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RESEARCH ARTICLE

Modelling the historic distribution and habitat of American chestnut (*Castanea dentata*) in Georgia, USA using edaphic and landform predictors

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Abstract

The loss of American chestnut (*Castanea dentata* Marsh. Bork.) caused ecological change in many community types of the eastern United States. Restoration is challenged by climate change and two naturalised invasive non-native diseases, chestnut blight (caused by *Cryphonectria parasitica* [Murrill] M.E. Barr) and Phytophthora root-rot (caused by *Phytophthora cinnamomi* Rands). Learning how to overcome these challenges in the southern portion of the former chestnut range may make range-wide restoration efforts more successful because these pressures are likely strongest in southern portions of the range. To establish a baseline of chestnut distribution and environmental correlates, we used ca. 1830 land lottery maps to document the historic abundance and distribution of chestnut in Georgia. Land lottery surveyors documented 717,901 trees within our study area, identifying 15,710 as chestnut. We used their data to create a species distribution model with soil and landform predictors, factors possibly related to disease risk and predicted the relative habitat suitability for chestnut throughout much of the State. Our results revealed that long-held assumptions about chestnut range and abundance in Georgia are incorrect. Chestnut was less common in northern Georgia and more common in the Piedmont than previously postulated, and chestnut ranged well into the Coastal Plain. Soil and landform variables adequately predicted chestnut distribution and habitat suitability models predicted that chestnut occupied a wide diversity of habitats; habitat preferences were complex and differed by physiographic province. All the models agreed that chestnut preferred higher elevation, more slope and landform curvature, but the relationship of chestnut to other variables was difficult to generalise and may have been context dependent. These results can be used to guide re-introduction and maximise success in the face of changing climate and non-native disease risk.

Highlights

- Anecdotal accounts limit the historic range of American chestnut in Georgia to the Blue Ridge, Appalachian Plateau and Ridge and Valley physiographic provinces; however, historic land lottery maps dating from the early 1800s documented chestnut throughout the Georgia Piedmont and much of the Coastal Plain;
- Chestnut was found in a wide range of Georgia habitats in every physiographic province before the introduction of non-native pathogens, sometimes in high abundance and sometimes as less dense components of habitats with other dominant or co-dominant species;
- Although patterns of chestnut distribution were largely driven by elevation and slope, other environmental factors including aspect, landform curvature, number of frost-free days, percentage clay in soil and soil pH significantly influenced chestnut distribution in Georgia. These patterns varied by physiographic province, suggesting chestnut habitat was not monotypic across Georgia;
- Restoration efforts that recognise regional differences and the full suite of diverse habitats that once included chestnut may be more likely to succeed. Our models and regional habitat suitability maps can be used to guide planting site selection, while also considering the large variability inherent in ecological restoration of chestnut across multiple physiographic provinces;
- As they are relatively fine scale, edaphic and landform factors are useful in predicting suitable habitat for plants and may be used in conjunction with climate change predictions to guide site selection for species reintroductions that will be sustainable into the foreseeable future.

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PENSOFT

Keywords

American chestnut, *Castanea dentata*, land lottery map, habitat suitability, historic distribution, landform, soil, species distribution model, witness tree

Introduction

American chestnut (*Castanea dentata* [Marshall] Borkhausen, henceforth chestnut) was once a fundamental component of forest ecosystems across 29 eastern U.S. States (covering > 800,000 km^2) and two eastern Canadian Provinces. The functional elimination of chestnut from its entire range has caused this species to be listed as vulnerable or critically imperilled in 14 States and provinces and caused a loss of diversity in numerous community types as well as unknown changes in plant and animal populations throughout its former range (Braun 1950; Hawkins 2006; Elliott and Swank 2008; Wright et al. 2022; NatureServe 2024). Genetic, breeding and restoration programmes have been established to restore the species (Griffin 2000; Anagnostakis 2012; Clark et al. 2014) and nearly a century of work has brought conservationists closer to this achievement (Westbrook et al. 2019; Westbrook et al. 2020).

The demise of chestnut was caused by two non-native invasive diseases; first, Phytophthora root rot (PRR) (causal organism: *Phytophthora cinnamomi* Rands) in the mid-1800s, followed by chestnut blight (causal organism: *Cryphonectria parasitica* [Murrill] Barr) in the early 20th century (Anagnostakis 2001). Both events were poorly documented by modern standards (Paillet 2002; Jacobs 2007) and little is known about the full historic chestnut distribution or range of ecological communities in which chestnut occurred before PRR (Woods 1953; Kane et al. 2020; NatureServe 2024). Remnant root-sprouts and an occasional mature chestnut tree remain throughout the former range, but these are a poor measure of the former full extent of the species. Although some anecdotal historic accounts describe stands of pure chestnut, this level of abundance could have been a misleading relict of prior timber harvest and was likely the exception (Frothingham 1924). Ultimately, there remains no consensus on the distribution or abundance of chestnut prior to these disease outbreaks to guide restoration, particularly in the southern portions of the range where PRR may have been the most destructive and where losses predate most forest and botanical inventories (Little 1977; Faison and Foster 2014).

Understanding chestnut in the southern portions of its former range and in Georgia, in particular, may be valuable to range-wide recovery efforts. With elevations ranging from sea level to near the upper limits of chestnut tolerance (Wang et al. 2013), information from Georgia may guide recovery across the southern U.S. and at higher latitudes (Von Humbolt et al. 1807). Due to climate change, the pressure from PRR which until recently was largely limited to latitudes below 40 degrees will likely shift northwards (Bergot et al. 2004; Gustafson et al. 2022), making southern strategies to overcome PRR germane to recovery efforts range-wide. Climate change may also make understanding chestnut habitat in the southern limits of its former range valuable to ensuring this species' survival to the north as chestnut range shifts northwards (Adeyemo and Grainger 2023).

Successful restoration will also depend on a better understanding of the habitat needs of this species, as evidenced by the mixed success of many test orchards and restoration test plantings. While breeding programmes show promise for disease resistance, improved chestnut stock will not be immune to PRR or chestnut blight (Westbrook et al. 2019; Westbrook et al. 2020). Finding the most suitable habitats for restoration using habitat modelling could help mitigate disease pressures, increase planting success, ensure that chestnut is restored to appropriate communities and improve use of limited resources. Knowing as many of the places where chestnut once occurred as possible, rather than only the most dominant or relict sites, may also ensure its restoration to the full range of communities and habitats possible, improving the resilience of restoration efforts (Frothingham 1924; Laport et al. 2022).

