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Consequences of Shifts in Abundance and Distribution of American Chestnut for Restoration of a Foundation Forest Tree

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Abstract: Restoration of foundation species, such as the American chestnut (*Castanea dentata*) that was devastated by an introduced fungus, can restore ecosystem function. Understanding both the current distribution as well as biogeographic patterns is important for restoration planning. We used United States Department of Agriculture Forest Service Forest Inventory and Analysis data to quantify the current density and distribution of *C. dentata*. We then review the literature concerning biogeographic patterns in *C. dentata*. Currently, 431 ± 30.2 million stems remain. The vast majority (360 ± 22 million) are sprouts <2.5 cm dbh. Although this number is approximately 10% of the estimated pre-blight population, blight has caused a major shift in the size structure. The current-day population has a larger range, particularly west and north, likely due to human translocation. While climate change could facilitate northward expansion, limited seed reproduction makes this unlikely without assisted migration. Previous research demonstrates that the current, smaller population contains slightly higher genetic diversity than expected, although little information exists on biogeographic patterns in the genetics of adaptive traits. Our research provides a baseline characterization of the contemporary population of *C. dentata*, to enable monitoring stem densities and range limits to support restoration efforts.

Keywords: *Castanea dentata*; chestnut blight; FIA; forest inventory and analysis; tree distribution

1. Introduction

Due to the rapid pace of human alterations of ecosystems, restoration is becoming an increasingly important tool in conservation biology [1,2]. In forests, foundation tree species are recognized as those that control population and community dynamics as well as ecosystem processes such as productivity and decomposition [3]. Restorations of foundation species can thus serve to both rejuvenate populations of these plants while simultaneously restoring ecosystem function.

The American chestnut (*Castanea dentata*) is considered a foundation species in eastern North American forests because of its influence over seed consuming populations [4] and its impact on nutrient cycling [3]. The dominance of *C. dentata* ended with the accidental introduction of the chestnut blight fungus (*Cryphonectria parasitica* (= *Endothia parasitica*)), which spread rapidly throughout the range (Figure 1) [5]. The filamentous ascomycete fungus colonizes wounded

cambium, causing a canker that eventually results in death of the aboveground stem [6]. The blight does not attack root systems that are protected in the soil, however, allowing trees to form root-collar sprouts. The asexual cycle of sprouting, infection with blight, and stem dieback can persist for decades, but sexual reproduction in natural forests is rare [7]. While it is fortunate that the blight did not cause the extinction of *C. dentata*, it did effectively extirpate it from the canopy, causing it to be functionally extinct in modern forests.

Since blight was discovered, many groups have attempted to create a blight resistant *C. dentata*. Jacobs *et al.* [8] review the three main approaches that have been pursued to develop blight resistance including biocontrol with hypovirulence, inter- and intra-species breeding programs, and, most recently, genetic engineering. Because of these efforts, restoration of *C. dentata* has become a viable possibility, which could have profound impacts on eastern forests through its effect on plant community composition, carbon cycling, and food web dynamics [8]. Breeding and biotechnology efforts are coming to fruition and, thus, researchers have begun to consider the ecology of *C. dentata* related to restoration efforts [8,9].

