Running Head: American chestnut at its southwest range limit

Environmental niche and demographic modeling of American chestnut near its southwestern range limit

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ABSTRACT—The inadvertent introduction and rapid spread of chestnut blight (caused by *Cryphonectria parasitica* (Murr.) Barr) in the early 20th century resulted in the demise of American chestnut (*Castanea dentata* (Marsh.) Borkh.; Fagaceae) as a major component of forest canopies and had negative impacts on eastern forest communities. Research efforts over the last century have documented the persistence of occasional trees and root crown/stump sprouts throughout much of the species' historic range providing the basis for ongoing breeding of blight-resistant stock and restoration efforts. Unfortunately, it remains unclear how much of the historic range remains climatically suitable for remnant trees that may harbor unique genetic variation for successful reintroduction efforts. Here we investigate whether the southwestern portion of the historical range remains environmentally suitable for undiscovered remnant populations of *C. dentata* using environmental niche modeling. We also use stage-structured matrix projection models to investigate the potential demographic future of *C. dentata* in W Tennessee, N Mississippi, SW Kentucky, and NW Alabama based upon observations of American chestnut in these areas over the last several decades. We found that suitable habitat associated with higher elevations and areas of high forest canopy cover occurs throughout much of the southwestern portion of the historical range and that populations of American chestnut in these areas are predicted to drastically decline over the next ~100-200 years without conservation interventions to mitigate the negative consequences of chestnut blight.

KEYWORDS—*Castanea dentata*, population matrix model, population size structure, restoration, species distribution modeling

INTRODUCTION

The unintentional introduction and rapid spread of chestnut blight (*Cryphonectria parasitica* (Murr.) Barr) in the early 20th century decimated American chestnut (*Castanea dentata* (Marsh.) Borkh.; Fagaceae) populations (Ziegler, 1920; Smith, 2000; Jacobs *et al.*, 2013; Dalgleish *et al.*, 2016). The loss of this species as a dominant canopy tree has profoundly impacted forest communities and the ecological dynamics of eastern hardwood forests. For example, the decline of annual large, edible seed production has impacted plant-animal interactions and wildlife population dynamics (Diamond *et al.*, 2000; Dalgleish and Swihart, 2012), and the loss of a major canopy tree has altered forest community dynamics, nutrient cycling, and fire regimes (Brooks, 1937, McCormick and Platt, 1980, Ellison *et al.*, 2005; Elliot and Swank, 2008, Jacobs *et al.*, 2013; De Bruijn *et al.*, 2014; Gustafson *et al.*, 2017). Given its previously widespread distribution, rapid demise, and ecological significance to the forests of eastern North America, policy and research efforts have been focused on the ultimate goal of breeding blight resistant trees and restoring American chestnut to its former range.

Research efforts since the middle of the 20th century aimed at conserving *C. dentata* have documented the persistence of root crown/stump sprouts, saplings, and occasional fruiting trees throughout much of the American chestnut's former distribution. For example, remnant populations of trees have been documented in parts of Connecticut (Stephens and Waggoner, 1980; Paillet, 1982, 2002), Massachusetts (Paillet, 1988, 2002), Virginia (Stephenson *et al.*, 1991), Ohio (Schwadron, 1995), southern Ontario (Tindall *et al.*, 2004, Van Drunen *et al.*, 2017), western New York (Laport, 2020), and southwest Tennessee (Laport *et al.*, 2020). Remnant trees are also continually being documented on crowd-sourcing mobile applications such as iNaturalist (www.inaturalist.org) and TreeSnap (www.treesnap.org), with many of these observations being

70 archived by the Global Biodiversity Information Facility (GBIF; www.gbif.org). These natural
71 history observations suggest the highest densities of remnant trees occur throughout the
72 Cumberland Plateau, Appalachian Mountains, and the northeastern US. Fewer contemporary *C.*
73 *dentata* occurrences are known from the southwestern range margin compared to core
74 distribution populations, but it is not clear to what degree this disparity reflects actual differences
75 in available habitat, population occurrence density, or whether this is because some parts of the
76 range have been under-surveyed (Jacobs *et al.*, 2013; Dalgleish *et al.*, 2016).
77 Ecological/Environmental Niche Modeling (ENM) or Species Distribution Modeling
78 (SDM) approaches provide one approach to identify areas that are environmentally suitable for
79 remnant American chestnut, and to aid conservation and reintroduction efforts. Recent studies
80 have implemented ENM/SDM approaches to investigate the current and future abiotic niche of
81 remnant American chestnut with the goal of identifying areas of ecological suitability throughout
82 the historical range to inform future restoration efforts. For example, models constructed using
83 known occurrences of American chestnut in Shenandoah National Park and Mammoth Cave
84 National Park projected suitable habitat in areas of relatively undisturbed upland forest, often on
85 slopes or at relatively high elevations. These studies also found that young forests on previously
86 cultivated lands were almost universally predicted as unsuitable for chestnut occurrence (Fei *et*
87 *al.*, 2007; Santoro, 2013). Another recent study using ENM/SDM approaches examined the
88 projected abiotic habitat suitability for American chestnut under multiple scenarios of climate
89 change over the next several decades. At a continental scale, this study found that suitable habitat
90 would shift northward into the northeastern US and southern Canada (Barnes and Delborne,
91 2019). These studies provide critical information for guiding the discovery, protection, and
92 reintroduction of American chestnut in mountainous core parts of its historical range where land

93 use history resulted in the preservation of relatively large areas of suitable habitat, or at the
94 northern range margin where the species may be expanding into new habitat in response to
95 climate change. Unfortunately, these previous models offer only a limited window into the
96 ecology of the species near the southern and western historical range limits by relying principally
97 upon occurrences from core parts of the range or by investigating continental scale patterns that
98 paint in broad strokes.

99 Populations occurring near species' range limits may inhabit marginal ecological
100 conditions not found within core parts of the distribution, which could promote the evolution and
101 maintenance of novel genetic variation and local adaptation (Halbritter *et al.*, 2015; Angert *et al.*,
102 2020). In addition to representing populations that may be locally adapted to the unique
103 environments of the Gulf Coastal Plain physiographic region, populations of *C. dentata* near the
104 southern and western historical range limits are also hypothesized to potentially harbor genetic
105 diversity more closely reflecting the ancestral populations that expanded from refugia following
106 the end of the Wisconsin glacial maximum (Russell, 1987; Huang, 1998; Kubisiak and Roberds,
107 2006, Dane, 2009). This genetic diversity could greatly aid breeding and restoration efforts under
108 a rapidly changing climate that is expected to push suitable habitat farther northward (Huang *et*
109 *al.*, 1998; Shaw *et al.*, 2012; Barnes and Delborne, 2019), but could also shed light on the
110 evolution and ecology of a species that was nearly extirpated prior to extensive study with
111 modern ecological methods.

112 In addition to experiencing atypical or marginal environments, populations near species
113 range limits also experience unique demographic processes arising, in part, from the challenges
114 of small population sizes (*e.g.*, mate limitation and inbreeding depression, local adaptation and
115 outbreeding depression, mutational load; Ellstrand and Elam, 1993; Angert *et al.*, 2020; Perrier

116 *et al.*, 2020). Range-edge populations can become locally adapted via the emergence of novel
117 genetic variation, but can also be demographically unstable, or transient, limiting their
118 demographic footprint (*e.g.*, Savolainen *et al.*, 2007; Angert *et al.*, 2008, 2020). Remnant
119 populations of *C. dentata* occurring in the southwestern portion of the historical range have
120 previously been noted to have higher levels of genetic variation than populations in other parts of
121 the distribution, potentially reflecting local adaptation or that these populations may more closely
122 reflect the genetic variation from populations that expanded from glacial refugia following the
123 last glacial maximum (Russell, 1987; Huang *et al.*, 1998, Shaw *et al.*, 2012). Prior evidence also
124 suggests that populations in the southwestern part of the historical distribution are relatively
125 small in comparison to the rest of the distribution and may have been afflicted by *Phytophthora*
126 *cinnamomi* (Rands) prior to the advent of chestnut blight (Anagnostakis, 2001; Dalgleish *et al.*,
127 2016). Yet, relatively little is known about the population dynamics of the species from this
128 region and few studies have investigated American chestnut population dynamics near its
129 historical range margins. The demography of American chestnut has been studied near its
130 northern distributional limit in southern Ontario (Van Drunen, 2018) and central Maine (Elwood,
131 2014), as well as beyond the historical range in naturalized populations in Michigan and
132 Wisconsin (Davelos and Jarosz, 2004; Stevens *et al.*, 2014). These studies reveal that in the
133 absence of chestnut blight, or when blight affliction is modest, populations of chestnut may
134 remain stable or expand into new habitat. It is unclear how the population dynamics of *C.*
135 *dentata* near its southwestern range margin compare to the demography of other remnant
136 populations near or beyond the native range, and whether such populations (and their novel
137 genetic variation) are at increased risk of local extinction. Recently, small populations near and
138 beyond the historical southwestern range limit in SW Tennessee and adjacent N Mississippi have

139 been documented (Laport *et al.*, 2020) suggesting the demography of the species in this region
140 remains poorly understood, particularly with respect to the prevalence of blight and population
141 persistence.

142 The paucity of ecological and demographic information for American chestnut
143 populations throughout W Tennessee, N Mississippi, SW Kentucky, and NW Alabama makes it
144 difficult to extend current research, breeding, and reintroduction efforts to southwestern parts of
145 the historical range. Yet, such populations are historically important components of the native
146 forest communities, and may also be extremely valuable sources of genetic variation for ongoing
147 restoration efforts that could increase the potential for successful regional reintroductions or for
148 mitigating the effects of climate change on reintroduced populations. Here we make an initial
149 attempt to (1) identify whether environmentally suitable habitat currently exists near the
150 historical southwestern range margin that could support undiscovered remnant populations of *C.*
151 *dentata* using ecological/environmental niche modeling approaches, and (2) to model the
152 demography of *C. dentata* in W Tennessee, N Mississippi, SW Kentucky, and NW Alabama
153 using simple projection matrix models to better understand the current status and future outlook
154 for persistence of American chestnut throughout the southwestern portion of its range. We found
155 that suitable habitat occurs throughout much of the southwestern range extent, but is most
156 strongly predicted to coincide with higher elevations and areas of high forest canopy cover.
157 Additionally, remnant populations of American chestnut in W Tennessee, N Mississippi, SW
158 Kentucky, and NW Alabama are predicted to drastically decline in number over the next ~100-
159 200 years, representing a significant loss to the local forest communities, as well as a loss of
160 potentially locally adapted genomes that may be crucial for breeding and restoration efforts
161 without conservation interventions.

METHODS

ENVIRONMENTAL NICHE MODELS

Population occurrence data—We obtained occurrence information for American chestnut throughout W Tennessee, N Mississippi, SW Kentucky, and NW Alabama from citizen science reports (iNaturalist), GBIF records (https://doi.org/10.15468/dl.gqv45a), and author-identified occurrences. Additional Mississippi records were obtained from herbarium records at the University of Mississippi (MISS), University of Southern Mississippi (USMS), Mississippi State University (MISSA), Northern Kentucky University (KNK), University of North Carolina at Chapel Hill (NCU), Louisiana State University (LSU), and the Mississippi Museum of Natural Science (MMNS). We additionally obtained occurrence records throughout the study region from a database comprising >3,000 individual occurrences documented since the late 1990s and early 2000s by J. Schibig and collaborators (Schibig *et al.*, 2005, 2006). After filtering to an area encompassing W Tennessee, N Mississippi, SW Kentucky, NW Alabama, and NE Arkansas (NW corner: 37.3583°, -91.1444°, SE corner: 32.8416°, -85.6044°) we obtained 583 occurrences. We thinned the dataset to 140 occurrences by retaining only a single point in any given ~1km^2 raster pixel (*i.e.*, removing all but a single point from within the same ~1 km^2 raster pixel; see below) to reduce autocorrelation among clustered occurrences within populations (Table 1).