Georgia is especially well-suited for this research because of a systematic survey of tree species composition conducted between 1804–1832 as part of the Georgia land lottery. "It shall be the duty of the surveyors … to mark, or cause to be marked, plainly and distinctly upon trees, if practicable, otherwise on posts, all stations and all lines which they may be required to run for the purpose of making the surveys (and) to cause all such lines to be measured with all possible exactness, within a half chain, containing thirty-three feet" (Georgia General Assembly 1825). Although the surveys were conducted to facilitate the redistribution of land following the forced removal and genocide of native peoples by the Georgia and United States governments (French 1978; Bleakley and Ferrie 2010), they inadvertently documented forest composition prior to large-scale forest clearing, the arrival of chestnut blight and possibly before PRR was widespread (Frothingham 1924; Crandall 1945; Anagnostakis 1995; Anagnostakis 2012) by recording 'witness trees' along land lot boundaries.

Other researchers have used species distribution modelling techniques to investigate environmental relationships of American chestnut (see Tulowiecki (2025) for a summary). Species distribution modelling, also known as habitat suitability modelling, was specifically developed to relate geospatial species occurrence data to environmental variables using various techniques that can accommodate virtually all types of predictor data (continuous and categorical), response data (presence/absence or presence only), relationships (simple linear to complex non-linear) and approaches (parametric and non-parametric) (Guisan and Zimmermann 2000; Peterson et al. 2011). Which approach works best is a matter of scale, the types of data available, the relationship of chestnut to its envi-

ronment within the range explored for the study and the intended use of the research (Tulowiecki 2025). For instance, some researchers are interested in range shifts due to climate change so they may use climate data at a scale relative to the species range (e.g. Barnes and Delborne (2019); Adeyemo and Granger (2023)), while other researchers are interested in species re-introduction so they may use edaphic factors at a more site-specific scale (e.g. Fei et al. (2007); Zhang et al. (2019)). While our effort lacked climate data that was contemporary with land lottery surveys, Georgia has other predictor variable data available on a scale ≤ 100 m^2 including a wide range of elevation, soil types and qualities and physiographic provinces with varying geologic origins that can be assumed to have changed little since the 1800s.

Our objectives were to: a) model the historical distribution (i.e. create a species distribution model, SDM) of chestnut in Georgia to determine which environmental variables were correlated with chestnut presence and b) to create a habitat suitability map, based on the best performing species distribution model or set of models for the purpose of assisting site selection for species re-introduction. In addition to modelling at the scale of the whole State, we also modelled chestnut distribution and habitat in each of Georgia's five distinct physiographic provinces (Fenneman and Johnson 1946) individually as prior research demonstrated that chestnut SDM results are dependent on scale (Henderson et al. 2023) and physiographic province (Black et al. 2002).

Materials and methods

Our study took place in the State of Georgia, United States of America. At 153,910 km^2, Georgia is a relatively large and diverse State. It contains five distinct physiographic provinces, several mountainous, others rolling or relatively flat. Soils vary widely from sandy to rocky to heavy clay. Georgia has the sixth highest tree species diversity of the 50 United States and the third highest tree diversity within the former range of chestnut. Modern and historic forest types within our study area range from pine dominated to hardwood dominated. Elevations range from sea level to 1,458 m, near the upper limits of chestnut tolerance (Wang et al. 2013).

Land lot surveyors located, blazed (marked) and identified witness trees at and near the boundary intersections of all lots which were typically 82 hectares, but with a minority of lots surveyed to 16, 65, 82, 101 or 198 ha lot sizes; lots were square. Witness trees were selected to be large enough to blaze and as close as possible to the lot boundary, within 10 metres. Trees were blazed where lot corners met, one tree at each boundary intersection (representing four lot corners) and a single tree on each boundary line extending from each intersection in the four cardinal directions; thus each boundary intersection where four land lots met, a total of five trees were blazed, arranged in the shape of a + sign with one tree in the middle and one tree in each of the cardinal directions. Tree species, their location and lot numbers were compiled on to hand drawn maps which we accessed at the Georgia State Archives and the Georgia GIS Clearinghouse (Georgia Spatial Association 2024). Remains of some blazed trees are also housed at the Georgia State Archives; lot numbers carved into the trees were approximately 15 cm tall and 10 cm wide, and many land lots were identified by three digits, thus we speculated blazed trees were likely 30–35 cm diameter at breast height or larger.

We downloaded digitised, georeferenced Georgia land lottery maps (1804–1832) from the Georgia GIS Clearinghouse (Georgia Spatial Association 2024). Using ArcGIS Pro v.3.1.0, we systematically searched all 392 maps for American chestnut locations (indicated on most maps by "Ches" or "chestnut", not be confused with chestnut oak which was designated by surveyors as "Mountain Oak", "M Oak", "Ch Oak" or "Ches O") and created a point in a vector layer for each location. For each physiographic province (Appalachian Plateau, Blue Ridge, Ridge and Valley, Piedmont and Coastal Plain as defined by Fenneman and Johnson (1946)), we divided the number of chestnuts detected in that province by the total number of trees sampled in that province to estimate the percentage of trees that were chestnut by physiographic province. We did not include areas beyond where land lottery surveyors documented chestnut when calculating percentage chestnut in the Coastal Plain.

We downloaded the Gridded Soil Survey Geographic (gSSURGO) Database (NRCS Data 2025) for the State of Georgia, clipped the extent to match the chestnut data extent (land lottery data only covered ~ 70% of the State, see Fig. 1) and using ArcGIS Pro joined "Component" and "Chorizon" tables to the 10 m map unit raster. We isolated the following soil attributes from the gSSURGO tables that were previously shown or assumed, based on expert opinion to affect American chestnut distribution (Russell 1987; Fei et al. 2007; Rhoades et al. 2009; Tulowiecki 2020; Henderson et al. 2023): particle size class, drainage class, percentage clay, erosion class, representative soil pH, number of frost-free days, parent material kind, parent material origin, soil taxonomic class (order, suborder, great group and subgroup) and we created independent raster layers for each of these variables (see SSURGO metadata tables and columns report [NRCS Data] and Keys to Soil Taxonomy Thirteenth Edition [Soil Survey Staff 2022] for descriptions of variables). We used 1/3 arc-second (10 m) digital elevation maps from the National Elevation Dataset (USGS 2022) to create an elevation raster layer in ArcGIS Pro. From the elevation raster layer, we used ArcGIS tools to calculate and create raster layers for elevation (m), aspect (degrees), slope (degrees) and curvature (amount of landform concavity or convexity [-1 to +1, respectively with 0 being flat]). As aspect is a radially distributed variable with 1° and 359° being nearly equal, we converted aspect raster data to two linear variables "eastness" (sin(aspect°(π/180)) and "northness" (cos(aspect°(π/180)). We processed all raster layers to