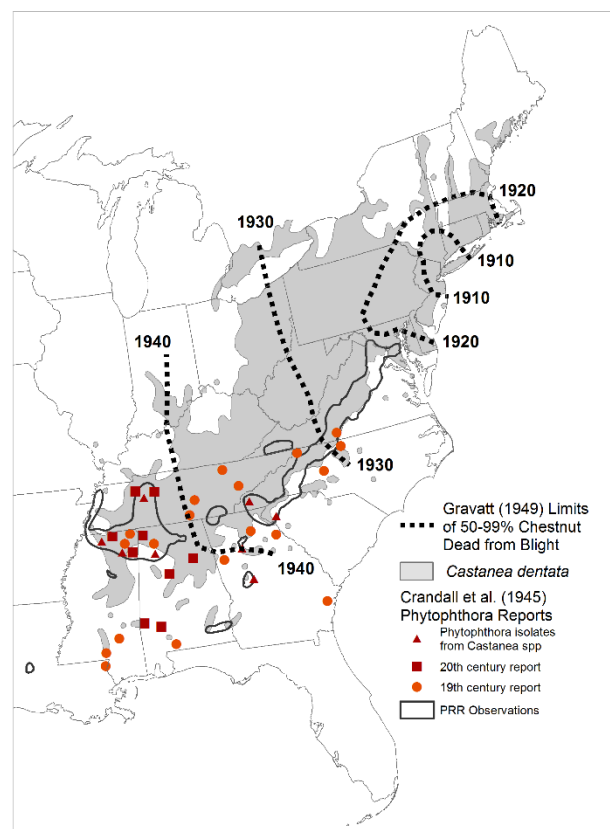


Figure 1. Pre-blight geographic range of *Castanea dentata* (Little 1977). Dotted lines indicate approximate blight progression (trees dead from blight) from Gravatt (1949). *Phytophthora* root rot (PRR) observations in the 19th and 20th centuries are from Crandall *et al.*, (1945).

Castanea dentata is a well-known case of a native species decline due to an imported species in North America, but it is unfortunately not the final case (e.g., emerald ash borer (*Agrilus planipennis*) on ash (*Fraxinus* spp.); hemlock woolly adelgid (*Adelges tsugae*) on eastern and Carolina hemlock (*Tsuga canadensis*, *T. caroliniana*). Because of the rapid pace of habitat destruction and climate change, discussions of species translocations and reintroductions have come to the forefront in conservation and restoration biology. *Castanea dentata* informs this dialogue and provides a case study for reintroduction biology of a foundation forest tree [8].

Our first aim in this paper is to characterize both the current distribution and abundance of *C. dentata* to create a new baseline to support restoration efforts. We use new United States Department of Agriculture Forest Service Forest Inventory and Analysis (FIA) program data to document the current abundance and distribution of *C. dentata*. Our second aim is to review what is known about biogeographic patterns in *C. dentata* with particular attention to climate change and genetic considerations, both of which will be important for restoration efforts.

2. Methods

Previous researchers have noted the limitations for using FIA data to assess *C. dentata* populations including the nature of the FIA sample, the rarity of *C. dentata*, inconsistency in the sampling of seedlings across states and inventory years, and species misidentifications [10]. In response to some of these limitations, the FIA program has implemented over the past two decades a nationally consistent sampling protocol and database system [11]. Data for seedling-sized trees are now available, along with approximate geographic locations and information by ecological regions, sections and subsections. *Castanea dentata* is still relatively rare and species misidentifications could occur, which may produce anomalies despite rigorous quality control procedures. Nevertheless, the FIA data are now significantly more useful for assessing contemporary *C. dentata* populations.

The current FIA sampling design consists of three phases. The first phase uses remote sensing to produce a stratification of land area to reduce estimation variance. In the second phase, field crews visit permanent ground plots to measure tree and stand variables. The ground plots are located at a density of approximately 1 plot per 2428 ha, one plot within a hexagon of a national array of hexagons covering the land area of the conterminous United States. The third phase is a 1/16th subset of the Phase 2 plots. Phase 3 plots are measured for additional variables related to forest ecosystem health. The estimates reported in this paper are derived from the Phase 1 stratification and the field measurements from Phase 2. The Phase 2 ground plot consists of a cluster of four subplot centers located 36.6 m apart. At each subplot center a 7.3 m radius subplot is used to measure all trees within that are 12.7 cm in diameter at breast height (dbh) or greater. Each subplot contains a 2.1-m radius microplot, which is used to sample all saplings (trees 2.5 cm–12.4 cm dbh) and seedlings (trees <2.5 cm dbh). The total area of the four subplots is 0.03 ha.

We used FIA data (Phase 1 and Phase 2) collected between 2002 and 2012 to develop an updated map of *C. dentata*'s distribution in the eastern United States. We included FIA inventories from 30 states (those with listings in the Biota of North America database [12] with native or naturalized occurrences of *C. dentata*). All 30 states had data meeting the new standards in 2013 [11]. We accessed the FIA database via a web tool, EVALIDator (VERSION 1.5.1.04) (<http://fiatools.fs.fed.us/Evalidator401/tmattribute.jsp>) on 1 March 2013. The query tool uses the methods of [13] regarding sampling protocols, estimation methods, methods for combining annual data for multi-year estimates, and estimation of sampling errors. *Castanea dentata* was observed in 16 of the 30 states in the FIA database, which covers most of the historical range (Table 1). Four states outside of Little's range, but with historical records of introduction, did not turn up any observations in the FIA sample, nor did 10 states on the periphery of Little's range. The geographic distribution of the surviving population was mapped by summarizing estimates by Bailey's ecological subsections [14] (Figure 2). Ecological subsections with densities of 1000 stems km^{-2} were mapped individually. Subsections with lower densities were combined at the section level in an effort to reduce noise from high estimation errors for these subsections. Ecological units were clipped to the counties with *C. dentata* listings in the Biota of North America Plant Atlas [12].