Environmental layers—We downloaded bioclim environmental variables (1970-2000 averages) plus elevation at 30 arcsecond resolution (~1km^2 at the equator) from Worldclim (ver. 2.1; www.worldclim.org; Hijmans *et al.*, 2005; Fick and Hijmans, 2017). We additionally downloaded the 2016 CONUS land cover and tree canopy cover datasets for the United States

185 from the Multi-Resolution Land Characteristics Consortium (https://www.mrlc.gov; Yang *et al.*,
186 2018). All environmental variable layers were scaled to the same pixel resolution (~1km^2;
187 0.00833° × 0.00833°) and cropped in QGIS (ver. 3.10.9; www.qgis.org) to span an area
188 encompassing our occurrence records, which were used as "projection" layers for our models
189 (above; Table 1; Fig. 1). We created additional independent sets of "calibration" environmental
190 layers by creating mask layers comprising 5km, 10km, and 30km radius buffers surrounding
191 each retained chestnut occurrence record in QGIS before trimming the original environmental
192 layers with these buffer masks. The three sets of "calibration" layers were used to evaluate the
193 set of environmental parameters that best predicted the observed occurrences (see Model
194 Calibration below). We evaluated sets of environmental layers trimmed to 5km, 10km, and 30km
195 buffers around each occurrence record in an effort to generate environmental niche models that
196 appropriately accounted for the current "patchy" occurrences, very low reproductive output, and
197 limited dispersal ability of remnant *C. dentata* when models were projected to the "projection"
198 layers (Paillet, 2002; Dalgleish *et al.*, 2016). Moreover, the current deciduous forest habitat in
199 the lower Mississippi River Valley and adjacent areas is fragmented, with high-quality upland
200 forest patches that could harbor *C. dentata* often being widely dispersed and adjacent to
201 unsuitable agricultural fields, silviculture, road corridors, and/or suburban development (Heilman
202 *et al.*, 2002; Riitters *et al.*, 2012; Yang *et al.*, 2018).
203 We performed correlation analyses on the calibration environmental layers using
204 ENMTools (ver. 1.3; Warren *et al.*, 2010) to reduce overfitting of the distribution model to the
205 occurrence points. Using an iterative approach, we removed environmental variables that
206 exhibited Pearson correlation coefficients ≥ 0.7 with another variable before running the
207 correlation analysis again to further evaluate pairwise correlations. When removing correlated

208 variables, we retained one variable of each correlated pair/set during each iteration of the
209 correlation analysis that is thought to be important for the life history of American chestnut
210 based upon prior research (*e.g.*, Griscom and Griscom, 2012; Fei *et al.*, 2012; Santoro, 2013;
211 Barnes and Delborne, 2019). Additionally, we excluded mean temperature of the wettest quarter
212 (Bio 8), mean temperature of the driest quarter (Bio 9), precipitation of the warmest quarter (Bio
213 18), and precipitation of the coldest quarter (Bio 19) as prior analyses indicate these
214 environmental layers may contain some apparent artifacts that can bias model construction (*e.g.*,
215 Escobar *et al.*, 2014; Campbell, 2015). We retained a combination of environmental variables
216 that exhibited low correlation coefficients (Pearson correlation coefficients ≤ 0.7) and/or are
217 important life history determinants for American chestnut for model calibration: annual mean
218 temperature (Bio 1), mean diurnal range (Bio 2), temperature seasonality (Bio 4), temperature
219 annual range (Bio 7), annual precipitation (Bio 12), precipitation of wettest quarter (Bio 16),
220 elevation, land cover, and canopy cover (Griscom and Griscom, 2012; Fei *et al.*, 2012; Santoro,
221 2013; Barnes and Delborne, 2019).
222 *Model calibration*—We conducted model calibration using the maximum entropy
223 ecological niche modeling application Maxent (ver. 3.4.1; Philips *et al.*, 2006; Philips *et al.*,
224 2020), following the procedure of Simões *et al.* (2020) to identify the combination of model
225 parameters and environmental variables that best fit our occurrence data. Maxent relies only on
226 georeferenced presence data to create complex models using machine learning to relate
227 environmental variables to occurrence points (Philips *et al.*, 2006; Merow *et al.*, 2013). We
228 created 34,782 candidate models (11,594 candidate models each for the 5km, 10km, and 30km
229 buffer sets) reflecting unique combinations of the retained environmental variables (see above),
230 regularization multipliers (0.1, 0.3, 0.5, 0.7, 0.9, 1, 2, 3, 4, 5, 6), and feature classes (l, q, p, t, h,

lq, lp, lt, lh, qp, qt, qh, pt, ph, th, lqp, lqt, lqh, lpt, lph, lth, qpt, qph, qth, pth, lqpt, lqph, lqth, lpth, qpth, lqpth, where l = linear, q = quadratic, p = product, h = hinge). The candidate models were implemented in Maxent using the R (ver. 4.0.2, R Core Team 2020) package kuenm (Cobos *et al.*, 2019) using an R script modified from the example file in Simões *et al.* (2020; Supplemental File 1). We randomly chose 80% of the 140 chestnut occurrence points for training the candidate models and 20% of the occurrence points for testing the candidate models. Candidate model performance was evaluated by partial ROC to evaluate the predictive fit of the model to the data via the receiver operating characteristic curve (ROC; Peterson *et al.*, 2008), omission rates (Anderson *et al.*, 2003), and model complexity (Akaike Information Criterion corrected for small sample size; AICc; Warren and Seifert, 2011).

Thirty candidate models met the statistical retention criteria of partial ROC, omission rate, and AICc (Simões *et al.*, 2020; Table 2). We implemented all of the models passing statistical criteria in Maxent (5km buffer = 22 models, 10km buffer = 7 models, 30km buffer =1 model) and projected them to the "projection" layers with clamping and Multivariate Environmental Similarity Surface (MESS) metrics. For all models, we evaluated variability in model predictions using 10 random bootstrap resampling replicates of 75% of the occurrence points (reserving 25% of occurrence points for testing each model replicate) in Maxent. To estimate land area with predicted environmental suitability for *C. dentata* we thresholded each of the median model outputs (cloglog format, WGS84 (EPSG:4326) projection) from Maxent to consider areas with an environmental suitability ≥0.5 as potential areas of occurrence (=1). Model areas with suitability <0.5 were considered environmentally unsuitable for occurrence (= 0).

DEMOGRAPHIC MODEL

Tree occurrence data—To model the population demography of chestnut in W Tennessee, N Mississippi, SW Kentucky, and NW Alabama we filtered the dataset within the area of interest (NW corner: 37.3583°, -91.1444°, SE corner: 32.8416°, -85.6044°) to include any observations that included information on tree size, demography, and/or blight infection status. For example, when explicit height or stem diameter measurements (*e.g.*, Diameter at Breast Height, DBH) were not available in the primary source data, we retained occurrences that included notations such as "resprout," "sapling," or "small tree." In total our thinned dataset comprised 558 occurrences that include information on tree size (Supplemental File 2), and we assigned each occurrence to one of five size classes representing life history transitions: resprouts (0-1.0 cm DBH), sprouts (1.1-2.5 cm DBH), saplings (2.5-10.0 cm DBH), trees (10.1-25.0 cm DBH), and mature trees (>25.0 cm DBH). Because of their prevalence in the dataset, trees noted as having a stem diameter "<1 cm" were assigned a DBH of 0.5 cm and retained as resprouts. This resulted in a "current" population structure of 23.7% resprouts, 47.5% sprouts, 19.7% saplings, 6.8% trees, and 2.3% mature trees. For modeling, we assumed that all of these trees were genetically independent, rather than treating spatially clustered occurrences as arising from a single root crown, and assumed that historical records were part of a "current" population throughout the area of interest. Blight affliction status among tree size classes was treated as a binary state (no blight = 0, blight = 1) based upon first-hand observation or collector notations. From these observations/notations we computed the proportion of trees in each size class that were blight-free and applied these proportions to the entire dataset. Blight-affliction was assumed to be lethal and result in tree mortality without size class regressions.

We modeled population growth rate, stable size class distributions, and the importance of different life history stages on American chestnut population growth rates in the area of interest using a stage structured Lefkovitch (1965) projection matrix model (Caswell, 2001; Morris and Doak, 2002). Our approach multiplies a transition matrix containing estimated probabilities of stasis/transition between demographic stages with a vector describing the observed distribution of individuals in the five demographic stages (Table 3a). To model the effect of blight on the chestnut population, we multiplied the transition rates in our transition matrix by the proportion of blight-free trees in each size class, thereby proportionally reducing the transition rates in the transition matrix to produce a "blight" matrix (Table 3b). We modeled the demography of the population (Fig. 1) under two different scenarios: 1) without blight, providing an expectation for the demographic future of the species in the absence of blight in the area of interest, and 2) with the inclusion of blight to examine the demographic future of the species in the area of interest under current conditions. To parameterize our transition matrix (Table 3), we modified individual transition rates between size classes from two prior studies of American chestnut demography with trees in similar size classes to our study: one near the historical northeastern range limit in Maine where chestnut was not strongly affected by blight (Elwood, 2014), and one focused on naturalized populations in Michigan exhibiting a range of blight affliction (Davelos and Jarosz, 2004). Where size regression was parameterized in prior studies, we assumed stage class stasis because we lacked life history information from our observations to confidently include these rates. Both models were implemented in R (ver. 4.0.0) using the package 'popbio' (Stubben and Milligan, 2007) for 100 time steps. Prior demographic studies of American chestnut have estimated each time step to represent multiple years (*e.g.*, ~13 years; Elwood, 2014; Van Drunen *et al.*, 2017). To summarize the output of our models we obtained the

299 dominant eigenvalues representing λ (where λ = 1 represents a stable population size, λ < 1
300 represents population contraction, and λ > 1 represents population growth) and the projected
301 stable size class distribution. We also estimated sensitivity and elasticity values from each model
302 to infer the importance of different life history stages and transition rates on population growth
303 rate.
304

305 ## RESULTS

306 ### ENVIRONMENTAL NICHE MODELS

307 The 5km buffer "calibration" layers (*i.e.*, 5km buffer around each occurrence point)
308 produced ENMs having AUCs (area under the curve of the receiver operating characteristic)
309 ranging from 0.629 (SD +/- 0.011) to 0.659 (SD +/- 0.025). Model response curves for Bio 2,
310 Bio 4, canopy cover, and elevation showed positive relationships with the predicted probability
311 of presence in models including variables in addition to elevation, canopy cover, and landcover.
312 In models including only elevation, canopy cover, and land cover as explanatory variables,
313 canopy cover and elevation showed positive relationships with the predicted probability of
314 presence. Canopy cover (49.0%-79.5%), elevation (9.9%-31.9%), and land cover (11.4%-31.8%)
315 made the largest contributions to most of the models with Bio 1 (10.1%-12.1%) contributing to
316 some models. In Maxent jackknife analyses, canopy cover, land cover, and elevation were the
317 most important for training gain, test gain, and AUC with Bio 1, Bio 2, Bio 4, and Bio 12 being
318 important for test gain and AUC in a few models (Table 2).
319 With the 10km buffer "calibration" layers (*i.e.*, 10km buffer around each occurrence
320 point) the resulting ENMs had AUCs ranging from 0.694 (SD +/- 0.009) to 0.712 (SD +/- 0.021).
321 Model response curves for Bio 7, canopy cover, and elevation showed positive relationships with
322 the predicted probability of presence in most models, with Bio 1 and Bio 16 having positive

323 relationships in some models. Canopy cover (46.5-59.5%), Bio 4 (15.4-25.9%), and land cover
324 (11.7-15.0%) made the largest contributions to the models. In Maxent jackknife analyses, canopy
325 cover, land cover, and Bio 4 were the most important for training gain, test gain, and AUC, with
326 elevation being important for test gain in one model (Table 2).

327 The 30km buffer "calibration" layer (*i.e.*, 30km buffer around each occurrence point)
328 produced an ENM with an AUC of 0.753 (SD +/- 0.021). Model response curves for Bio 1, Bio
329 7, Bio 12, canopy cover, and elevation all showed positive relationships with the predicted
330 probability of presence. Bio 2 (28.3%), canopy cover (20.6%), and land cover (17.3%) made the
331 largest contributions to the model, and in Maxent jackknife analyses, canopy cover, land cover,
332 and Bio 2 were most important for training gain, test gain, and AUC (Table 2).

333 Projecting the ENMs to the "projection" layers indicated relatively high environmental
334 suitability for American chestnut throughout much of W Tennessee, N Mississippi, SW
335 Kentucky, and NW Alabama (Fig. 2). The 30 model predictions were roughly visually similar,
336 though many models differed appreciably in areas of predicted environmental suitability
337 (Supplemental File 3). The areas of highest environmental suitability were most consistently
338 predicted to occur throughout eastern portions of the area of interest (*e.g.*, Hardeman, McNairy,
339 Chester, Henderson, Hardin, Decatur, and Benton Counties in Tennessee; Yalobusha, Lafayette,
340 Marshall, Benton, Tippah, Union, Alcorn, Prentiss, Tishomingo, Itawamba, and Monroe
341 Counties in Mississippi; Lauderdale, Colbert, Franklin, Marion, and Lamar Counties in
342 Alabama) that comprise higher elevations and areas of high canopy cover (as inferred from the
343 elevation and canopy cover layers downloaded from WorldClim and MRLCC, respectively).
344 However, areas of relatively high predicted environmental suitability also occurred along river

drainages and uplands otherwise surrounded by low elevation areas of agriculture in the western portion of the area of interest between the Tennessee R. and the Mississippi R. (Fig. 2).