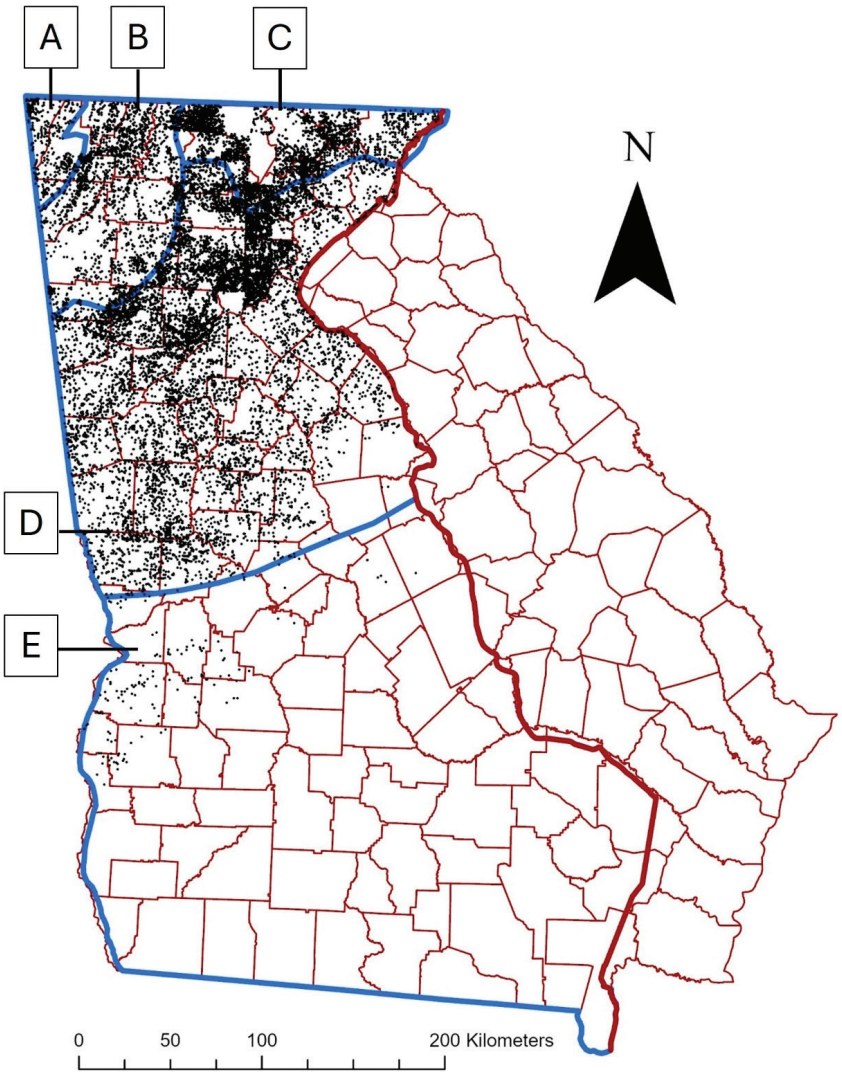


Figure 1. Locations of American chestnut (black dots) on Georgia land lottery maps (1804–1832). Thin red lines are GA county boundaries, thick red lines are extent of land lottery maps, blue lines distinguish physiographic provinces: **A.** Appalachian Plateau, **B.** Ridge and Valley, **C.** Blue Ridge, **D.** Piedmont and **E.** Coastal Plain.

match the projection and extent of the chestnut layer produced from the land lottery data.

For species distribution modelling, we used the sdm package v.1.1-8 (Naimi and Araújo 2016) for R v.4.2.1 (R) that allows users to compare various relationships and approaches to find the best fit for datasets and desired outputs (Naimi and Araújo 2016). We checked all 18 predictor variables for collinearity; none had collinearity issues, so we retained them all for modelling. We classified class, drainage, great group, order, particle size class, parent material kind, subgroup and suborder as categorical predictors (NRCS Data 2025). As we did not have independent training data, we used a subset of chestnut occurrence data for model training. As we did not have absence data, (surveyors did not record if a chestnut tree was not observed), we created 47,130 random background points, three times the number of chestnut locations (Barbet-Massin et al. 2012; Naimi and Araújo 2016; Sillero and Barbosa 2020; Whitford et al. 2024), using the 'gRandom' function (random in geographic space). To compensate for limited computing power, we converted predictors to 100 m resolution from a 10 m resolution using ArcGIS Spatial Analyst Resample tool.

Using the processed environmental raster data, the chestnut occurrence points and the background points, we created a chestnut species distribution model using the sdm package for R. We evaluated model performance using standard model selection metrics generated by the sdm for R package such as area under the curve (AUC), correlation score (COR) and true skill statistic (TSS) (for an explanation of these statistics, see Santini et al. (2021)). We intended to use the ensemble method that averages several user-selected modelling methods including boosted regression tree, generalised additive, generalised linear, maximum entropy and random forest, all commonly used SDM techniques for American chestnut (Tulowiecki 2025). We replicated each model run three times and tried both subsampling and bootstrapping data partitioning methods with 30% of the data reserved for testing models. The original land survey methods and our sdm methods ensured no spatial autocorrelation between training and

test data (Naimi and Araújo 2016). Random forest with the bootstrapping data partitioning method consistently produced significantly higher AUC scores and less overlap in density plots that demonstrated better ability to differentiate between chestnut occurrences and background points, so we only report results from random forest. We generated variable importance factors (normalised to sum to 1) to determine which environmental variables had the most influence on the model and species response curves for the random forest model to visualise how chestnut responded to individual variables that had significant influence on the model.

We divided all the processed raster and vector data by physiographic province: Appalachian Plateau, Ridge and Valley, Blue Ridge, Piedmont and Coastal Plain (Fenneman and Johnson 1946), then repeated the entire process from checking for collinearity to modelling to generating variable importance factors and species response curves for each individual physiographic province. Once we had models for the whole State (i.e. all portions covered by the land lottery maps) and each of the five provinces, we ran the 'predict' function in sdm for r to predict relative habitat suitability, based on the models we created and wrote the results to raster files that we mapped in ArcGIS Pro.

Results

A thorough inspection of the land lottery maps revealed that not all trees were identified to species, for example, 'pine' and 'bay' and many colloquial names required some research to confirm species; 66 recognisable species were documented including many intriguing species such as 'chinquapin' (*Castanea pumila* [Linnaeus] P. Miller) and 'wahoo' (*Ulmus alata* Michaux). Within our study area 717,901 trees were sampled, of which 15,710 were identified as chestnut (2% of trees sampled, Fig. 1). In the Coastal Plain portion of our study area (within the range of chestnut occurrences), 0.25% of trees sampled were chestnut, 3.1% in the Piedmont, 2.8% in the Blue Ridge, 1.0% in the Ridge and Valley and 1.0% Appalachian Plateau. Chestnut abundance, however, was not distributed homogeneously or randomly across the landscape; many discrete regions had higher or lower abundance than these values (Fig. 1).

