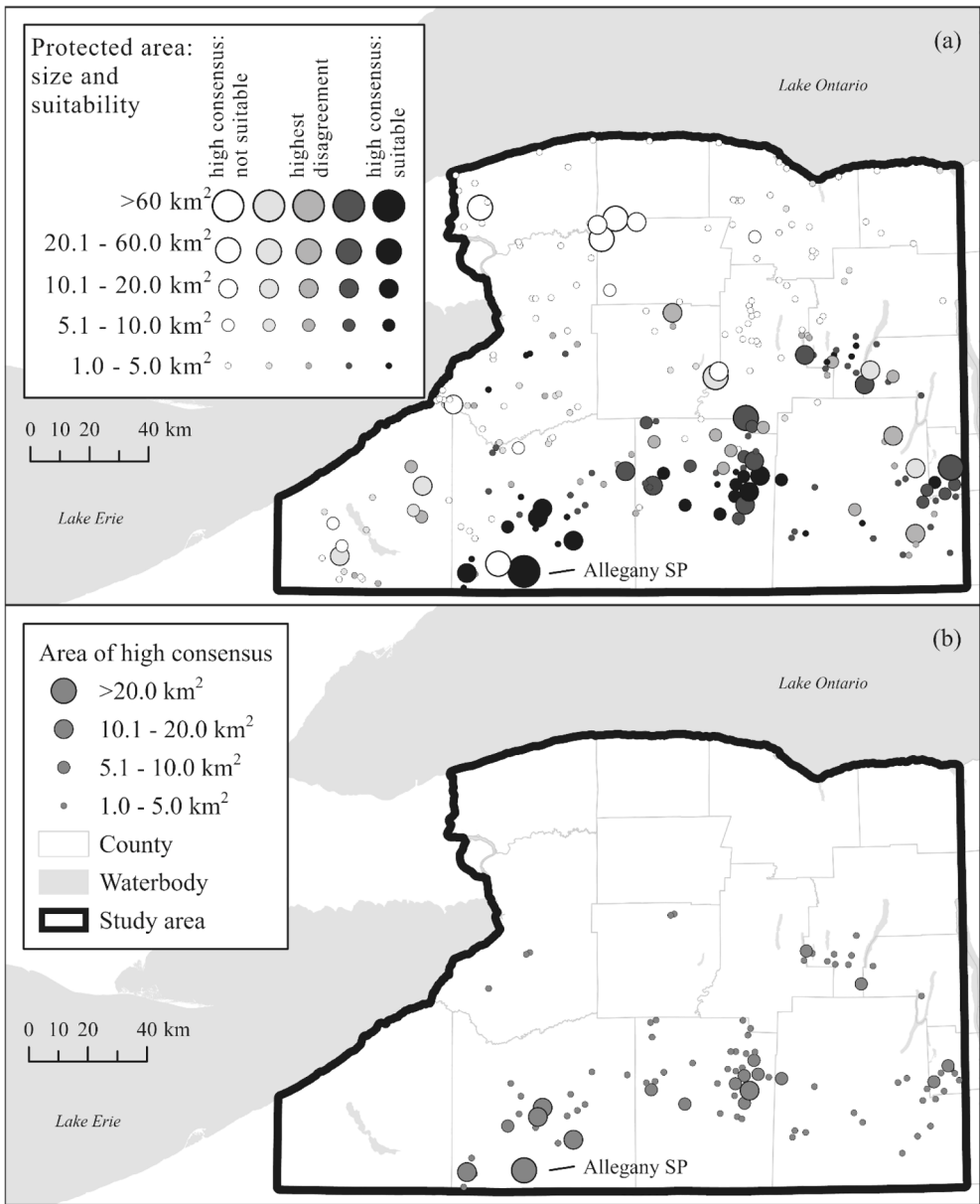


Fig. 4. A proportional symbol map showing the locations of protected land parcels and predictions of suitable habitat made by species distribution models. (a) Size of protected land parcel and mean committee average. (b) Size of contiguous patches of high-consensus predicted suitable habitat within protected land parcels. Allegheny SP = Allegheny State Park.

error, stating that their maps may “suggest corrections” and “localities where further field work is needed for revision and where range extensions and State records may be sought” (Little and Viereck, 1971, p. 7). Third, in creating range maps for New York State, Little and Viereck created their maps through herbarium records, State publications, and field trips, but did not consult OLSRs. In light of these issues, this

study’s SDM results may provide an important revision to chestnut distribution in western NYS and motivate additional study of chestnut range there.

Regarding differences between SDM predictions and the Paciorek et al. map (2016; Fig. 1b), ecological processes dictating species presence versus abundance may differ, leading to the observed

Table 6
A summary of protected lands, along with high-consensus predicted suitable habitat for chestnut within protected lands, across different land managers within the study area. “High-consensus” suitable habitat is where ≥ 7 out of 9 species distribution models predicted suitable habitat. NGO = non-governmental organization.