Visual inspection of the top model outputs constructed from each of the environmental layer buffer sets suggested several of the models resulting from the 5km and 10km buffers produced the most realistic predictions for the potential distribution of *C. dentata* in the area of interest, as they apparently better reflected areas of high canopy cover (Fig. 1; Supplemental File 3). Models resulting from the 30km buffer (and several resulting from the 5km and 10km buffers) made either apparent under- or over-predictions of habitat suitability given the patchiness of available forest habitat throughout W Tennessee, N Mississippi, SW Kentucky, and NW Alabama (Supplemental File 3). Models that included other environmental variables in addition to elevation, canopy cover, and land cover tended to have broader predictions of environmental suitability than those relying only on elevation, canopy cover, and land cover. Models resulting from the 10km buffer tended to underpredict suitability in N Mississippi relative to the models resulting from the 5km buffer. All of the models also predicted areas of high environmental suitability in parts of E Arkansas comprising uplands and areas of high canopy cover (*e.g.*, Crowley's Ridge, foothills of E Ozark Mountains) beyond the western extreme of the accepted distribution. After thresholding the models resulting from the 5km buffers, approximately 14,589,787ha (range: 5,529,005-28,464,967ha) of land area, representing ~47% of the total projection area, was predicted to contain environmentally suitable habitat (environmental suitability ≥0.5) for *C. dentata*. From the 10km buffers approximately 3,532,389ha (range: 21,187-9,700,077ha) of land area, representing ~11% of the total projection area, was predicted to represent environmentally suitable habitat (environmental suitability ≥0.5). Approximately 9,856,276ha of land area, representing ~32% of the total projection area,

368 was predicted as environmentally suitable for American chestnut by the model resulting from the
369 30km buffer.
370
371 DEMOGRAPHIC MODEL
372 Without blight, the model for the American chestnut population in W Tennessee, N
373 Mississippi, SW Kentucky, NW Alabama produced a dominant eigenvalue (λ) of 1.09
374 representing a growing population. Projecting the population over 100 time steps produced
375 exponentially growing trajectories for all size classes (Fig. 3). The projected stable size class
376 distribution indicated a population comprising 34.2% resprouts, 52.5% sprouts, 5.4% saplings,
377 5.6% trees, 2.4% mature trees. Sensitivities were largest for the transition between sprouts and
378 saplings, and for the transition between trees and mature trees indicating life-history transitions
379 from small stages to mid-size stages, and to reproductive maturity, are important for population
380 growth in the absence of blight. Summed elasticities were higher for matrix elements
381 representing stasis (S = 0.863) than for elements representing growth (G = 0.107) or fecundity (F
382 = 0.030; Fig. 2) indicating stage class stasis is also important for population growth in the
383 absence of blight.
384 After proportionally reducing the transition rates between stage classes by accounting for
385 only blight-free trees, the model produced a dominant eigenvalue (λ) of 0.92 indicating a
386 shrinking population. Projecting the population over 100 time steps produced rapidly declining
387 trajectories for all size classes (Fig. 3). The projected stable size class distribution indicated a
388 population comprising 7.7% resprouts, 82.4% sprouts, 8.3% saplings, 1.6% trees, and 0.04%
389 mature trees. Sensitivities were largest for the stasis of sprouts, and for the transition between
390 sprouts and saplings (Fig. 2) indicating stasis and transition from small stages to mid-size stages

is important for population growth in the presence of blight. Summed elasticities were higher for matrix elements representing stasis (S = 0.945) than for elements representing growth (G = 0.041) or fecundity (F = 0.013) also indicating that in the presence of blight persistence is important for population growth.

DISCUSSION

The functional extinction of *C. dentata* after the introduction of *C. parasitica* in the early 1900s is thought to have drastically altered the ecology and community dynamics of eastern North American forests (Jacobs *et al.*, 2013, Dalgleish *et al.*, 2016). Unfortunately, the rapid near-extirpation of an integral component of eastern deciduous forest communities before many formal ecological theories and methods were established, makes current efforts to reconstruct pre-blight *C. dentata* ecology, and the consequences of its loss from eastern forests, a difficult task. For example, historical records give some indication of pre-blight forest composition (Zon, 1904; Mattoon, 1909; Ashe, 1912; Brooks, 1937; Russell, 1987; Paillet, 2002) and how these forests may have responded to the loss of *C. dentata* (Ziegler, 1920; Keever, 1953; Stephenson *et al.*, 1991; Jacobs *et al*., 2013), but it remains unclear whether such descriptions can be extrapolated throughout the large and ecologically variable historical range of *C. dentata*. Studies after blight spread throughout the historical range of American chestnut have inferred significant community-level consequences, including replacement of chestnut by other tree species (*e.g.*, *Quercus* spp., *Carya* spp. and *Acer rubrum*; Keever, 1953; Stephenson *et al.*, 1991; Davelos and Jarosz, 2004; Griscom and Griscom, 2012), and the probable extinction of interacting species (*e.g.*, greater chestnut weevil; *Curculio caryatrypes* Boheman 1843; Anderson, 2017). Yet, *C. dentata* persists throughout much of its historical range as a minor component of eastern forests

414 comprising small individuals that continue to re-sprout from the root systems of blight-killed
415 trees, which typically succumb to blight prior to reaching reproductive size, though occasional
416 reproductive trees have also been noted (*e.g.*, Paillet, 1984; Boucher, 2000; Dalgleish *et al.*,
417 2016). Recent efforts to characterize the extent of remaining suitable habitat likely to harbor
418 extant *C. dentata* have made it clear that additional effort is needed to locate remnant
419 individuals/populations and to more fully characterize the current ecological and demographic
420 status of the species throughout its formerly native range to aid conservation and restoration
421 efforts (Fei *et al.*, 2007; Santoro, 2013; Jacobs *et al.*, 2013; Dalgleish *et al.*, 2016). In this study,
422 we focused on an area of the historical American chestnut range that has been relatively
423 understudied to identify potential new areas in which remnant populations of *C. dentata* may
424 occur but remain undiscovered, and to gain insight into the current and future population
425 dynamics of remnant trees in an area with high genetic diversity that could bolster breeding and
426 restoration efforts by increasing the heterozygosity of breeding stock (Stilwell *et al.*, 2003).
427

428 ENVIRONMENTAL NICHE MODELS

429 Prior applications of environmental niche modeling to *C. dentata* have sought to
430 investigate the ecology of American chestnut and identify suitable habitat for discovering
431 remnant populations, as well as to explore areas suitable for reintroduction. Some of these
432 studies have focused on restricted portions of the historical range, carefully investigating the
433 environmental parameters associated with the presence of *C. dentata* in areas of relatively intact
434 forest (Fei *et al.*, 2007; Santoro, 2013; Elwood, 2014). Predictions from these studies indicate
435 that suitable habitat for *C. dentata* in Shenandoah National Park occurs in primarily well-drained
436 upland forests at relatively high elevations in the Blue Ridge Mountains of Virginia (Santoro,

437 2013) and in areas of high canopy cover on steep upper- and mid-slope areas overlying
438 sandstone in topographically diverse parts of Mammoth Cave National Park in Kentucky with
439 young forests on previously cultivated lands being unsuitable for chestnut occurrence (Fei *et al.*,
440 2007). At a continental scale that sacrifices microscale variation and nuance, environmental
441 suitability is predicted to shift northward and beyond the current northern range limit in response
442 to climate change (Fei *et al.*, 2012; Barnes and Delborne, 2019). However, none of these studies
443 have included many occurrences from the southwestern distribution of American chestnut and
444 offer only limited insight into environmental suitability near the historical southwestern range
445 limit.

446 Though our study is focused on a relatively restricted portion of American chestnut's
447 historical range we found that much of W Tennessee, N Mississippi, SW Kentucky, and NW
448 Alabama remain environmentally suitable and that many potentially undiscovered *C. dentata*
449 may persist in remaining forests of the region. The 30 environmental niche models satisfying
450 statistical test criteria produced modest (AUC <0.9), roughly similar, but widely variable habitat
451 suitability predictions throughout the area of interest (Fig. 1; Supplemental File 2). Over-
452 predictions seemed apparent when models included bioclimatic variables compared to those that
453 only included elevation, canopy cover, and land cover, while under-predictions seemed apparent
454 with some sets of environmental layer buffers (Supplemental File 2). The variability among
455 model predictions likely reflects, in part, the difficulty in producing a multivariate model that
456 captures the environmental niche represented by the disparate environments where chestnut
457 observations occur (Vale *et al.*, 2014; Barnes and Delborne, 2019). Prior to the introduction of
458 chestnut blight, *C. dentata* was one of the most broadly distributed tree species in eastern North
459 America, ranging from southern Maine to southern Mississippi (Peattie, 1950; Little, 1977;

460 Paillet, 2002; Jacobs *et al.*, 2013; Dalgleish *et al.*, 2016). Given this historical distribution, the
461 species likely also occupied a much broader set of ecological conditions than currently realized
462 by extant populations (Fei *et al.*, 2007; Griscom and Griscom, 2012). Indeed, historical
463 documents note the occurrence of the species at or beyond the currently accepted distributional
464 limits in SW Tennessee (Fraser, 1864; Williams, 1873), though likely as relatively minor forest
465 components (Ashe 1912). Although our environmental niche models incorporate historical
466 observations of *C. dentata* from the time *C. parasitica* had arrived in W Tennessee and N
467 Mississippi, well within the lifespan of healthy *C. dentata* (Zon, 1904; Ashe, 1912), they likely
468 underestimate the full range of environmental conditions that could be occupied by the species.
469 This may reflect non-representative historical reporting or collection of specimens due to
470 sampling bias against a common species (prior to blight), but remnant populations may also
471 occur in habitats where blight was slower to arrive. Moreover, populations at distributional limits
472 are rare and may occupy environmental conditions not typically experienced by core distribution
473 populations or be found in small patches of suitable environmental conditions embedded within
474 unsuitable environments (Vale *et al.*, 2014; Angert, 2020). These possibilities would make it
475 difficult to accurately identify the set of environmental parameters that reliably predict species
476 occurrences (Galante *et al.*, 2018). Thus, most of our model predictions, especially those
477 produced from the 5km buffers, likely represent conservative projections of suitable habitat (Fig.
478 1). Search efforts for remnant populations of *C. dentata* in under-explored parts of the historical
479 distribution may prove fruitful, and intact forest with high predicted suitability beyond the
480 currently accepted range should be considered as possibly viable habitat. In Mississippi, for
481 example, apparently relatively little contemporary search effort has occurred, even though this
482 area may harbor crucial genetic diversity for breeding and restoration efforts by representing

483 potential genetic relicts that more closely reflect populations that expanded from refugia
484 following the last glacial maximum (Russell, 1987; Kubisiak and Roberds, 2006; Dane, 2009).
485 Interestingly, most of our models also predict suitable American chestnut habitat in upland areas
486 of NE Arkansas. While observations of *C. dentata* are not known from these areas, some of these
487 areas are habitat for the closely-related congeners *Castanea ozarkensis* Ashe and *Castanea*
488 *pumila* Mill, but could potentially harbor rare *C. dentata*.

489 As with all environmental niche models, caution is warranted in interpreting these
490 projections. Our model calibration approach produced several "equally-good" models that when
491 implemented and projected to the area of interest produced widely differing predictions of
492 environmental suitability. One challenge to producing accurate models of habitat suitability
493 appears to be determining the scale at which environmental heterogeneity influences the
494 presence of *C. dentata* (Fei *et al.*, 2007; Santoro, 2013). Because of adult mortality caused by
495 chestnut blight, the population dynamics of American chestnut are likely not currently strongly
496 influenced by pollen and seed dispersal, or seedling recruitment, and the probability of
497 occurrence in many areas (including the southwestern historical range limit) is probably highest
498 within or adjacent to intact forests that have persisted since the arrival of blight (*e.g.,* >50 years)
499 with relatively low disturbance (Paillet, 1988; 2002; Fei *et al.*, 2007; Griscom and Griscom,
500 2012; Gustafson *et al.*, 2017). The frequency and intensity of *C. parasitica* affliction also plays a
501 role in the occurrence and persistence of chestnut, and environmental variation over relatively
502 small scales might strongly influence blight affliction (Van Drunen *et al.*, 2018). Thus, model
503 construction using relatively small environmental layer "buffers" around each occurrence point
504 may more accurately capture the environmental covariates of *C. dentata* occurrence and
505 persistence over the last several decades.