The ranges of environmental variables differed by province (Table 1). There were no collinearity issues amongst variables for the whole-State model or any of the individual province models, so we retained all variables for further analyses. For the whole State and each province, we constructed chestnut species distribution models that included all variables (full models), but some variables (percentage clay, erosion class, pH and parent material origin) had too many data gaps in the gSSURGO database to use them to build a useful predictive habitat suitability map, so we also constructed species distribution models (reduced models) and predictive habitat suitability maps without these variables.

The full State-wide mean model performance had an AUC score of 0.96, COR score of 0.74 and TSS score of 0.77, which is considered good to very good, but not overfitted (Allouche et al. 2006; Shabani et al. 2018) (Table 2). Elevation had the greatest influence on the model by an order of magnitude (normalised variable importance score of 0.66 compared to 0.04–0.10 for other variables), followed in order of importance by number of frost-free days, slope, percentage clay, curvature, pH, northness and eastness (Fig. 2). Other variables (all soil taxonomy variables, particle size class, drainage class, erosion class, parent material kind and parent material origin) did not contribute significantly to the model. The species response curves indicated that the probability of chestnut occurrence increased with elevation, slope, eastness, pH, percentage clay and any type of landform curvature, convex or concave (Table 2). The probability of chestnut occurrence decreased with number of frost-free days. The relationship of chestnut to northness was too complex to be generalised (Fig. 3).

The reduced whole-State mean model performance was nearly the same as the full model (Table 2). Elevation had the greatest influence on the probability of chestnut occurrence, followed by slope, number of frost-free days, curvature, northness and eastness (Fig. 4). Species response curves were similar to those of the full model, except that chestnut was positively related to northness and the relationship to number of frost-free days was too complex to be generalised (Table 2, Fig. 5).

As the full model produced a habitat suitability map with numerous data gaps (due to data gaps in some of the SSURGO soils variables), we used the reduced whole-State model to construct a State-wide habitat suitability map (Fig. 6). Due to the overwhelming influence of elevation on the species distribution model and the differences in elevation amongst the State's physiographic provinces, the whole-State model suggests the highest concentra-

Table 1. Range of continuous environmental variables considered in this study.

Physiographic province	Curvature (1/m)	Eastness and Northness (transformed degrees)	Elevation (m)	Frost-free days	pH	Slope (degrees)	Clay (%)
Appalachian Plateau	-1.19–1.07	-1 - 1	194–717	180–217	4.6–7.0	0–77	9–55
Blue Ridge	-1.08–0.95	-1 - 1	234–1458	140–235	4.6–7.3	0–74	6–53
Coastal Plain	-0.97–0.91	-1 - 1	3–248	180–287	3.2–7.9	0–74	1–70
Piedmont	-1.06–1.46	-1 - 1	61–1003	140–275	4.5–7.0	0–77	3–60
Ridge and Valley	-0.90–0.86	-1 - 1	171–868	180–241	4.5–7.5	0–69	3–69
Whole State	-1.19–1.46	-1 - 1	3–1458	140–287	3.2–7.9	0–77	1–70

Table 2. Model performance scores and generalised species responses to environmental variables for reduced models (top) and full models (bottom). + and – symbols indicate positive and negative relationships, respectively. For curvature, the first symbol indicates if chestnut had a relationship with curvature (convex or concave) and the symbol in parenthesis indicates preference for convex (+) or concave (-). Question marks indicate no clear unidirectional pattern in species response. AUC = area under the curve, COR = correlation score, TSS = true skill statistic.

Reduced Model											
Model	**AUC**	**COR**	**TSS**	**Curvature**	**Eastness**	**Elevation**	**Frost-free days**	**Northness**	**Slope**		
Whole State	0.95	0.76	0.77	+(+,-)	+	+	?	+	+		
Coastal Plain	0.95	0.79	0.82	+(-)	+	+	-	-	+		
Piedmont	0.89	0.66	0.61	+(-)	?	+	+	?	+		
Ridge and Valley	0.88	0.65	0.57	+(-)	?	+	?	+	+		
Appalach. Plateau	0.86	0.62	0.56	+(+)	?	+	-	-	+		
Blue Ridge	0.86	0.63	0.54	+(-)	+	+	+	-	+		
Full Model											
Model	**AUC**	**COR**	**TSS**	**Curvature**	**Eastness**	**Elevation**	**Frost-free days**	**Northness**	**Slope**	**pH**	**%Clay**
Whole State	0.96	0.74	0.77	+(+,-)	+	+	-	?	+	+	+
Coastal Plain	0.96	0.77	0.84	+(-)	+	+	-	-	+	?	?
Piedmont	0.89	0.67	0.60	+(-)	?	+	+	+	?	?	?
Ridge and Valley	0.86	0.62	0.54	+(-)	+	+	-	+	+	?	+
Appalach. Plateau	0.87	0.64	0.60	+(+)	?	+	-	-	+	-	-
Blue Ridge	0.86	0.61	0.56	+(+)	+	+	+	?	?	-	?

tion of highly suitable habitat is in the upper elevations of the State, especially the upper Piedmont and Blue Ridge.

Individual physiographic province models ranged in performance from good to very good (AUC score 0.86–0.95). The full and reduced Coastal Plain models performed best (Table 2). The same variables that significantly influenced the full and reduced whole-State models significantly influenced each of the physiographic province models, with elevation the most influential variable in every model, except the full Coastal Plain model where slope influenced probability of chestnut occurrence more than elevation (Figs 2, 3, Table 2). The relative importance of elevation compared to other significant variables was less in the mountainous regions of the State (Ridge and Valley, Appalachian Plateau and Blue Ridge) than in the Piedmont or Coastal Plain, true for both full and reduced models. Probability of chestnut occurrence was positively associated with elevation and slope, except for the full models for the Piedmont and Blue Ridge where the relationship with slope was difficult to generalise (Figs 3–5). The relationships of eastness, northness, number of frost-free days, pH and percentage clay with chestnut occurrence were not consistent amongst full versus reduced models or amongst physiographic provinces. In no case was a relationship one di-