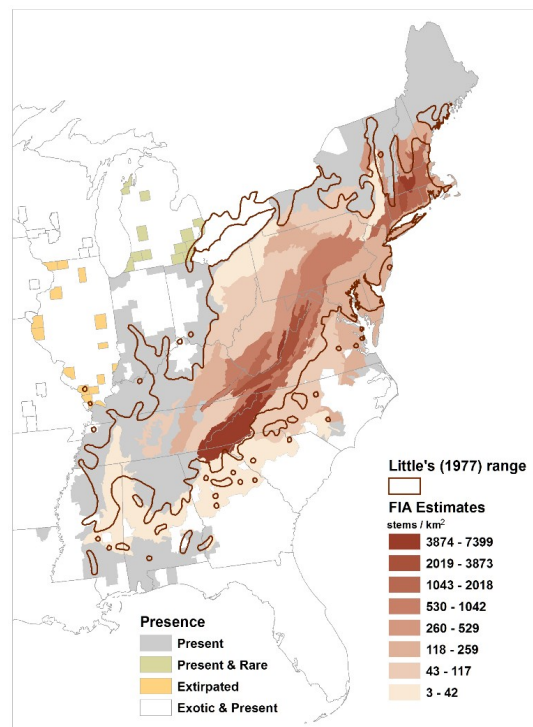


Figure 2. Geographic distribution of surviving *Castanea dentata* populations, with presence data taken from the Biota of North America (Kartesz 2013) and stem densities estimated from the Forest Inventory and Analysis (FIA) data.

Table 1. FIA state evaluation groups used in the estimation of chestnut populations. States listed in italics have no chestnuts in the FIA database.

| State | Evaluation Group |
|-----------------------|------------------|
| Alabama | 2006–2012 |
| <i>Arkansas</i> | 2006–2012 |
| Connecticut | 2007–2011 |
| <i>Delaware</i> | 2007–2011 |
| Florida | 2002–2010 |
| Georgia | 2005–2011 |
| <i>Illinois</i> | 2007–2011 |
| <i>Indiana</i> | 2007–2011 |
| Kentucky | 2005–2011 |
| <i>Louisiana</i> | 2001–2009 |
| <i>Maine</i> | 2007–2011 |
| Maryland | 2007–2011 |
| Massachusetts | 2007–2011 |
| <i>Michigan</i> | 2007–2011 |
| <i>Minnesota</i> | 2009–2012 |
| <i>Mississippi</i> | 2006–2012 |
| <i>Missouri</i> | 2007–2011 |
| New Hampshire | 2007–2011 |
| New Jersey | 2007–2011 |
| New York | 2007–2011 |
| North Carolina | 2003–2010 |
| <i>Ohio</i> | 2007–2011 |
| Pennsylvania | 2007–2011 |
| Rhode Island | 2007–2011 |
| <i>South Carolina</i> | 2007–2011 |
| Tennessee | 2005–2011 |
| <i>Vermont</i> | 2007–2011 |
| Virginia | 2008–2011 |
| West Virginia | 2007–2011 |
| <i>Wisconsin</i> | 2008–2012 |

3. Results

The estimated number of live seedling-sized stems (diameter at breast height <2.5 cm) was 360 million with sampling error of 6.13% (22 million). The estimated number of live trees with diameter at breast height \geq 2.5 cm was 70.9 million with sampling error of 11.56% (8.2 million). Combining the estimates gives a population total of 431 million stems with sampling error of 7.1% (30.2 million). *Castanea dentata* densities were highest in the Blue Ridge Mountains, the Allegheny Mountains, Lower New England, the Northern Ridge and Valley, and the Northern Cumberland Mountains (Figure 2). The Biota of North America [12] noted the species as present in each state included in Little's [15] range map (Figure 2). In addition, *C. dentata* was found outside the historic range in Louisiana, Missouri, Iowa, Wisconsin, Michigan, and Florida, apparently due to human translocation (Figure 2).