506 Variability in niche model prediction might also be expected near a species range limit if
507 the observed distribution represents the realized rather than the fundamental ecological niche
508 (Warren, 2012; Broennimann *et al.*, 2021). The naturalization of *C. dentata* beyond the accepted
509 historical range limit in Michigan, Wisconsin, Iowa, and Nova Scotia (Paillet and Rutter, 1989;
510 Barnes and Delborne, 2019), suggests that *C. dentata* may not have been at ecological
511 equilibrium when standardized range maps were established (Little, 1977) and may still have
512 been expanding from glacial refugia before the arrival of chestnut blight (Russell, 1987; Huang
513 *et al.*, 1998). Some of this expansion would likely have been contingent upon ongoing
514 evolutionary responses (*i.e.*, mutation, fitness differences, selection, local adaptation, etc.) to
515 changing and novel climatic conditions encountered during expansion, and may not be
516 adequately accounted for in environmental niche modeling approaches that make predictions
517 assuming niche conservatism (Weins and Graham, 2005). The accuracy of our environmental
518 niche models may also have been affected by lowered habitat residency of *C. dentata* as a
519 consequence of a root rot pathogen (*Phytophthora cinnamomi*) that is thought to have diminished
520 the range extent and population densities of *C. dentata* in the southern US by the late 1800s
521 (Russell, 1987; Anagnostakis, 2001; Dalgleish *et al.*, 2016). Environmental niche models relying
522 upon post-*P. cinnamomi* and post-*C. parasitica* occurrences of American chestnut are likely less
523 representative of the habitat once occupied by *C. dentata*, though further investigation is
524 warranted to better understand how models might be impacted by pathogenic mortality.
525

526 DEMOGRAPHIC MODEL

527 Demographic modeling of remnant chestnut populations can reveal important population
528 dynamics that may guide conservation priorities and highlight the challenges of restoration

529 efforts (Boucher, 2000; Davelos and Jarosz, 2004; Jacobs, 2007, 2013; Elwood, 2014; Baines *et*
530 *al.,* 2014). With our simple models, we aimed to investigate the general population trajectories
531 for remnant trees in W Tennessee, N Mississippi, SW Kentucky, and NW Alabama, a relatively
532 understudied portion of the historical American chestnut range. After making several simplifying
533 assumptions about a relatively modest sampling of individuals spread throughout the region
534 across several decades we found that the small starting population was projected to either expand
535 exponentially ($\lambda > 1$) in the absence of blight or decline rapidly ($\lambda < 1$) when blight is accounted
536 for over the next several decades (Fig. 3). In the absence of blight we projected exponential
537 growth of ~9% per time step across all size classes, while accounting for blight resulted in a
538 projection of a ~8% decrease per time step across all size classes (Fig. 3).

539 In the modeled blight and non-blight scenarios, the high stasis element elasticities (Fig. 2)
540 indicate individual tree persistence over many years as having the greatest proportional influence
541 on population growth rates and that this trait has likely structured the current stage class
542 distribution of remnant American chestnut in W Tennessee, N Mississippi, SW Kentucky, and
543 NW Alabama. Approximately 70% of individuals in our observed data are represented by the
544 smallest size classes (resprouts or sprouts). In the presence of recurrent *C. parasitica* infection
545 these stage classes indicate regrowth from previously blight-afflicted individuals and are crucial
546 for longer-term persistence of the species in relatively undisturbed habitat where blight-afflicted
547 root crowns remain viable (Zon, 1904; Paillet, 1988). Large sensitivities for transitions to larger
548 and mature trees in the demographic model also suggest that even rare trees transitioning to
549 reproductive maturity can play an outsized role in population growth. In the model accounting
550 for blight, the chestnut population in W Tennessee, N Mississippi, SW Kentucky, and NW
551 Alabama is projected to decline rapidly toward extinction within ~20 time steps (~100-200

552 years) at minimum. However, the population could persist much longer if time steps are assumed
553 to span a decade or longer (Van Drunen *et al.*, 2017). Yet, these individuals cannot persist
554 indefinitely and will eventually experience mortality from blight, senescence, or stochastic
555 environmental influences (*e.g.*, storms, tree fall, land development, etc.) without interventions to
556 preserve them.

557 The actual population of extant trees in the area of interest is likely much larger than the
558 observed set of trees in our dataset, and the actual stage transition rates for individuals in W
559 Tennessee, N Mississippi, SW Kentucky, and NW Alabama likely differ from those in southern
560 Maine and Michigan. Nevertheless, the model projections presented here are qualitatively similar
561 to the demographic projections from other studies of *C. dentata* populations suggesting that
562 currently the major determinant of chestnut population dynamics is *C. parasitica* and the
563 presence of relatively undisturbed forest (Paillet, 1988; Elwood, 2014; Van Drunen *et al.*, 2017;
564 2018). Pre-blight estimates suggest *C. dentata* comprised up to 5-10% of forest trees west of the
565 Tennessee R. (Ashe, 1912). Though current densities are certainly much lower than historical
566 occurrences, the species was an important component of forest communities between the
567 Mississippi and Tennessee Rivers, and continues to contribute to the ecological dynamics of
568 forests in this area. However, we emphasize that our model projections should be considered
569 with caution and serve as a starting point for more robust investigations of a species that has long
570 attracted attention from land managers, biologists, and the general public (Kummer, 2003;
571 Steiner and Carlson, 2006; Rosen, 2013; Popkin, 2020). Continued surveys to discover remnant
572 trees and more consistent documentation of blight affliction, especially in under-explored areas,
573 would help refine model projections while serving the dual purpose of aiding conservation
574 efforts.

575

576 *Conclusions*—Despite being nearly extirpated in the mid-20th century by introduced
577 chestnut blight, *C. dentata* continues to persist throughout its range primarily as small
578 resprouting individuals. Recent research emphasis has been centered on core parts of the
579 historical distribution where remnant trees appear to be plentiful. Much less effort has focused on
580 the southwestern part of the range—where the species exemplifies its classification as a species
581 of "Special Concern" (Tennessee Flora Committee, 2015; Tennessee Natural Heritage Program,
582 2016)—and the degree to which suitable habitat and undiscovered populations persist in under-
583 surveyed parts of the historical distribution is not well known. We found that suitable habitat for
584 *C. dentata* occurs throughout much of the historical southwestern range extent in W Tennessee,
585 N Mississippi, SW Kentucky, and NW Alabama using environmental niche modeling
586 parameterized from locations where American chestnut has been observed over the last several
587 decades. However, variability among modest model predictions also suggests that the extreme
588 western portions of the historical native range represent marginal habitat for the species and
589 areas of highest environmental suitability are predicted to be restricted to higher elevations and
590 current areas of high forest canopy cover (Fig. 1). Although W Tennessee, N Mississippi, SW
591 Kentucky, and NW Alabama is a region that has been impacted over the last ~150 years by
592 timber harvesting, forest fragmentation (Heilman *et al*., 2002; Riitters *et al.*, 2012), and other
593 introduced plant pathogens (*i.e.*, *Phytophthora cinnamomi*; Anagnostakis, 2001) our ENMs
594 suggest the area has not supported very large populations of *C. dentata* in recent times.
595 Demographic modeling using historical and contemporary observations of *C. dentata* across the
596 region also supports this inference and suggests a dire near-term future for the persistence of the
597 species near its southwestern range margin. The density of recently-documented American

chestnut was generally low throughout the area of interest (but higher in some large areas of relatively intact forest), and demographic modeling accounting for the observed effects of blight suggests drastic declines across all size classes over the next ~100-200 years. Continued population decline appears to be the rule in the presence of *C. parasitica* given the devastating effects the fungus has had on *C. dentata* populations over the past ~120 years (Ziegler, 1920; Paillet, 2002; Davelos and Jarosz, 2004; Jacobs, 2007, 2013; Dalgleish *et al.*, 2016), though local climatic and habitat variability might moderate the effects of blight in some areas leaving relatively healthy populations (Van Drunen *et al.*, 2018). Taken together, our ENM and stage-structured demographic projections highlight the continued presence of suitable *C. dentata* habitat throughout the southwestern extent of its historical distribution, and emphasize the need for efforts to locate, conserve, and introduce genetic material from individuals with potentially novel and locally adapted genotypes from these areas into currently active restoration programs.

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LITERATURE CITED

ANAGNOSTAKIS, S. L. 2001. The effects of multiple importations of pests and pathogens on a native tree. *Biol. Invasions,* **3**:245-254.

ANGERT, A. L., H. D. BRADSHAW, JR., AND D. W. SCHEMSKE. 2008. Using experimental evolution to investigate geographic range limits in monkeyflowers. *Evolution,* **62**:2660–2675.

ANGERT, A. L., M. G. BONTRAGER, AND J. ÅGREN. 2020. What do we really know about adaptation at range edges? *Annu. Rev. Ecol. Evol. S.,* **51**:341-361.

ASHE, W. W. 1912. Chestnut in Tennessee. Tennessee Geological Survey Bulletin 10-B. Nashville, TN, U.S.A.

ANDERSON, R. 2017. Co-extinction and the case of American chestnut and the greater Chestnut weevil (*Curculio caryatrypes*). *Canadian Museum of Nature Blog*. https://canadianmuseumofnature.wordpress.com/2017/02/02/co-extinction-and-the-case-of-american-chestnut-and-the-greater-chestnut-weevil-curculio-caryatrypes/.

ANDERSON, R. P., D. LEW, AND A. T. PETERSON. 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecol. Model.,* **162**:211–232.

BAINES, A. D., E. A. EAGER, AND A. M. JAROSZ. 2014. Modeling and analysis of American chestnut populations subject to various stages of infection. *Lett. Biomath.,* **1**:235-247.

BARNES, J. C., AND J. A. DELBORNE. 2019. Rethinking restoration targets for American chestnut using species distribution modeling. *Biodivers. Conserv.,* **28**:3199-3220.

BOUCHER, D. H. 2000. Population dynamics of American chestnut sprouts: the projection matrix approach. *J. Am. Chestnut Found.,* **14**:38-45.

BROOKS, A. B. 1937. *Castanea dentata*. *Castanea,* **2**:61-67.

BROENNIMANN, O., B. PETITPIERRE, M. CHEVALIER, M. GONZÁLEZ-SUÁREZ , J. M. JESCHKE, J. ROLLAND, S. M. GRAY, S. BACHER, AND A. GUISAN. 2021. Distance to native climatic niche margins explains establishment success of alien mammals. *Nat. Commun.,* **12**:2353 dx.doi.org//https://doi.org/10.1038/s41467-021-22693-0.

CAMPBELL, L. P., C. LUTHER, D. MOO-LLANES, J. M. RAMSEY, R. DANIS-LOZANO, AND A. T. PETERSON. 2015. Climate change influences on global distributions of dengue and chikungunya virus vectors. *Philos. T. Roy. Soc. B,* **370**:1-9.

CASWELL, H. 2001. *Matrix Population Models: Construction, Analysis, and Interpretation,* second edition. Sinauer, Sunderland, MA, U.S.A.

COBOS, M. E., A. T. PETERSON, N. BARVE, AND L. OSORIO-OLVERA. 2019. kuenm: an R package for detailed development of ecological niche models using Maxent. *PeerJ* **7**:e6281.

DALGLEISH, H. J., AND R. K. SWIHART. 2012. American chestnut past and future: implications of restoration for resource pulses and consumer populations of eastern U.S. forests. *Restor. Ecol.,* **20**:490-497.

--------, C. D. NELSON, J. SCRIVANI, AND D. JACOBS. 2016. Consequences of shifts in abundance and distribution of American chestnut for restoration of a foundation forest tree. *Forests,* **7** dx.doi.org//10.3390/f7010004.

DANE, F. 2009. Comparative phylogeography of *Castanea* species. *Acta Hortic.,* **844**:211-222.

DAVELOS, A. L., AND A. M. JAROSZ. 2004. Demography of American chestnut populations: effects of a pathogen and a hyperparasite. *J. Ecol.,* **92**:675-685.