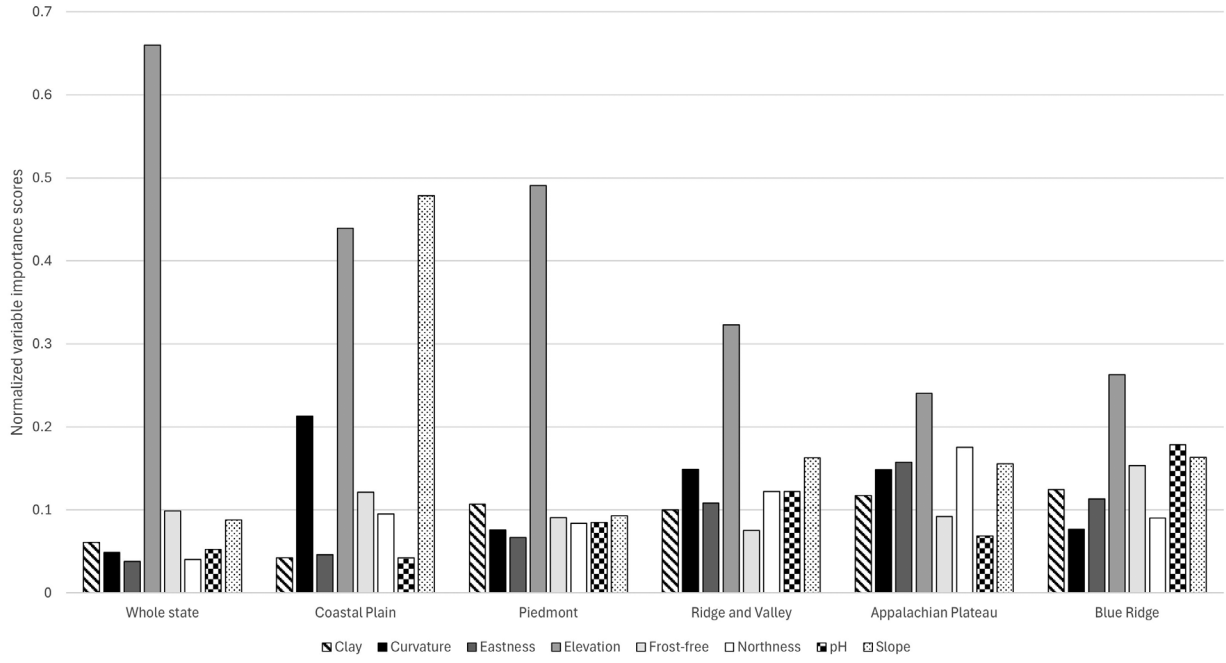


Figure 2. Normalised variable importance scores for full chestnut species distribution models.

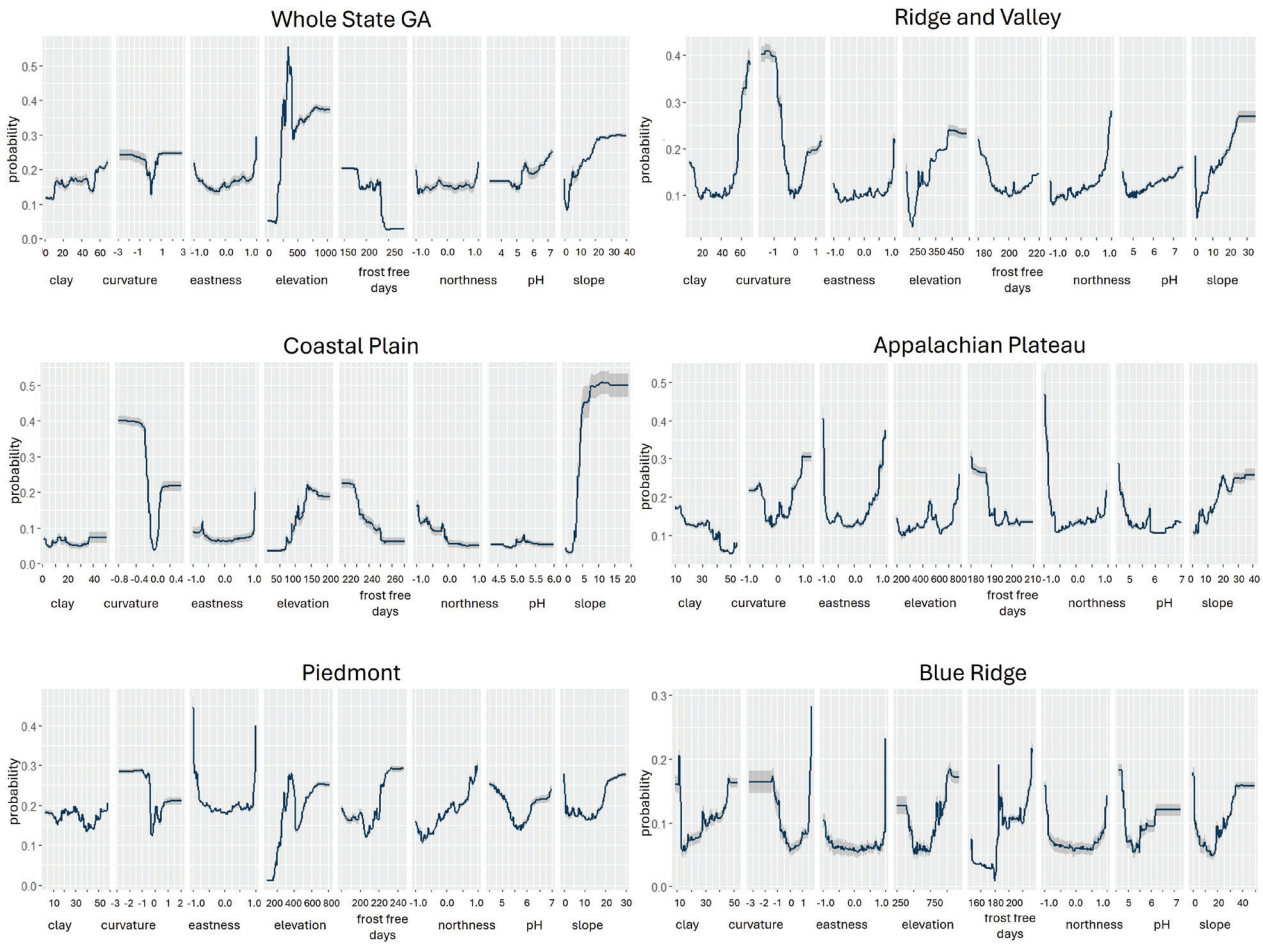


Figure 3. Species response curves for full species distribution models of American chestnut distribution in the whole State of Georgia and in each of its provinces individually.