	State	Local	NGO	Federal	Tribal	Other
Total protected land (km ²)	1251.2	239.5	131.0	176.2	84.5	10.2
Percent of total protected land	66.1%	12.7%	6.9%	9.3%	4.5%	0.5%
High-consensus predicted suitable habitat (km ²)	620	37	20	7	3	2
Percent of total high-consensus predicted suitable habitat	89.9%	5.4%	2.9%	1.0%	0.5%	0.3%
High-consensus predicted suitable habitat (km ²), ≥ 1 km ² patches only	532	13	6	–	–	–
Percent of total high-consensus suitable habitat, ≥ 1 km ² patches only	96.6%	2.3%	1.1%	–	–	–

dissimilarities between maps. At least one study found that while plant SDMs provided some insight into where relative abundance would be high, they overestimated the range of habitats where high species abundance would occur (Van Couwenberghe et al., 2013). Similarly in this study, high estimated relative abundance in previous work (Paciorek et al., 2016) coincided with high-consensus suitable areas predicted by SDMs, but not always vice-versa. Future work could explore estimating chestnut abundance at fine-resolution using timber descriptions from OLSRs, since research has suggested that the order of taxa listed in timber descriptions might approximate relative abundance in accordance with rank abundance distribution models (Larsen et al., 2015).

This study contributes to an understanding of which environmental conditions are favored by chestnut. SDMs agreed with previous knowledge regarding the importance of acidic soils and steeper, well-drained upland sites to chestnut distribution (see literature in Section 1), including in regions bordering the study area (i.e. southern Ontario; Tindall et al., 2004). Given the high importance of these two predictors across most SDMs (Table 3), and the disagreement on the importance and nature of the relationship between chestnut and other predictors (Table 4), results suggest that within the study area, soil acidity and terrain slope were the main drivers of chestnut distribution at the extent and resolution of analysis. Unlike previous studies (Thomas-Van Gundy and Strager, 2012; Tindall et al., 2004), this study did not find that soil sand was an important predictor of chestnut distribution, although sandy soils within the study area often correspond with acidic soils. In focusing on environmentally-suitable sites for chestnut reintroduction, this study did not incorporate Native American variables as predictors of chestnut; Native American land use may have promoted chestnut in the study area within approximately 10 km of village sites (Black et al., 2006; Tulowiecki and Larsen, 2015).

Despite containing a portion of the northerly limit of chestnut, this study's SDMs suggest that the observed limit in the study area is due to soil and topography rather than climate conditions as might be expected. Even though chestnut is sensitive to frost (Gurney et al., 2011), the northern portion of the study area where chestnut is absent is actually warmer (including warmer winters) than the southern portion. The warmer northern portion, however, contains flat terrain and mildly acidic to neutral soils that are less preferable to chestnut, with only highly localized sites favorable for chestnut (Fig. 3). Supporting this study's findings is the observation that chestnut is presently found at higher latitudes on gentle slopes and sandy acidic soils in neighboring southern Ontario (Tindall et al., 2004). Older range maps for chestnut compiled by Russell (1987) also suggest a higher latitudinal limit for chestnut.

This study shows that predicted suitable habitat for chestnut in the study area falls largely on private lands (Table 5). While chestnut restoration has been explored largely on federal lands (Clark et al., 2014), the results suggest that within the study area, chestnut restoration may require the participation of mainly private landowners to facilitate reintroduction. Where it is desired to reintroduce chestnut to protected lands, results suggest that it should occur largely on those managed by New York State. This study did not evaluate actual land cover at each protected land parcel to assess the feasibility of reintroducing chestnut into existing forests or within afforestation sites, but rather provided a more parcel-level understanding of protected lands that may contain suitable habitat for chestnut.

One potential limitation in using historical data to model suitable sites for chestnut is that hybrid or transgenic chestnut might have different habitat requirements than pure American chestnut. However, one modeling study suggested that the climatic requirements of Chinese chestnut and American chestnut strongly overlap (Fei et al., 2012). At least one seedling growth study found that optimal habitat for pure American chestnut and hybrid chestnut were statistically the same in Virginia, and that both preferred dry upper slopes and ridges (Griscom and Griscom, 2012). Another study found comparable survival of pure

American chestnut and hybrid chestnut growing on acidic abandoned surface mines (Skousen et al., 2013). Other guides suggest Chinese chestnut prefers acidic, well-drained soils similar to American chestnut (Gilman and Watson, 1993).

6. Conclusion

In a novel synthesis of historical data, SDMs, and current data on land ownership, this study expands upon the body of literature concerning the distribution of chestnut and issues surrounding its potential reintroduction to eastern US forests. Within the study area, this study found that chestnut prefers acidic soils on steeper terrain, and offers a revision to chestnut range at a fine resolution. The study suggests that the historical distribution of chestnut falls mostly on private lands, manifesting that chestnut reintroduction will depend upon the co-operation of private landowners along with governmental and non-governmental agencies. The maps and findings of this study serve to identify sites to prioritize for potential reintroduction of chestnut to maximize success.

CRedit authorship contribution statement

Stephen J. Tulowiecki: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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