DE BRUIJN, A., E. J. GUSTAFSON, D. M. KASHIAN, H. J. DALGLEISH, B. R. STURTEVANT, AND D. F. JACOBS. 2014. Decomposition rates of American chestnut (*Castanea dentata*) wood and implications for coarse woody debris pools. *Can. J. Forest Res.,* **44**:1575-1585.

DIAMOND, S. J., R. H. GILES, R. L. KIRKPATRICK, AND G. J. GRIFFIN. 2000. Hard mast production before and after the chestnut blight. *South. J. Appl. For.,* **24**:196-201.

ELLIOT, K. J., AND W. T. SWANK. 2008. Long-term changes in forest composition and diversity following early logging (1919-1923) and the decline of American chestnut (*Castanea dentata*). *Plant Ecol.,* **197**:155-172.

690

691 ELLISON, A. M., M. S. BANK, B. D. CLINTON, E. A. COLBURN, K. ELLIOTT, C. R. FORD, D. R.
692 FOSTER, B. D. KLOEPPEL, J. D. KNOEPP, G. M. LOVETT, J. MOHAN, D. A. ORWIG, N. L.
693 RODENHOUSE, W. V. SOBCZAK, K. A. STINSON, J. K. STONE, C. M. SWAN, J. THOMPSON, B. VON
694 HOLLE, AND J. R. WEBSTER. 2005. Loss of foundation species: consequences for the structure and
695 dynamics of forested ecosystems. *Front. Ecol. Environ.*, **3**:479-486.

696

697 ELLSTRAND, N. C., AND D. R. ELAM. 1993. Population genetic consequences of small population
698 size: implications for plant conservation. *Annu. Rev. Ecol. Syst.,* **24**:217-242.

699

700 ELWOOD, E. C. 2014. Population matrix model for American chestnut (*Castanea dentata*) and the
701 implications for re-introduction [Honors thesis]. The College of William and Mary.
702 Williamsburg, VA, U.S.A.

703

704 ESCOBAR, L. E., A. LIRA-NORIEGA, G. MEDINA-VOGEL, AND A. T. PETERSON. 2014. Potential for
705 spread of the white-nose fungus (*Pseudogymnoascus destructans*) in the Americas: use of
706 Maxent and NicheA to assure strict model transference. *Geospatial Health,* **9**:221-229.

707

708 FEI, S., J. SCHIBIG, AND M. VANCE. 2007. Spatial habitat modeling of American chestnut at
709 Mammoth Cave National Park. *Forest Ecol. Manag.,* **252**:201-207.

710

--------, L. LIANG, F. L. PAILLET, K. C. STEINER, J. FANG, Z. SHEN, Z. WANG, AND F. V. HEBARD. 2012. Modelling chestnut biogeography for American chestnut restoration. *Divers. Distrib.,* **18**:754-768.

FICK, S. E., AND R. J. HIJMANS. 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.,* **37**:4302-4315.

FRASER, H. 1864. Hattie Fraser Diary 1861-1864. Craddock Book Club, Somerville, TN, U.S.A.

GALANTE, P. J., B. ALADE, R. MUSCARELLA, S. A. JANSA, S. M. GOODMAN, AND R. P. ANDERSON. 2018. The challenge of modeling niches and distributions for data-poor species: a comprehensive approach to model complexity. *Ecography,* **41**:726-736.

GRISCOM, H. P., AND B. W. GRISCOM. 2012. Evaluating the ecological niche of American chestnut for optimal hybrid seedling reintroduction sites in the Appalachian ridge and valley province. *New Forest.,* **43**:441-455.

GUSTAFSON, E. J., A. DE BRUIJN, N. LICHTI, D. F. JACOBS, B. R. STURTEVANT, J. FOSTER, B. R. MIRANDA, AND H. J. DALGLEISH. 2017. The implications of American chestnut reintroduction on landscape dynamics and carbon storage. *Ecosphere,* **8**:e01773.

HALBRITTER, A. H., R. BILLETER, P. J. EDWARDS, AND J. M. ALEXANDER. 2015. Local adaptation at range edges: comparing elevation and latitudinal gradients. *J. Evolution. Biol.,* **28**:1849-1860.

HEILMAN JR., G. E., J. R. STRITTHOLT, N. C. SLOSSER, AND D. A. DELLASALA. 2002. Forest fragmentation of the conterminous United States: Assessing forest intactness through road density and spatial characteristics. *BioScience*, **52**:411-422.

HIJMANS, R. J., S. E. CAMERON, J. L. PARRA, P. G. JONES, AND A. JARVIS. 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.,* **25**:1965-1978.

HUANG, H. W., F. DANE, AND T. L. KUBISIAK. 1998. Allozyme and RAPD analysis of the genetic diversity and geographic variation in wild populations of the American chestnut (Fagaceae). *Am. J. Bot.,* **85**:1013-1021.

JACOBS, D. F. 2007. Toward development of silvical strategies for forest restoration of American chestnut (*Castanea dentata*) using blight-resistant hybrids. *Biol. Conserv.,* **137**:497-506.

--------, H. J. DALGLEISH, AND C. D. NELSON. 2013. A conceptual framework for restoration of threatened plants: the effective model of American chestnut (*Castanea dentata*) reintroduction. *New Phytol.,* **197**:378-393.

KEEVER, C. 1953. Present composition of some stands of the former oak-chestnut forest in the southern Blue Ridge Mountains. *Ecology,* **34**:44-55.

KUBISIAK, T. L., AND J. ROBERDS. 2006. Genetic structure of American chestnut populations based on neutral DNA markers. p. 109–122. *In*: Steiner, K.C. and J.E. Carlson (eds.). Restoration of American chestnut to forest lands—Proceedings of a conference and workshop. May 4–6, 2004, The North Carolina Arboretum. Natural Resources Report NPS/NCR/CUE/NRR-2006/001. National Park Service, Washington, D.C., U.S.A.

KUMMER, C. 2003. A new chestnut. *The Atlantic*, 1 June 2003. https://www.theatlantic.com/magazine/archive/2003/06/a-new-chestnut/302742/?utm_source=copy-link&utm_medium=social&utm_campaign=share.

LAPORT, R. G. 2020. Remnant American chestnut (*Castanea dentata* (Marsh.) Borkh.; Fagaceae) in upland forests of western New York. *Proc. Rochester Acad. Sci.,* **21**:5-14.

--------, D. SMITH, AND J. NG. 2020. Remnant American chestnut (*Castanea dentata*) near the historical western range limit in southwestern Tennessee. *Castanea,* **85**:232-243.

LEFKOVITCH, L. P. 1965. The study of population growth in organisms grouped by stages. *Biometrics,* **21**:1-18.

LITTLE, E. L., JR. 1977. Minor eastern hardwoods. Volume 4. Atlas of United States trees. Miscellaneous Publication 1342. USDA Forest Service, Washington, D.C., U.S.A.

MATTOON, W. R. 1909. The origin and early development of chestnut sprouts. *Forest Quarterly,* **7**:34-37.

MCCORMICK, J. F., AND R. B. PLATT. 1980. Recovery of an Appalachian forest following the chestnut blight. *Am. Midl. Nat.*, **104**:264-273.

MEROW, C., M. J. SMITH, AND J. A. SILANDER, JR. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography,* **36**: 1058-1069.

MORRIS, W. F., AND D. F. DOAK. 2002. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis.* Sinauer, Sunderland, MA, U.S.A.

PAILLET, F. L. 1982. The ecological significance of American chestnut (*Castanea dentata* (Marsh.) Borkh.) in the Holocene forests of Connecticut. *B. Torrey Bot. Club,* **109**:457-473.

--------. 1988. Character and distribution of American chestnut sprouts in southern New England woodlands. *B. Torrey Bot. Club,* **115**:32-44.

--------. 2002. Chestnut: history and ecology of a transformed species. *J. Biogeogr.,* **29**:1517-1530.

--------, AND P. A. RUTTER. 1989. Replacement of native oak and hickory tree species by the introduced American chestnut (*Castanea dentata*) in southwestern Wisconsin. *Can. J. Botany,* **67**:3457-3469.

PEATTIE, D. 1950. A Natural History of Trees of Eastern and Central North America. Houghton Mifflin Company, Boston, MA, U.S.A.

PERRIER, A., D. SÁNCHEZ-CASTRO, AND Y. WILLI. 2020. Expressed mutational load increases toward the edge of a species' geographic range. *Evolution,* **74**:1711-1723.

PETERSON, A. T., M. PAPEŞ, AND J. SOBERÓN. 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecol. Model.,* **213**:63-72.

PHILLIPS, S. J., R. P. ANDERSON, AND R. E. SCHAPIRE. 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.,* **190**:231-259.

--------, M. DUDÍK, AND R. E. SCHAPIRE. 2020. Maxent software for modeling species niches and distributions (Version 3.4.1). URL http://biodiversityinformatics.amnh.org/open_source/maxent/, accessed 15 August 2020.

POPKIN, G. 2020. Can genetic engineering bring back the American chestnut? *The New York Times Magazine*, 30 April 2020. https://www.nytimes.com/2020/04/30/magazine/american-chestnut.html?smid=url-share.

R CORE TEAM. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

RIITTERS, K. H., AND J. D. WICKHAM. 2012. Decline of forest interior conditions in the conterminous United States. *Sci. Rep.,* **2**:653 dx.doi.org//10.1038/srep00653.

ROSEN, R. 2013. Genetically engineering and icon: can biotech bring the chestnut back to America's forests? *The Atlantic*, 31 May 2013. https://www.theatlantic.com/technology/archive/2013/05/genetically-engineering-an-icon-can-biotech-bring-the-chestnut-back-to-americas-forests/276356/?utm_source=copy-link&utm_medium=social&utm_campaign=share.

RUSSELL, E. W. B. 1987. Pre-blight distribution of *Castanea dentata* (Marsh.) Borkh. *Bull. Torrey Bot. Club,* **114**:183-190.

SANTORO, J. 2013. American chestnut (*Castanea dentata*) habitat modeling: identifying suitable sites for restoration in Shenandoah National Park, Virginia [M.Sc. thesis]. Duke University. Durham, NC, U.S.A.

SAVOLAINEN, O., T. PYHÄJÄRVI, AND T. KNÜRR. 2007. Gene flow and local adaptation in trees. *Annu. Rev. Ecol. Evol. S.,* **38**:595-619.

SCHIBIG, J., C. NEEL, M. HILL, M. VANCE, AND J. TORKELSON. 2005. Ecology of American chestnut in Kentucky and Tennessee. *J. Am. Chestnut Found.,* **19**:42-48.

--------. VANCE, S. CUMING, L. FLY, C. NEEL, AND J. TORKELSON. 2006. Ecology of the American chestnut and Allegheny chinquapin on the Cumberland Plateau of Kentucky and Tennessee. *J. Am. Chestnut Found.,* **20**:44-50.

SCHWADRON, P. A. 1995. Distribution and persistence of American chestnut sprouts, *Castanea dentata* (Marsh.) Borkh., in northeastern Ohio woodlands. *Ohio J. Sci.,* **95**:281-288.

SHAW, J., J. H. CRADDOCK, AND M. A. BINKLEY. 2012. Phylogeny and phylogeography of North American *Castanea* Mill. (Fagaceae) using cpDNA suggests gene sharing in the southern Appalachians. *Castanea,* **77**:186-211.

SIMÕES, M., D. ROMERO-ALVAREZ, C. NUÑEZ-PENICHET, L. JIMÉNEZ, AND M. E. COBOS. 2020. General Theory and Good Practices in Ecological Niche Modeling: A Basic Guide. *Biodiversity Informatics,* **15**:67-68.

SMITH, D. M. 2000. American chestnut: Ill-fated monarch of the eastern hardwood forest. *J. Forest.,* **98**:12-15.

STEINER, K. C. AND CARLSON, J. E, EDS. 2006. Restoration of American chestnut to forest lands: proceedings of a conference and workshop. May 4-6, 2004, The North Carolina Arboretum.

Natural Resources Report NPS/NCR/CUE/NRR 2006/001. National Park Service, Washington, D.C., U.S.A.

STEPHENS, G. R. AND P. E. WAGGONER. 1980. A half century of natural transitions in mixed hardwood forests. Bulletin 783. The Connecticut Agricultural Experiment Station, New Haven, CT, U.S.A.

STEPHENSON, S. L., H. S. ADAMS, AND M. L. LIPFORD. 1991. The present distribution of chestnut in the upland forest communities of Virginia. *Bull. Torrey Bot. Club,* **118**:24-32.