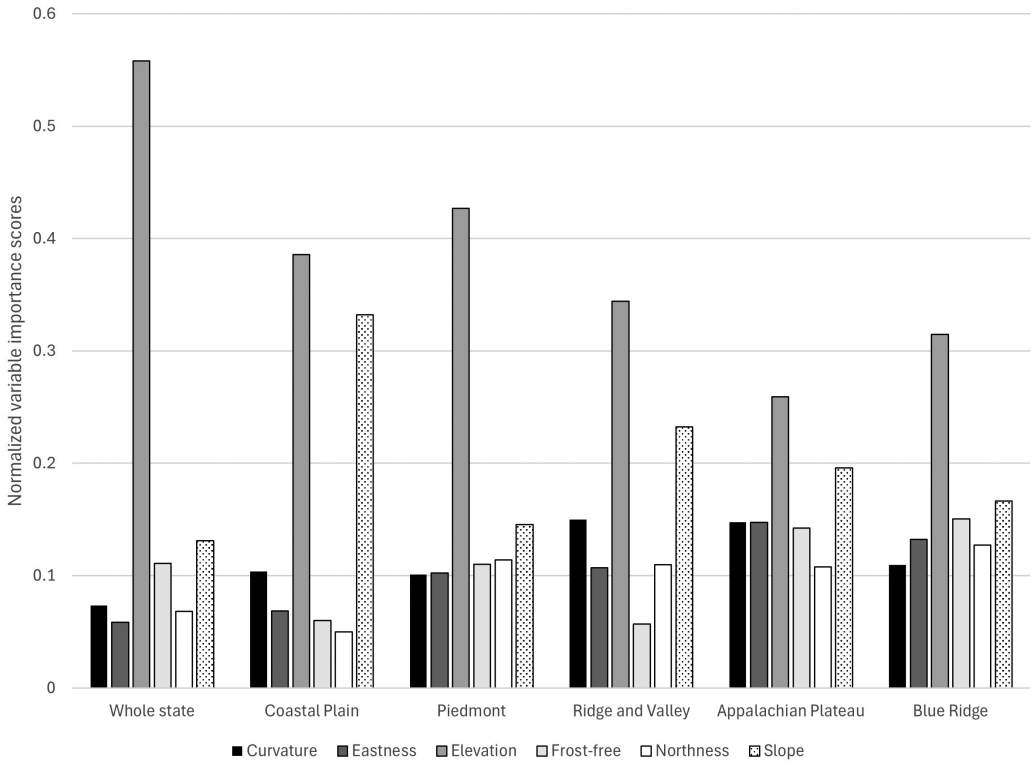


Figure 4. Normalised variable importance scores for reduced chestnut species distribution models.

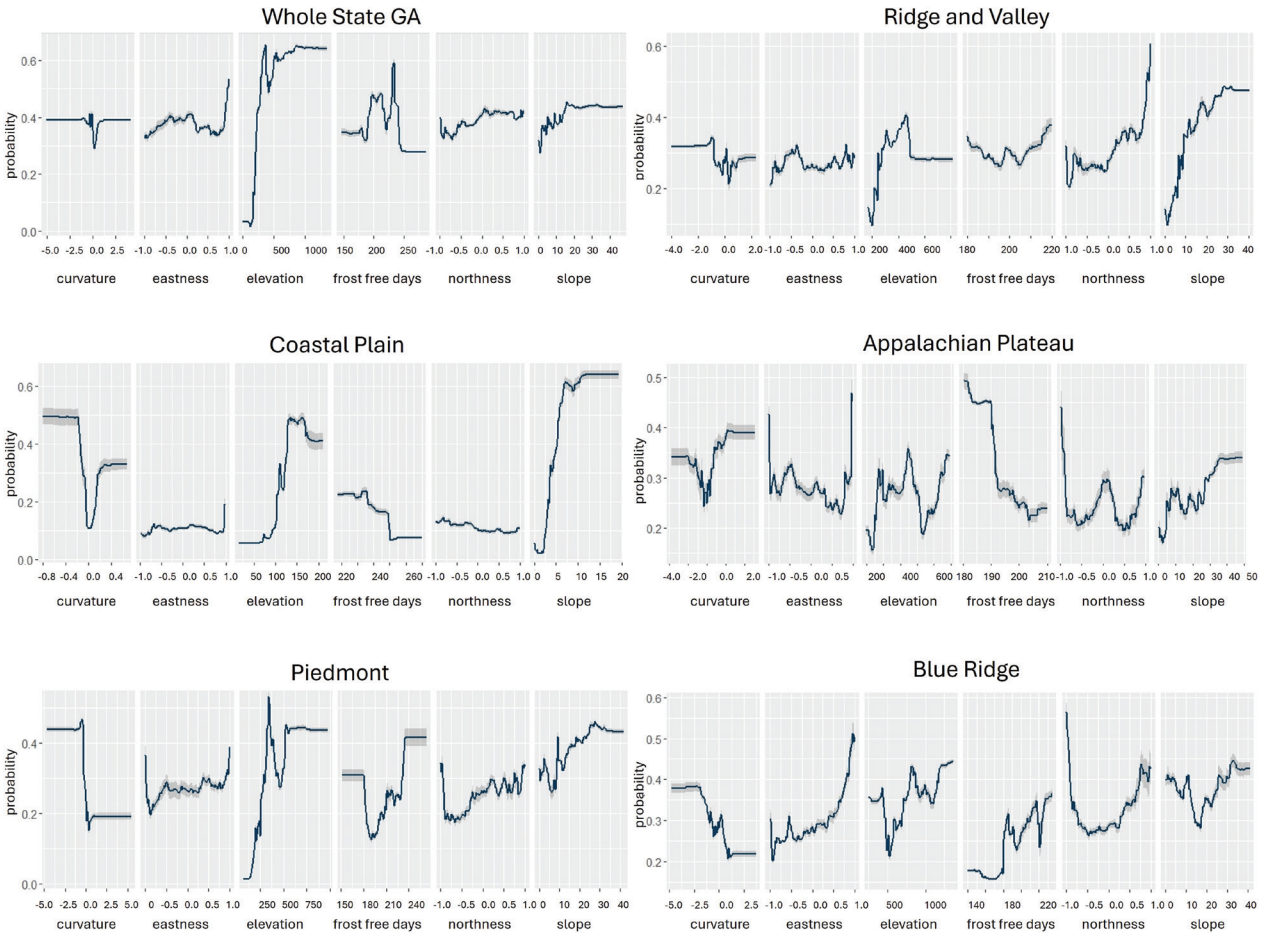


Figure 5. Species response curves for reduced species distribution models of American chestnut distribution in the whole State of Georgia and in each of its provinces individually.