Our estimate of 431 million *C. dentata* stems remaining in eastern North America can be contrasted with a historic population estimate of 4.2 billion trees [16]. This suggests that 10% of the pre-blight *C. dentata* population remains. It is unclear whether the historical estimate includes seedlings or only canopy trees. If the population size is only for canopy trees, then our estimates of the remaining population size are high. Despite this uncertainty, it is clear that the current-day population of *C. dentata* is significantly smaller in numbers but also spread over a larger range than the historical population (Figure 2). In addition, the size distribution is greatly skewed, with 84% of the population in the seedling-size class and only 16% of trees being larger than 2.5 cm dbh.

4. Discussion

4.1. Density and Distribution of *Castanea Dentata*

Previous analysis of FIA data designed to quantify extant *C. dentata* populations was limited by the lack of quality seedling (<2.5 cm dbh) data [10]. However, McWilliams *et al.* [10] were able to estimate that 1.13 million ha of forest contain *C. dentata* stems at least 2.54 cm in dbh. The states with the highest frequency of *C. dentata* included Pennsylvania, Virginia, North Carolina, West Virginia, Massachusetts, and New York [10]. The frequency measure of abundance used by McWilliams *et al.* [10] aligns well with our current analysis based upon density of *C. dentata* stems.

Long-lived trees, such as *C. dentata*, that are relatively shade tolerant [17,18] and rely upon advanced regeneration for successful reproduction, would be expected to have a large proportion of their population in seedling size classes. We observed 84% of the population in the seedling size classes for contemporary *C. dentata* populations. This proportion is larger than the 73% of the population reported in the seedling class for mature stands of American chestnut in Michigan [19]. Indeed, our number is much closer to the 81% reported by Davleos and Jarosz [19] for populations in Michigan that were experiencing an epidemic of blight. This comparison indicates that *C. dentata* is still experiencing the blight epidemic throughout its range and that the proportion of trees in the seedling size class is likely much higher than in historical populations.

Interestingly, the range of *C. dentata* seems to have expanded from the pre-blight distribution reported by Little [15] (Figure 1). Frost sensitivity may have limited its proliferation at higher latitudes in some northern forests [20]. An outbreak of the introduced soil borne oomycete pathogen, *Phytophthora cinnamomi* Rands, during approximately 1825–1875 (Figure 1) may have been responsible for permanently retracting the southern portion of the range of *C. dentata* from the southeastern Piedmont, the Atlantic and Gulf Coastal Plains and western Tennessee [21,22]. In the late 1800's most *C. dentata* in the Piedmont region of North Carolina had disappeared, while its natural range was still expanding before the introduction of the blight in other areas [20]. For example, *C. dentata* was still spreading northwestward into Michigan at the time of blight introduction [23]. Many of the populations we document to the west of the original range, particularly those in Wisconsin and Michigan, are known translocations [23,24]. These populations were often initially

started through plantings that spread through natural reproduction, though some populations in Michigan may also have been initiated without human assistance [19].

Understanding the current density and distribution of *C. dentata* in contemporary forests can provide fundamental knowledge to aid in future *C. dentata* restoration. Major landscape-level changes have occurred since introduction of blight that may influence which specific regions and site types should be ideally targeted for restoration. Climate change is among the most prominent examples and FIA data are currently being used to examine potential range shifts in response to this phenomenon [25,26]. Our data can serve as a baseline for similar studies in *C. dentata*. In addition, the population we describe provides an indication of the potential genetic reserve of *C. dentata*, which is a basis for breeding and genetic engineering efforts aimed at developing blight resistance for restoration efforts [8,27]. Below we review what is known in the literature about biogeographic patterns in climate and genetic diversity relevant to *C. dentata* in light of our new results.

4.2. Climate

The historical distribution of *C. dentata* encompasses a slightly smaller climatic space compared to other species in the genus, particularly relative to *C. mollissima* [28]. Average annual precipitation across the entire range is between 100 and 120 cm, ranging from a low of about 81 cm in western New York to a high of 200 cm in the southern Appalachians [29]. Snowfall in the northern portions of the range can be significant and exceed 2.5 m annually [29]. Along with *C. crenata*, *C. dentata* inhabits some of the coldest conditions compared to other *Castanea* species worldwide [28].