STEVENS, D. L., K. SOLTAU, A. DAVELOS BAINES, AND A. M. JAROSZ. 2014. American chestnut sprout dynamics. *Acta Hortic.,* **1019**:223-227.

STILWELL, K. L., H. M. WILBUR, C. R. WERTH, AND D. R. TAYLOR. 2003. Heterozygote advantage in the American chestnut, *Castanea dentata* (Fagaceae). *Am. J. Bot.,* **90**:207-213.

STUBBEN, C., AND B. MILLIGAN. 2007. Estimating and analyzing demographic models using the popbio package in R. *J. Stat. Softw.,* **22**:1-23.

TENNESSEE FLORA COMMITTEE. 2015. Guide to the Vascular Plants of Tennessee. University of Tennessee Press, Knoxville, TN, U.S.A.

TENNESSEE NATURAL HERITAGE PROGRAM. 2016. Rare Plant List. Department of Environment and Conservation, Nashville, TN, U.S.A.

TINDALL, J. R., J. A. GERRATH, M. MELZER, K. MCKENDRY, B. C. HUSBAND, AND G. J. BOLAND. 2004. Ecological status of American chestnut (*Castanea dentata*) in its native range in Canada. *Can. J. Forest Res.,* **34**:2554-2563.

VALE, C. G., P. TARROSO, AND J. C. BRITO. 2014. Predicting species distribution at range margins: testing the effects of study area extent, resolution and threshold selection in the Sahara–Sahel transition zone. *Divers. Distrib.,* **20**:20-33.

VAN DRUNEN, S. G., K. SCHUTTEN, C. BOWEN, G. J. BOLEN, AND B. C. HUSBAND. 2017. Population dynamics and the influence of blight on American chestnut at its northern range limit: Lessons for conservation. *Forest Ecol. Manag.,* **400**:375-383.

--------, S. G., J. L. MCCUNE, AND B. C. HUSBAND. 2018. Distribution and environmental correlates of fungal infection and host tree health in the endangered American chestnut in Canada. *Forest Ecol. Manag.,* **427**:60-69.

WARREN, D.L. 2012. In defense of 'niche modeling.' *Trends Ecol. Evol.,* **27**:497-500.

--------, AND S. N. SEIFERT. 2011. Ecological niche modeling in Maxent: The importance of model complexity and the performance of model selection criteria. *Ecol. Appl.*, **21**:335-342.

--------, R. E. GLOR, AND M. TURELLI. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography,* **33**:607-611.

WIENS, J. J, AND C. H. GRAHAM. 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Evol. S.,* **36**:519-539.

WILLIAMS, J. S. 1873. Old times in west Tennessee: reminiscences, semi-historic, of pioneer life and the early emigrant settlers in the Big Hatchie country. W. G. Cheeney, Memphis, TN, U.S.A.

YANG, L., S. JIN, P. DANIELSON, C. HOMER, L. GASS, S. M. BENDER, A. CASE, C. COSTELLO, J. DEWITZ, J. FRY, M. FUNK, B. GRANNEMAN, G. C. LIKNES, M. RIGGE, AND G. XIAN. 2018. A new generation of the United States National Land Cover Database: Requirements, research priorities, design, and implementation strategies. *ISPRS J. Photogramm.,* **146**:108-123.

ZIEGLER, E.A. 1920. Problems arising from the loss of our chestnut. *Forest Leaves,* **17**:152-155.

ZON, R. 1904. Chestnut in southern Maryland. U.S. Department of Agriculture, Bureau of Forestry, Bulletin No. 53. Washington, D.C., U.S.A.

1409 Table 1.--American chestnut observations and locality information throughout W. Tennessee, N.
1410 Mississippi, S.W. Kentucky, and N.W. Alabama used for environmental niche modeling.
1411 Observations included historical collections from herbaria, personal observations by the authors
1412 and colleagues, and engaged citizen-scientist observations from GBIF recorded and verified with
1413 the iNaturalist application. Detailed latitude/longitude location information is available upon
1414 request
1415

Date	Latitude	Longitude	County	State	Collectors	Collector Code/Voucher Accession
16-Jul-1969	34.76	-88.43	Alcorn	Mississippi	T. M. Pullen	MISS0018279
12-May-2019	35.03	-88.73	McNairy	Tennessee	R.G. Laport, D. Smith & J. Ng	SWMT05622
12-May-2019	35.03	-88.74	McNairy	Tennessee	R.G. Laport, D. Smith & J. Ng	SWMT05625
31-Oct-1981	33.91	-89.26	Calhoun	Mississippi	R. A. Stewart	MISS0018280
12-May-1967	34.11	-89.50	Calhoun	Mississippi	T. M. Pullen	MISS0018282
22-Jun-1980	33.29	-89.10	Choctaw	Mississippi	S. McDaniel	MMNS021400
15-Jun-1980	33.36	-89.14	Choctaw	Mississippi	S. McDaniel	MMNS021294
14-Jun-2013	33.42	-89.26	Choctaw	Mississippi	K. Philley	MMNS034856
21-Apr-1967	33.77	-88.89	Clay	Mississippi	T. R. Simmons, Jr	MISS0018284
22-Aug-1979	33.79	-88.91	Clay	Mississippi	K. E. Rogers	MMNS021663
14-Sep-2019	35.39	-88.77	Chester	Tennessee	R.G. Laport, D. Smith & J. Ng	SWMT05640
10-Nov-2019	35.38	-88.77	Chester	Tennessee	R.G. Laport, D. Smith & J. Ng	CSP19
1-May-1884	34.17	-86.83	Cullman	Alabama	C. Mohr	UNA00032071
6-Jun-2002	36.06	-86.79	Davidson	Tennessee	S. J. Baskauf	http://bioimages.vanderbilt.edu/ind-baskauf/11845#2002-06-06
15-Sep-1994	33.69	-89.67	Grenada	Mississippi	J. R. MacDonald	MISS0018287
20-Jun-1986	33.70	-89.53	Grenada	Mississippi	M. W. Morris	MISS_Morris2115
24-Apr-1994	33.71	-89.69	Grenada	Mississippi	J. R. MacDonald	MMNS013157
12-Jul-1980	33.73	-89.76	Grenada	Mississippi	R. A. Stewart II	MMNS004275
17-Jun-1986	33.75	-89.58	Grenada	Mississippi	M. W. Morris	MISS_Morris2107
27-Apr-1980	33.76	-89.83	Grenada	Mississippi	R. A. Stewart II	MMNS004504
unknown	36.31	-88.26	Henry	Tennessee	N/A	USDA_NPGS_3395807
12-Jun-2020	34.94	-89.04	Benton	Mississippi	R.G. Laport, D. Smith & J. Ng	SWMT05659
29-Aug-2004	36.75	-86.23	Allen	Kentucky	J. Schibig & M. Vance	KALL1
23-May-2004	36.66	-87.35	Christian	Kentucky	Caudell & J. Schibig	KCHR1
15-Jun-2004	36.76	-88.43	Marshall	Kentucky	J. Schibig & M. Vance	KMAR1
28-Jun-2003	36.73	-85.87	Monroe	Kentucky	J. Schibig & J. H. Craddock	KMON4
15-May-2003	36.72	-88.05	Trigg	Kentucky	J. H. Craddock	KTRI123
13-Aug-2003	36.71	-88.07	Trigg	Kentucky	J. Schibig & J. H. Craddock	KTRI148
26-May-2002	36.77	-88.11	Trigg	Kentucky	J. Schibig, Barber, J. H. Craddock & Torkelson	KTRI16

14-Jul-2002	36.72	-88.08	Trigg	Kentucky	J. Schibig	KTRI60
29-Sep-2002	36.78	-88.11	Trigg	Kentucky	J. Schibig, Barber, J. H. Craddock & Torkelson	KTRI86
3-May-2003	36.76	-88.11	Trigg	Kentucky	J. Schibig & M. Vance	KTRI98
11-May-2004	36.97	-86.56	Warren	Kentucky	J. Schibig & M. Vance	KWAR1
11-May-2004	36.96	-86.56	Warren	Kentucky	J. Schibig & M. Vance	KWAR6
20-May-1964	34.22	-89.36	Lafayette	Mississippi	B. W. Haglan	MISS0018293
20-Oct-2000	34.37	-89.29	Lafayette	Mississippi	B. A. Connolly & M. Duffy	MISS0018290
18-Sep-1980	34.43	-89.39	Lafayette	Mississippi	K. L. Gordon	MMNS006950
3-Nov-1965	34.54	-89.49	Lafayette	Mississippi	L. Dowdy	MISS0018292
29-Jul-1955	34.24	-88.62	Lee	Mississippi	J. D. Ray, Jr.	MISSA014060
13-Sep-2005	33.44	-88.32	Lowndes	Mississippi	M. Whitson	KNK31973000000000
11-Jul-1969	34.17	-88.00	Marion	Alabama	R. Kral	KANU212195
29-Sep-1967	34.66	-89.47	Marshall	Mississippi	S. Lassetter	MISS0018297
26-Jun-2005	34.32	-89.47	Lafayette	Mississippi	M. Alexander	MLAF1
28-Jun-1955	33.89	-88.25	Monroe	Mississippi	J. D. Ray, Jr.	MISSA014059
13-May-1993	34.00	-88.57	Monroe	Mississippi	R. G. Wieland	MMNS026542
10-May-1952	34.05	-88.56	Monroe	Mississippi	R. M. Schuster	MISSA014058
26-Jun-1980	33.34	-89.63	Montgomery	Mississippi	K. L. Gordon	MMNS006740
1-Sep-1968	36.44	-87.49	Montgomery	Tennessee	J. Schibig	NCU00153931
6-Dec-2004	34.59	-88.19	Tishomingo	Mississippi	Maddox, C. Neel	MTIS1
4-Aug-1996	34.24	-89.22	Pontotoc	Mississippi	C. T. Bryson	MMNS012849
4-Aug-1996	34.24	-89.19	Pontotoc	Mississippi	C. T. Bryson	MISS0018298
24-Jun-1951	33.57	-86.45	Saint Clair	Alabama	C. G. Hollis	UNA00032086
20-Aug-1962	33.94	-86.26	Saint Clair	Alabama	P. E. Bostick	NCU00153908
13-Oct-2018	35.18	-89.29	Fayette	Tennessee	R.G. Laport, D. Smith & J. Ng	SWMT05626
13-Oct-2018	35.16	-89.29	Fayette	Tennessee	R.G. Laport, D. Smith & J. Ng	SWMT05627
18-Jul-1966	36.57	-87.97	Stewart	Tennessee	B. Evans	NCU00153932
9-May-1980	34.12	-90.07	Tallahatchie	Mississippi	R. A. Stewart II	MMNS004476
20-Jul-2002	35.45	-86.27	Bedford	Tennessee	C. Neel	TBED1
8-Oct-2005	35.43	-86.25	Bedford	Tennessee	C. Neel	TBED14
1-Jan-2004	35.36	-86.53	Bedford	Tennessee	C. Neel	TBED4
1-Dec-2003	35.87	-85.98	Cannon	Tennessee	C. Neel	TCAN1
5-Aug-2005	35.80	-85.99	Cannon	Tennessee	M. Vance	TCAN36
9-Jan-2005	35.89	-88.46	Carroll	Tennessee	J. Schibig & M. Vance	TCAR1
8-Oct-2005	35.49	-86.14	Coffee	Tennessee	C. Neel	TCOF3
18-Aug-2002	36.07	-86.82	Davidson	Tennessee	J. Schibig	TDAV4
14-Sep-2002	36.27	-86.90	Davidson	Tennessee	J. Schibig	TDAV7
15-Jul-2003	36.09	-85.82	Dekalb	Tennessee	J. Schibig & J. H. Craddock	TDEK15
4-Aug-2002	36.06	-85.86	Dekalb	Tennessee	J. Schibig, Barber, J. H. Craddock & Torkelson	TDEK4
June-02	35.04	-89.23	Fayette	Tennessee	B. Turner	TFAY25
1-May-2002	35.04	-89.24	Fayette	Tennessee	B. Turner	TFAY6
20-Jul-2002	35.28	-86.14	Franklin	Tennessee	C. Neel	TFRA1
25-Sep-2005	35.07	-86.05	Franklin	Tennessee	P. Tarpley	TFRA3