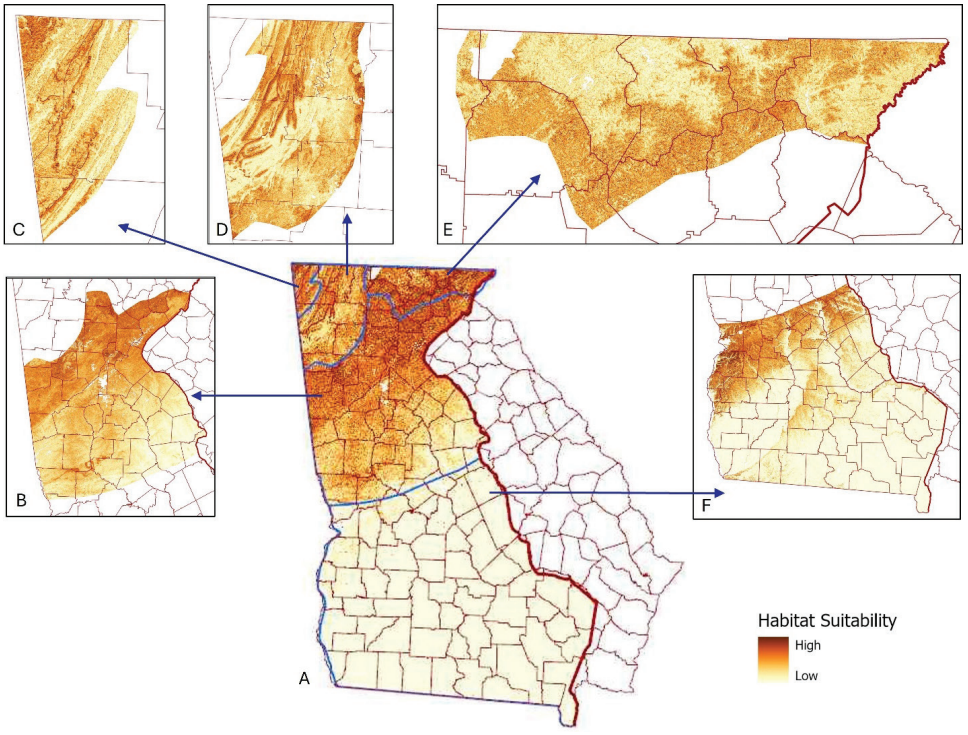


Figure 6. American chestnut habitat suitability map for **A.** Whole State model of Georgia and individual physiographic province models; **B.** Piedmont; **C.** Appalachian Plateau; **D.** Ridge and Valley; **E.** Blue Ridge and **F.** Coastal Plain. Thin red lines are county boundaries; thick red lines mark the extent of the land lottery maps. Darker orange is higher chestnut suitability; lighter orange is lower chestnut suitability.

rection in the full model (e.g. positive) and the opposite direction in the reduced model (e.g. negative) for the same physiographic province. If there was a difference between the full and reduced model, it was because the relationship of a variable in one model had a clear pattern (positive or negative) and, in the other model, was too complex to generalise as positive or negative (Table 2, Figs 3–5).

Discussion

The methods employed by land lottery surveyors documented a heterogeneous distribution of chestnuts across the 1800s landscape. Surveys documented a chestnut abundance far below most conventional estimates for the Blue Ridge, Ridge and Valley and Appalachian Plateau and much higher in the Piedmont and Coastal Plain (Frothingham 1912; Braun 1950; Saucier 1973; Little 1977; Griffin 2000; TACF 2024). Although some bias is apparent in the witness tree data and differences in land lot size complicated our analysis, the land lottery surveys remain the most comprehensive and least biased dataset available for American chestnut distribution before chestnut blight and likely before large-scale effects of PRR (Anagnostakis 2012). While our estimates of chestnut abundance contradict many earlier studies, several other researchers have also concluded that accounts of a chestnut dominated landscape are apocryphal. A review of land lottery maps in the north-eastern United States by Thompson et al. (2013) also found chestnut did not comprise more than 3% of trees in the region and a study of land lottery maps in the upper Midwest came to a similar conclusion (Faison and Foster 2014). Other lines of evidence using pollen records (Watts 1980; Delcourt and Delcourt 1998) also concluded that American chestnut was not a dominant species in their respective study areas. The widespread acceptance of these overestimates, most often given as '25% or more' likely originated with observations of exceptional stands documented by E. Lucy Braun (1956). There she documented several stands of exceptionally high chestnut abundance, yet taken in whole, her study clearly documented that chestnut was not a dominant tree on the landscape (Faison and Foster 2014). Frothingham (1924) noted that, because of chestnut's ability to re-sprout prolifically after clearcutting, dense nearly pure stands of chestnut were most likely anthropogenic in nature. Despite several decades of strong science to the contrary, the myth of a landscape dominated by American chestnut remains stubbornly present.

It is worth noting several instances of apparent surveyor bias, where the frequency of chestnuts documented by surveyors abruptly changed along north/south or east/west lines. These were found at several locations where two or more land lottery maps joined and where a survey crew was apparently more or less inclined to use chestnuts as witness trees. The reasons for this are unknown, but, fortunately for our purposes, appear to be limited to few instances and a very small percentage of the trees sampled, with the preponderance of the land lottery dataset lacking these surveyor artefacts. Bias in these early surveys has been extensively studied (see Cogbill (2023) for a review) and can take other subtle forms. However, surveyor biases are most problematic when using relatively small sample sizes or when researchers are attempting to estimate tree density (Cogbill et al. 2018), neither of which are true for our work.

Soils data were problematic in several ways: the original format (Microsoft Access database or standalone tables that had to be linked to map units) was difficult to use, there were large amounts of missing data and data quality was sometimes questionable. The National Cooperative Soil Survey (NRCS NCSS 2024) that collects soils data in the United States relies on volunteers from different agencies to collect soils data, allows for different collection and testing methods and has been collecting data over a long time span and with different technologies (USDA 2017). This may explain why only three of the 12 soils variables we used (pH, frost-free days and % clay) had a significant influence on the species distribution models and may have resulted in some of the complex chestnut responses that were difficult to interpret. Nevertheless, our study and others provide evidence that these environmental factors are influential to chestnut distribution and, although we could not include pH, frost-free days and percentage clay in our predictive maps, they influenced the full species distribution models and should be given consideration when prioritising chestnut re-introduction sites.