Over the past decade, the northern areas of *C. dentata*'s range have experienced increases in mean annual temperature while the southern portions of the range have seen no net change in mean annual temperatures, due to increased cooling in the winter months combined with increased warming in the summer months [26]. Such changes in temperatures are expected to shift range distributions of species, including forest trees. FIA data have been used to examine indirect evidence for tree range shifts in response to climate change [25,26]. Woodall *et al.* [25] present evidence that 70% of the 15 northern species they examined are shifting northward, while the 15 southern species' ranges remain mostly unchanged. In an updated analysis using the most recent seedling FIA datasets, Zhu *et al.* [26] argue that 58% of the 92 species examined showed evidence of range contraction while only 20% display the expected pattern for northward range expansion.

The limited seed production that occurs in current-day *C. dentata* populations [7] means that range shifts northward in response to climate change will be extremely unlikely. However, contraction of sprout-based populations is entirely possible if temperatures become unfavorable or interact with other climate factors such as an increase in the frequency of late spring frosts or decreases in winter snowpack [30].

All of the areas with the highest current density of *C. dentata* occur within the historical range (Figure 2). In addition, our data show that *C. dentata* is currently present in areas that are north of the historical range (Figure 2); it is less clear whether this is due to natural northward expansion or human-assisted planting. Although the mechanism is unclear, the presence of *C. dentata* north of its historical range indicates that these areas may be climatically suitable for restoration. Although climate change may not be as problematic in the southern portion of *C. dentata*'s range, the prevalence of *Phytophthora* root rot disease is a persistent threat to *C. dentata*'s viability in this region [21]. Indeed, the observation that *Phytophthora* is expanding northward due to warming temperatures is a major threat posed by climate change [31]. Our results illustrate very low stem densities in the southwest portion of the historical range. This is most likely caused by high rates of chestnut mortality due to *Phytophthora*, which underscores the strong threat that *Phytophthora* poses to restoration (Figure 2).

4.3. Genetic Diversity

The post-blight extant stems that we describe here are the basis for breeding and genetic engineering efforts aimed at developing blight resistance for restoration. As such, understanding

biogeographic patterns in genetic diversity will be important for breeding locally adapted sources for restoration. Studies have estimated genetic diversity in contemporary populations of *C. dentata* using protein (isozymes) and non-coding (*i.e.*, neutral) DNA markers (reviewed in [8]). Isozyme diversity is higher in the southern parts of the *C. dentata* range. An exception to this general pattern is that less diversity is found in some lower and intermediate latitude populations of *C. dentata* [32]. Additional neutral DNA markers and population sampling strongly support the southwest to northeast clinal trend in decreasing genetic diversity with no or very limited indication of regional boundaries [33,34]. Kubisiak and Roberds [33] also found low but positive correlations between genetic and geographic distances, suggesting that *C. dentata* was a single metapopulation established by high gene flow with some genetic drift and is apparently maintained by persistence (through root collar sprouting) of a large sample of pre-blight genotypes. Although we calculate that only 7% to 11% of the pre-blight population remains, significant genetic diversity has been retained [33]. Further, our data indicate an area of high stem density in the southern Appalachians, which coincides with areas of greatest genetic diversity (Figure 2) and areas that contain hybridized (with *C. pumila* var. *pumila*) individuals [34–36].

Although gene diversity studies, using neutral allele frequencies, over large areas of the *C. dentata* native range have found low levels of genetic differentiation with little to no regional pattern [32,33,37], essentially no information is available on geographic variation for adaptive traits such as bud flushing date, thermal and moisture tolerances, or growth rate. While data from a close relative with a similar wide-range (such as European chestnut, *C. sativa*, [38,39]) can be helpful as an initial guide, the lack of this critical information on these traits in *C. dentata* limits our ability to create optimally adapted genotypes for re-introduction and restoration programs for this species.

5. Conclusions

In the United States, 431 ± 30.2 million *C. dentata* stems remain with the vast majority of these stems (360 ± 22 million, 84%) having a dbh of <2.5 cm. Both the southern and northern portions of the range have lower density of stems than the central portion comprising the Appalachians and southern New England. Analyses of FIA data collected with improved methods provide an important baseline for tree monitoring that will enable further examination of future changes in stem densities and range limits. Furthermore these data indicate expansion of the range north and west, most likely due to human-assisted translocation. Although expansion of the range through natural seed dispersal is extremely unlikely given the persistence of blight, contraction of sprout populations is a possibility in the face of climate change. Previous genetic research indicates that the southern portion of the range contains the highest genetic diversity, which coincides with areas of high stem density reported in our data. Further research into biogeographic patterns of genetic traits is needed, particularly those associated with adaptive traits such as bud flush and cold tolerance.

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Conflicts of Interest: The authors declare no conflict of interest.

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