25-Sep-2005	35.08	-86.03	Franklin	Tennessee	P. Tarpley	TFRA4
25-Sep-2005	35.07	-86.02	Franklin	Tennessee	P. Tarpley	TFRA5
25-Sep-2005	35.07	-86.03	Franklin	Tennessee	P. Tarpley	TFRA6
6-Jun-2000	35.38	-87.19	Giles	Tennessee	J. Schibig	TGIL1
2-Jun-1998	35.08	-87.22	Giles	Tennessee	C. Neel	TGIL3
1-Jun-1998	35.09	-87.22	Giles	Tennessee	C. Neel	TGIL4
24-Feb-2002	35.80	-87.58	Hickman	Tennessee	J. Schibig, Barber & J. H. Craddock	THIC1
2-Aug-2005	36.36	-87.62	Houston	Tennessee	J. Schibig & M. Vance	THOU1
1-Feb-2003	35.96	-87.91	Humphreys	Tennessee	J. Schibig & M. Vance	THUM1
28-Oct-2006	36.18	-87.79	Humphreys	Tennessee	J. Schibig, Leach, Greenwell & Dreaden	THUM4
15-Sep-1982	34.84	-88.973	Tippah	Mississippi	D. Meeks	MMNS013370
10-Sep-1978	34.53	-88.16	Tishomingo	Mississippi	K. E. Rogers	MMNS000789
15-Nov-2003	34.61	-88.17	Tishomingo	Mississippi	H. M. Sullivan	MMNS022035
3-Jun-2006	34.61	-88.28	Tishomingo	Mississippi	L. Majure & G. N. Ervin	MISSA014053
unknown	34.74	-88.24	Tishomingo	Mississippi	A. Allison	MISS0018300
5-May-2015	34.81	-88.19	Tishomingo	Mississippi	T. G. Harbison, M. T. Perkins, J. H. Craddock	NCU00085298
4-Oct-1978	34.89	-88.11	Tishomingo	Mississippi	K. E. Rogers	MMNS007370
5-Oct-1978	34.92	-88.17	Tishomingo	Mississippi	K. E. Rogers	MMNS002655
21-Jul-2002	35.31	-86.54	Lincoln	Tennessee	C. Neel	TLIN1
21-Jul-2002	35.04	-86.56	Lincoln	Tennessee	C. Neel	TLIN2
20-Jul-2002	35.03	-86.47	Lincoln	Tennessee	C. Neel	TLIN3
19-Jun-2004	36.59	-85.86	Macon	Tennessee	J. Schibig & M. Vance	TMAC1
8-Oct-2005	36.49	-85.94	Macon	Tennessee	J. Schibig, M. Vance & Torkelson	TMAC2
20-Jul-2002	34.67	-86.52	Madison	Tennessee	C. Neel	TMAD1
2-Oct-1999	34.66	-86.51	Madison	Tennessee	C. Neel	TMAD3
5-Jan-2002	35.34	-86.78	Marshall	Tennessee	J. Schibig, C. Neel & Torkelson	TMAR1
1-Oct-1998	35.46	-87.12	Maury	Tennessee	Estes	TMAU1
20-Jul-2002	35.40	-86.30	Moore	Tennessee	C. Neel	TMOO1
15-Oct-2004	35.54	-87.98	Perry	Tennessee	C. Neel	TPER1
7-Jan-2006	35.63	-87.91	Perry	Tennessee	C. Neel	TPER2
7-Jan-2006	35.68	-87.88	Perry	Tennessee	C. Neel	TPER3
8-Jul-2004	36.04	-86.60	Davidson	Tennessee	M. Vance	TPUT2
9-Jun-2002	36.44	-86.74	Robertson	Tennessee	Torkelson	TROB3
5-Jan-2003	36.44	-86.75	Robertson	Tennessee	Torkelson	TROB4
14-Mar-2003	35.71	-86.22	Rutherford	Tennessee	C. Neel	TRUT1
23-Jan-2003	36.40	-85.88	Smith	Tennessee	J. Schibig, Draper & Kemp	TSMI1
26-Jun-2003	36.21	-85.87	Smith	Tennessee	M. Vance, J. Schibig & J. H. Craddock	TSMI2
26-Jun-2002	36.62	-88.03	Stewart	Tennessee	J. Schibig	TSTE1
5-Sep-2002	36.57	-88.01	Stewart	Tennessee	J. Schibig	TSTE13
5-Sep-2002	36.57	-88.02	Stewart	Tennessee	J. Schibig	TSTE17
5-Aug-2002	36.61	-88.04	Stewart	Tennessee	J. Schibig	TSTE2
12-Sep-2002	36.61	-88.04	Stewart	Tennessee	J. Schibig	TSTE37
14-Jul-2003	36.66	-88.05	Stewart	Tennessee	J. H. Craddock	TSTE47

24-Jul-2003	36.67	-88.05	Stewart	Tennessee	J. H. Craddock	TSTE72
12-Sep-2003	36.60	-88.01	Stewart	Tennessee	J. H. Craddock	TSTE73
23-Apr-2002	36.51	-86.45	Sumner	Tennessee	J. Schibig	TSUM10
28-Apr-2002	36.51	-86.39	Sumner	Tennessee	J. Schibig	TSUM17
28-Apr-2002	36.43	-86.68	Sumner	Tennessee	J. Schibig	TSUM18
23-Oct-2003	36.38	-86.66	Sumner	Tennessee	J. Schibig	TSUM21
22-Jul-2004	36.62	-86.21	Sumner	Tennessee	J. Schibig & M. Vance	TSUM23
20-Nov-2003	36.30	-88.66	Weakley	Tennessee	J. Schibig & B. Turner	TWEA1
2-Feb-2003	35.83	-87.00	Williamson	Tennessee	J. Schibig	TWIL1
13-Jul-2004	35.82	-87.06	Williamson	Tennessee	J. Schibig & M. Vance	TWIL13
31-Aug-1996	33.20	-89.04	Winston	Mississippi	J. R. MacDonald	MMNS024435
31-Aug-1996	33.21	-89.06	Winston	Mississippi	J. R. MacDonald	MISSA014056
11-Oct-1978	33.21	-88.97	Winston	Mississippi	K. L. Gordon	MMNS005245
10-May-1967	34.02	-87.36	Winston	Alabama	R. C. Clark	NCU00153909
14-May-1999	33.87	-89.57	Yalobusha	Mississippi	R. A. Stewart II	MMNS034421
12-Jun-1996	33.98	-89.82	Yalobusha	Mississippi	J. R. MacDonald	MMNS012824
9-Apr-2020	34.40	-86.20	Marshall	Alabama	michaelezell	iNaturalist
20-Apr-2020	34.74	-86.71	Madison	Alabama	N. Cash	iNaturalist
29-May-2019	35.06	-85.84	Marion	Tennessee	N. Parrish	iNaturalist
3-Aug-2019	35.06	-88.73	McNairy	Tennessee	A. J. Trently	iNaturalist
9-Jul-2019	35.21	-85.86	Marion	Tennessee	dmp83178	iNaturalist
1-Jul-2020	35.56	-87.45	Lewis	Tennessee	M. Mayfield	iNaturalist
17-May-2020	36.07	-86.90	Davidson	Tennessee	N. Parrish	iNaturalist
16-Sep-2019	36.89	-86.95	Logan	Kentucky	rustyduck	iNaturalist
14-Apr-2020	36.97	-86.82	Logan	Kentucky	rustyduck	iNaturalist

Table 2. Summary statistics of the 30 environmental niche models passing model calibration criteria after implementation in Maxent. Model names take the form: buffer layer size (5km, 10km, or 30 km), regularization multiplier (ranging from 0.1-6.0), feature classes (l = linear, q = quadratic), and environmental variables (E = elevation, L = land cover, C = canopy cover, 1 = Bio 1, 2 = Bio 2, 4 = Bio 4, 7 = Bio 7, 12 = Bio 12, 16 = Bio 16). Environmental variable abbreviations are the same for all columns. Variables with negative model effects are indicated with a "-" in parentheses

								Top 3 Contributing Variables in Jackknife Analyses		
Model	**AUC**	**SD**	**Variables with Positive Response Curves**	**Environmental Variable with ≥10% Contributions to the Model (variable: % contribution)**				**Training Gain**	**Test Gain**	**AUC**
5km0.1qE,1,2,4,12,L,C	0.648	0.023	2, 4, C, E	C: 51.8	E: 16.2	Bio1: 10.1		C, E, L	C, L, 1(-)	C, L, 12
5km0.1qE,L,C	0.639	0.026	C, E	C: 55.3	E: 31.9	L: 12.8		C, E, L	C, L, E(-)	C, L, E
5km0.3qE,1,2,4,12,L,C	0.646	0.017	2, 4, C, E	C: 49.8	L: 25.7			C, L, E	C, L, E	C, L, 1
5km0.3qE,L,C	0.641	0.021	C, E	C: 56.4	L: 28.2	E: 15.4		C, E, L	C, L, E	C, L, E
5km0.5qE,1,2,4,12,L,C	0.659	0.025	4, C, E	C: 52.3	E: 12.4			C, L, E	C, L, E	C, L, 2
5km0.5qE,L,C	0.642	0.035	C, E	C: 67.7	E: 16.7	L: 15.5		C, L, E	C, L, E	C, L, E
5km0.7qE,1,2,4,12,L,C	0.655	0.031	2, 4, C, E	C: 49.0	L: 18.0	E: 12.3	Bio1: 11.0	C, L, E	C, L, 4	C, L, E
5km0.7qE,L,C	0.635	0.021	C, E	C: 62.5	L: 22.7	E: 14.7		C, L, E	C, L, E	C, L, E
5km0.9qE,1,2,4,12,L,C	0.658	0.019	2, 4, C, E	C: 51.7	L: 18.4	E: 11.8	Bio1: 10.6	C, L, E	C, L, E	C, L, 4
5km0.9qE,L,C	0.629	0.011	C, E	C: 55.4	E: 24.6	L: 20.0		C, L, E	C, L, E(-)	C, L, E
5km1.0qE,1,2,4,12,L,C	0.642	0.018	2, 4, C, E	C: 59.9	L: 12.8	E: 9.9		C, L, E	C, L, 12(-)	C, L, 1
5km1.0qE,L,C	0.635	0.028	C, E	C: 59.6	L: 21.9	E: 18.4		C, L, E	C, L, E(-)	C, L, E
5km2.0qE,L,C	0.641	0.024	C, E	C: 66.9	E: 17.7	L: 15.4		C, L, E	C, L, E	C, L, E
5km3.0qE,L,C	0.635	0.028	C, E	C: 79.5	E: 10.8			C, L, E	C, L, E(-)	C, L, E

5km4.0qE,1,2,4,12,L,C	0.655	0.020	2, 4, C, E	C: 69.8	L: 11.4			C, L, E	C, L, E	C, L, 2
5km4.0qE,L,C	0.631	0.024	C, E	C: 53.3	L: 35.2	E: 11.6		C, L, E	C, L, E(-)	C, L, E
5km5.0qE,1,2,4,12,L,C	0.656	0.030	2, 4, C, E	C: 56.2	L: 19.7	Bio1: 12.1		C, L, E	C, L, E	C, L, 1
5km5.0qE,L,C	0.630	0.018	C, E	C: 62.7	L: 20.2	E: 17.1		C, L, E	C, L, E(-)	C, L, E
5km5.0qtE,1,2,4,12,L,C	0.656	0.014	2, 4, C, E	C: 65.1	L: 14.4			C, L, E	C, L, 12(-)	C, L, 1
5km5.0qtE,L,C	0.650	0.025	C, E	C: 67.8	L: 22.3	E: 9.9		C, L, E	C, L, E	C, L, E
5km6.0qE,L,C	0.634	0.031	C, E	C: 52.9	L: 31.8	E: 15.3		C, L, E	C, L, E	C, L, E
5km6.0qtE,L,C	0.632	0.028	C, E	C: 59.7	L: 24.5	E: 15.7		C, L, E	C, E(-), L	C, L, E
10km0.1lE,1,4,7,12,L,C	0.705	0.017	1, 7, C, E	C: 48.8	Bio4: 24.6	L: 13.5		C, 4, L	C, 4, E(-)	C, 4, L
10km0.1lE,1,2,4,7,12,16,L,C	0.709	0.011	1, 7, C, E	C: 53.1	Bio4: 19.8	L: 15.0		C, L, 4	C, L, 4	C, L, 4
10km0.3lE,1,4,7,12,L,C	0.704	0.032	1, 7, C, E	C: 53.2	Bio4: 23.0	L: 12.5		C, 4, L	C, L, 4	C, L, 4
10km0.3lE,1,2,4,7,12,16,L,C	0.702	0.018	16, 7, C, E	C: 50.4	Bio4: 15.4	L: 13.7		C, L, 4	C, 4, L	C, 4, L
10km0.5lE,1,4,7,12,L,C	0.712	0.021	7, C, E	C: 55.2	Bio4: 25.9	L: 11.7		C, 4, L	C, L, 4	C, L, 4
10km0.7lE,1,4,7,12,L,C	0.694	0.009	7, C, E	C: 46.5	Bio4: 25.8	L: 17.0		C, 4, L	C, 4, L	C, 4, L
10km1.0lE,1,4,7,12,L,C	0.708	0.021	7, C, E	C: 59.5	Bio4: 17.2			C, 4, L	C, L, 4	C, L, 4
30km0.5lqE,1,2,4,7,12,16,L,C	0.753	0.021	1, 12, 7, C, E	Bio2: 28.3	C: 20.6	L: 17.3	Bio7: 10.6	C, L, 2	C, 2, L	C, 2, L