Despite the challenges, our study revealed some results of particular interest, notably, the high abundance of chestnut in the Georgia Piedmont, 11% higher than in the Blue Ridge and over 200% higher than in the Ridge and Valley and Appalachian Plateau, provinces where high chestnut abundance was better documented and is widely accepted. Our findings contradict anecdotal accounts and many range maps which exclude most of the Georgia Piedmont from the chestnut range (Little 1977); i.e. prior to chestnut blight and PRR chestnut was widespread in the Georgia Piedmont and abundant throughout much of this physiographic province at levels comparable to or higher than any other province in Georgia. Crandall et al. (1945), Woods (1953), Anagnostakis (2001) and others have speculated that chestnut was first lost in the Georgia Piedmont because of PRR which may have thrived in the warmer climate, lower slopes and heavier clay soils, however, the loss was poorly documented. PRR typically kills chestnuts on poorly drained or disturbed sites, leaving little evidence of their former occupancy, whereas chestnut blight more often top-kills chestnuts, leaving a legacy of chestnut sprouts to vouch for their former presence (Wang et al. 2013). The distribution of chestnut in the Coastal Plain is also notable where other maps exclude it entirely. Although it was apparently restricted to ridges, hilltops and steep river bluffs, chestnut was present and a significant component of some Coastal Plain ecosystems.

In our study, elevation was the only variable to which chestnut responded consistently across every province in

Georgia. Elevation has been a significant and often driving factor in nearly every chestnut distribution study that examined it (Tulowiecki 2025). Nearly every researcher has found that chestnut is positively correlated with elevation, likely due to a suite of factors associated with elevation (e.g. drainage, frost, exposure, community type, soil moisture etc.). These factors are often modelled and found to have no collinearity issues with elevation; however, the data may not be accurate enough or fine enough in scale to detect collinearity or significant effects on chestnut distribution or there may be an interaction of variables that is difficult to examine with currently available methods. While elevation could be interpreted as a proxy for climate factors, it is likely to have effects beyond climate alone. Laport et al. (2022) found that, even when accounting for several climate factors, their models indicated that habitat was less suitable at lower elevations. Tulowiecki and Larson (2015) concluded that climate variables were significant only in areas of extremely cold weather and Zhang et al. (2019) found that the significance of climate variables was reduced in areas with more suitable climate. The relative importance of elevation versus climate may also vary by scale; Henderson et al. (2023) found that, in their State-wide model, climate had the greatest influence on their model, but the factors most predictive of chestnut distribution in their park-level (smaller scale) model were edaphic and landform variables. As the purpose of our study was to provide information for restoration site selection at a more local scale, elevation was an essential variable to be considered even if climate is considered.

The relationship of chestnut to some environmental variables may be context dependent. Context can explain shifts between full and reduced models in the relative importance of environmental variables and context can explain the differences between the physiographic provinces in the direction of the relationship between chestnut and some environmental variables. For example, the range of environmental factors within the geographic area being described likely determines the strength of chestnut response to those factors. In our study, elevation was frequently the most influential of all the environmental factors, but elevation exerted the greatest influence on chestnut occurrence in the Piedmont and Coastal Plain where there is a much smaller range of elevations. As chestnut is cold-sensitive (Russell 1987; Laport et al. 2022; Henderson et al. 2023), within geographic areas with very high elevations, chestnut distribution is limited to lower elevations (Fei et al. 2007). In another example, slope was important in several studies throughout the range of chestnut, but the effect differed by physiographic province or region (Black et al. 2002; Santoro 2013; Zhang et al. 2019; Tulowiecki 2020). Slope was the second most important variable in many of our models, although it was much more influential in the Coastal Plain than any of the other Georgia provinces. In addition to chestnut varying in response to environmental factors throughout its range and across physiographic provinces, there may be interactive or synergistic effects amongst environmental factors that we were unable to examine. For example, the relationship of chestnut to northness in our whole-State model and in the Ridge and Valley province was positive, but the relationship was negative in the Coastal Plain and Appalachian Plateau. One explanation for this result was an interaction between aspect, province and other variables. This explanation is supported by the findings of Black and others (2002) who found chestnut was most probable on a north aspect with high relief and that species response to landforms varied across physiographic provinces.

Conclusion

American chestnut was more of a generalist species than a specialist that was limited mainly by elevation, but occurred in a wide variety of community types throughout a large range. Attempting to describe former chestnut distribution, based on where extant trees and sprouts are found today or a few anecdotal accounts, would lead to a very incomplete picture. As documented by Georgia land lottery maps, the current realised niche of American chestnut is a tiny fragment of the historic niche space due to recent anthropogenic filters, especially introduced pathogens. It should be alarming that we can make such a common wide-spread species functionally extinct, but resources dedicated to breeding combined with distribution and habitat modelling could enable successful re-introduction and conservation. Fine-scale edaphic and landform modelling could be used in conjunction with larger scale climate projection and range modelling to determine the suitability of habitat for American chestnut into the foreseeable future (Barnes and Delborne 2019; Adeyemo and Granger 2023; Henderson et al. 2023).

Although the whole-State habitat suitability map illustrated a much higher density of high-quality habitat in the upper Piedmont and mountainous regions of Georgia, we recommend restoration practitioners use our individual physiographic province models and habitat suitability maps to select areas of the province in which they work for re-introduction of chestnut. Far from a monotypic forest limited to the coves and ridges of Appalachia, the American chestnut once ranged across dozens of described ecosystems in Georgia, from mesic Coastal Plain bluffs to Piedmont montane longleaf pine (*Pinus palustris* P. Miller) and shortleaf (*Pinus echinata* P. Miller)-post oak (*Quercus stellata* Wangenheim) ecosystems, as well as numerous Appalachian communities (Tuttle and Kramer 2005); the American chestnut was highly adaptable with a varied and complex niche that was likely distinct in each physiographic province. Next steps towards restoration should endeavour to better describe the many communities where chestnut was present. By placing chestnut across the range of conditions and ecosystems where it once thrived, such efforts are more likely to succeed in a genuine and resilient restoration of this species.

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Author contributions

Nathan Klaus conceived the project, worked to have the land lottery maps digitised, searched all maps, created the shapefile of chestnut locations, researched the documentation of land lottery surveys, analysed the relative frequency of chestnut locations by province, wrote sections of this paper relevant to those activities plus the introduction and nagged Joyce for years to get this project done. Joyce Klaus manipulated soils and landform data in GIS to create working rasters, completed all modelling, created predictive maps, created all figures and tables, wrote the sections of this paper pertaining to those activities and procrastinated working on this project as much as possible. Each author also consulted the other on their portions of the work and edited the other's writing.

Data accessibility statement

Chestnut occurrence data and habitat suitability maps (TIFFs) produced by this research can be found at https://american-chestnut-data-gadnrwrd.hub.arcgis.com.

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Supplementary materials

Supplementary material 1

Locations of American chestnut (*Castanea dentata*) in Georgia, USA on circa 1800's land lottery maps (.txt)
Link: https://doi.org/10.21425/fob.18.161937.suppl1