Table 3. Transition matrices showing estimated stasis (on diagonal), growth (below diagonal), and reproductive (upper right) elements A) without blight and B) with blight for a population of American chestnut in W Tennessee, N Mississippi, SW Kentucky, and NW Alabama. Matrix elements were derived from rates estimated for populations of American chestnut in S Maine (Elwood, 2014) and Michigan (Davelos and Jarosz, 2004). Size class regressions in prior studies were included in rates for size class stasis

A. w/o Blight	**1. Resprout**	**2. Sprout**	**3. Sapling**	**4. Tree**	**5. Mature Tree**
1. Resprout	0.826	0	0	0.693	2.167
2. Sprout	0.171	0.977	0	0	0
3. Sapling	0	0.023	0.866	0	0
4. Tree	0	0	0.134	0.957	0
5. Mature Tree	0	0	0	0.043	0.987
B. w/ Blight	**1. Resprout**	**2. Sprout**	**3. Sapling**	**4. Tree**	**5. Mature Tree**
1. Resprout	0.765	0	0	0.693	2.167
2. Sprout	0.159	0.905	0	0	0
3. Sapling	0	0.021	0.709	0	0
4. Tree	0	0	0.110	0.338	0
5. Mature Tree	0	0	0	0.015	0.380

Figure 1. Life cycle diagram for a stage-classed *Castanea dentata* population in W Tennessee, N Mississippi, SW Kentucky, and NW Alabama. All trees were assigned to stage classes based on diameter at breast height (DBH) measurements. Stage classes are represented by squares (Resprout (stage 1) ≤ 1cm DBH, Sprout (stage 2) = 1.1-2.5cm DBH, Sapling (stage 3) = 2.6-10cm DBH, Tree (stage 4) = 10.1-20cm DBH, Mature Tree (stage 5) ≥ 20cm DBH). Arrows represent growth (G) transitions between stages, stasis (S) within a stage class, and fecundity (F) of reproductive stage classes. Values associated with transitions are elasticities for a model without blight (A) and a model with blight (B), representing the proportional importance of changes to a transition/stasis/fecundity rate on population growth

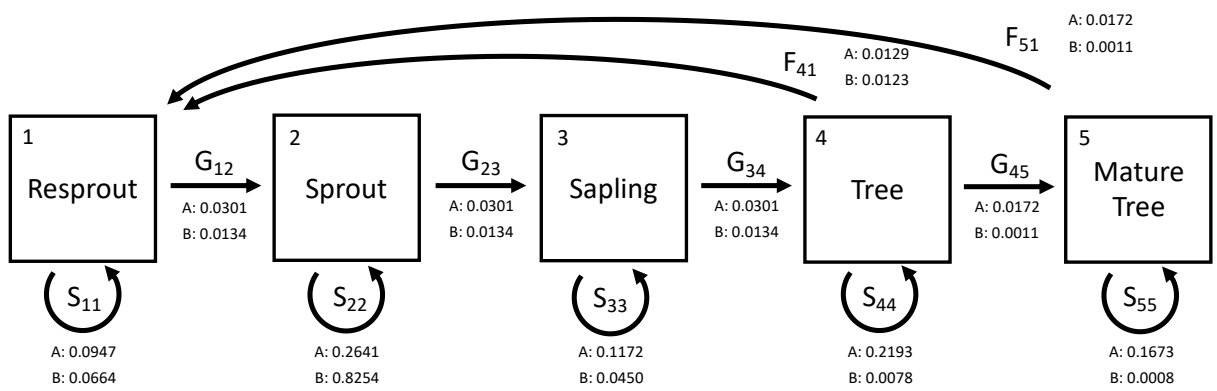


Figure 2. A) The estimated historical range of *Castanea dentata* (gray shading; Little, 1977) in W Tennessee (Tenn.), N Mississippi (Miss.), SW Kentucky (Ken.), and NW Alabama (Ala.). The black square in the inset map indicates the study location. Representative ENM projections using B) 5km, C) 10km, and D) 30km environmental layer buffers around each point for model construction. In B, C, and D, warmer (*i.e.*, more orange) colors indicate higher predicted environmental suitability. The model projections resulting from the 5km buffers were generally more apparently "realistic" compared to those arising from the 10km and 30km buffers (Supplemental File 2). Black dots in all panels show the location of occurrence records within the area of interest that were used for ENM construction. County boundaries are indicated by the lighter borders within each state

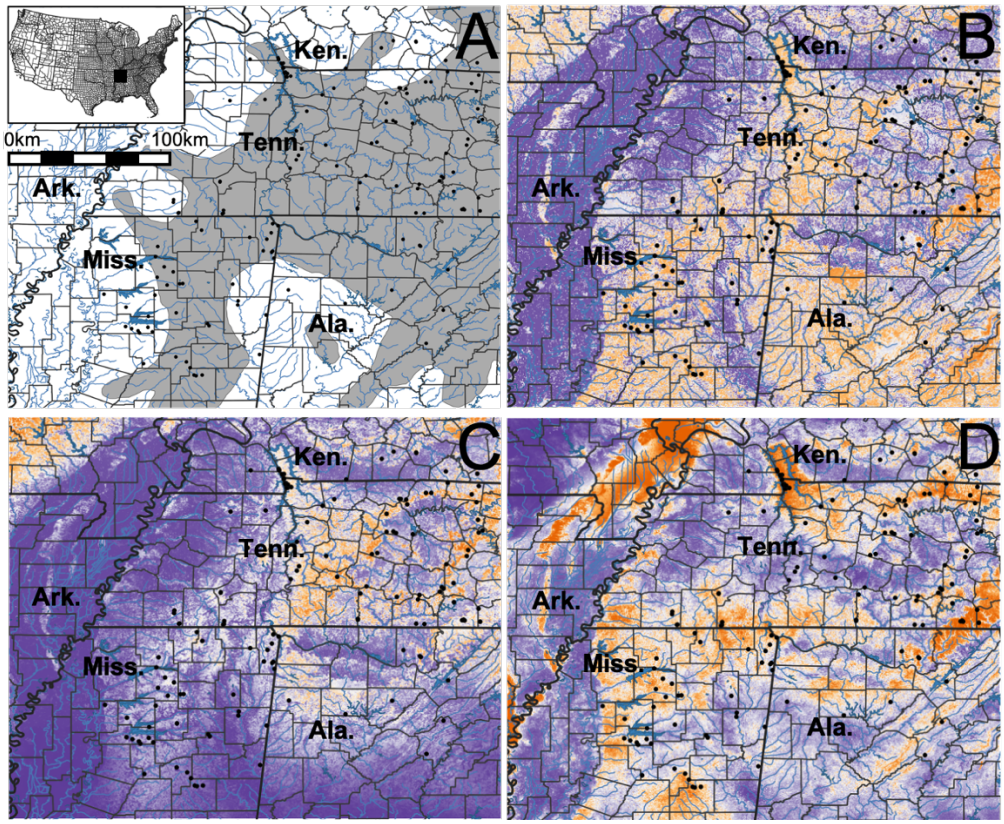
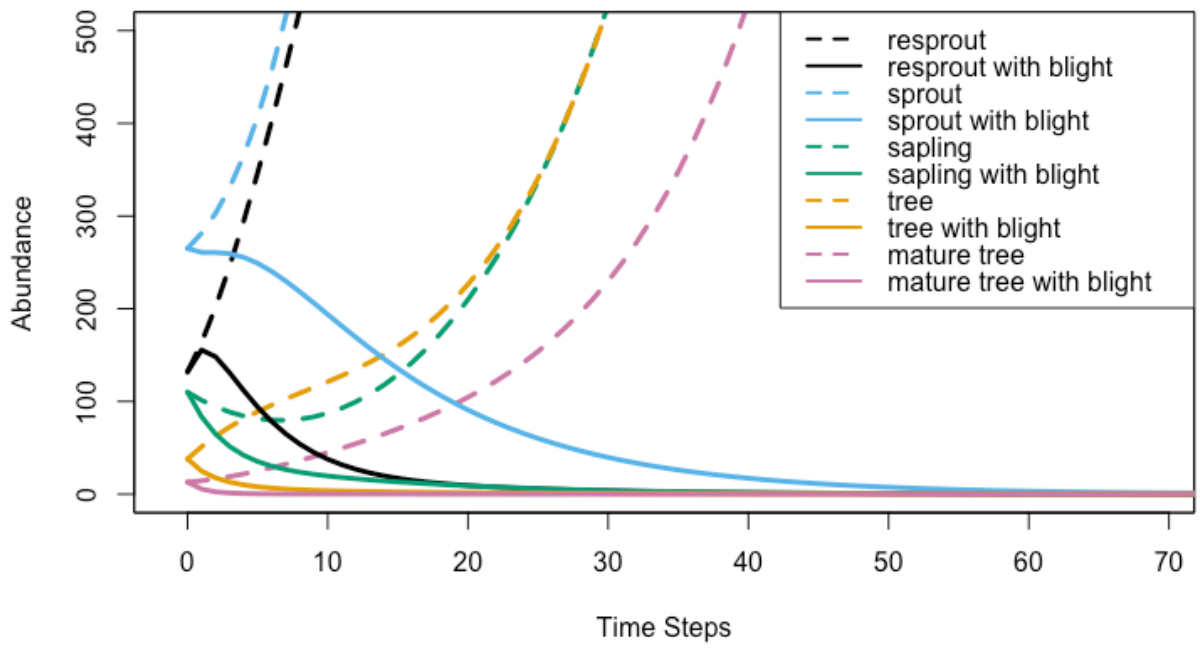


Figure 3. Demographic model projections for a *Castanea dentata* population in W Tennessee, N Mississippi, SW Kentucky, and NW Alabama without blight (dashed lines) and with blight (solid lines). Each line represents the demographic trajectory for a different size class as indicated in the inset key. Without blight, the population was predicted to have a $\lambda = 1.09$ indicating an increase ~9% per time step, while with blight the population is predicted to have a $\lambda = 0.92$ indicating a decrease of ~8% per time step. The duration of each time step is not known for the study population, but is estimated to extend over multiple years for a similar population in southern Ontario, Canada (~13 years; Van Drunen *et al.*, 2018), suggesting extinction of American chestnut throughout the study region could occur in ~100-200 years



995 Supplemental File 1. R scripts used for environmental niche model calibration (adapted from
996 Simões *et al.*, 2020) and demographic matrix modeling in 'popbio' (Stubben and Milligan,
997 2007).
998
999 Supplemental File 2. Locality and size information for all W Tennessee, N Mississippi, SW
1000 Kentucky, and NW Alabama American chestnut observations comprising the demographically
1001 modeled population. Observations included historical collections from herbaria, personal
1002 observations by the authors and colleagues, and citizen naturalist observations from GBIF
1003 recorded and verified with the iNaturalist application.
1004
1005 Supplemental File 3. Environmental niche model projections from Maxent across W Tennessee,
1006 N Mississippi, SW Kentucky, and NW Alabama for all 30 models passing model calibration
1007 criteria. The models arising from the 5km buffer calibration layers (the first 12 models) generally
1008 produced more apparently realistic projections for suitable habitat compared to the models
1009 arising from the 10km buffer calibration layers (next 7 models) or the 30km buffer calibration
1010 layers (last model). Many of the 10km buffer models underestimated parts of the N Mississippi
1011 range, while the 30km buffer model predicts suitable habitat in many areas where chestnut is not
1012 observed. Some of the 5km buffer models that incorporate Bioclim variables with elevation, land
1013 cover, and canopy cover also make apparent overpredictions of environmental suitability.