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Reconsidering the fire ecology of the iconic American chestnut

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Abstract. The iconic American chestnut (*Castanea dentata*) once spanned a large portion of eastern North America before its functional extinction in the early 20th century due primarily to non-native fungal pathogens. The pronounced loss of this species likely resulted in an abrupt alteration of many ecological processes, including fire. The potential to resurrect this species through resistance breeding or other methods holds promise, but more information on the fire ecology of American chestnut may provide helpful information to assist restoration. Here we summarize the existing direct and indirect research on the fire history and fire ecology within the former range of American chestnut. We found multiple lines of evidence to suggest fire was frequent throughout much of its historical range. A broadscale analysis of historical fire frequency revealed that 88% of the American chestnut range had a mean fire return interval of 20 yr or less, corresponding to finer-scale fire history and forest structure studies. In much of the historical range of American chestnut, the stand structure was much more open, fire scar studies of associated species were very frequent (mean fire return interval ranged between 1.9 and 19.8 yr), and, in many cases, charcoal abundance and American chestnut pollen were positively related. This evidence coupled with American chestnut's suite of traits associated with tolerance of frequent fire, such as highly flammable litter, tall stature, rapid growth, and resprouting ability, reinforce concepts that fire was historically an important component of many woodlands and forests containing American chestnut. While these lines of evidence are strongly suggestive, we provide potential areas of further inquiry to expand and refine our understanding of American chestnut fire ecology.

Key words: American chestnut; *Castanea dentata*; fire-adaptive traits; fire ecology; fire history; foundation species; restoration.

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Introduction

While fire is an important process in many eastern North American forest ecosystems, debate on the role of fire in some deciduous forests persists (Matlack 2013, Stambaugh et al. 2015, Hanberry et al. 2020*a*). This uncertainty is largely due to the limited extent of existing studies and numerous gaps in our understanding, a circumstance particularly evident for forests containing the once widespread and iconic American chestnut, *Castanea dentata*. The extensive range of American chestnut (Fig. 1) was in part due to its ability to coexist with many other species across a wide range of environmental conditions, from xeric woodlands with highly fire-adapted pines and oaks (e.g., *Pinus rigida, Quercus montana*; see Table 5 in Nowacki and Abrams 2008) to mixed mesophytic and cove forests containing more fire-sensitive species (e.g., *Fagus grandifolia*, *Liriodendron tulipifera*, *Acer saccharum*; Braun 1950). In the early to mid-1900s, American chestnut went functionally extinct primarily because of the non-native fungal pathogens, *Cryphonectria parisitica* and *Phytophthora cinnamomi*. The loss of American chestnut resulted in numerous changes that varied depending on the pre-invasion stand composition, disturbance history, and other biophysical factors (Korstian and Stickel 1927, Nelson 1955, Elliott and Swank 2008). Since American chestnut is widely considered a foundation species (Ellison et al. 2005), the functional extinction of this species likely had numerous ecological consequences, including potential alterations to fire regimes.

Most early observations highlighted a negative role of fire in American chestnut forests, often commenting on how sensitive mature trees were to fire damage and that fire hindered seedling regeneration (Reed 1905, Ashe 1911). Zon (1904) briefly mentions that American chestnut was deeply rooted and capable of withstanding fires that burn through the litter layer. These early perspectives are informative, but were often based on anecdotal observations that focused on economic impacts through the loss of timber due to tree mortality and injury. Even by the mid-20th century, consideration of the possible positive role of fire in American chestnut ecosystems was still lacking. In Braun's (1950) classic book, "Deciduous Forests of North America," consideration of fire was generally lacking despite more recent evidence that indicates fire was prominent in many of these ecosystems (Lafon et al. 2017). In almost 100 pages of Braun (1950) that describes the ecology and geography of forests containing American chestnut, there are only three references to fire in these sections. Over the past half century, a deeper understanding about the role of fire in the eastern USA, including ecosystems containing American chestnut, has begun to emerge (Nowacki and Abrams 2008, Fesenmyer and Christensen 2010, Hanberry et al. 2020*b*). A recent synthesis on the silvics of American chestnut demonstrates this progress by highlighting some positive responses of the species to fire (Wang et al. 2013).

Over the past few decades, success in developing a putatively pathogen-resistant backcross hybrid between American chestnut and Chinese chestnut (*Castanea mollissima*) has resulted in extensive small-scale test outplantings of chestnut hybrids throughout much of the species' historical range, with increased interest in broader scale reintroductions (Clark et al. 2014, American Chestnut Foundation 2019). More recently, the development of a transgenic American chestnut that is pathogen-resistant also holds much promise for reintroducing the species (Zhang et al. 2013, Steiner et al. 2017). While more research is needed on the efficacy of larger scale reintroductions of pathogen-resistant American chestnut, studies of site suitability and silvicultural considerations have been conducted in an effort to facilitate landscape-level reintroduction (Jacobs 2007, Zhang et al. 2019, Tulowiecki 2020). As demonstrated by restoration efforts with other co-occurring species (e.g., *P. rigida*, *P. echinata*; Stambaugh et al. 2019), successful reintroduction of American chestnut may benefit from a better understanding of its disturbance ecology and the potential to incorporate fire in its recovery and management.

Here, we aim to extend the conversation about the historic role of fire in forests that contained American chestnut by proposing that fire was historically frequent and that this species had numerous traits that promoted resilience to fire. Specifically, our objectives are to (1) summarize the current understanding of the fire ecology of American chestnut based on fire history and fire-adaptive trait studies; (2) develop a conceptual framework that indicates the possible consequences of American chestnut loss on fire and forest dynamics; and (3) provide some salient areas for future research. The information and perspectives presented here have implications that may help efforts in reestablishing American chestnut in woodlands and forests of the eastern USA.

Evidence of Fire in American Chestnut Forests

Multiple lines of evidence suggest fire was frequent throughout much of the historical range of

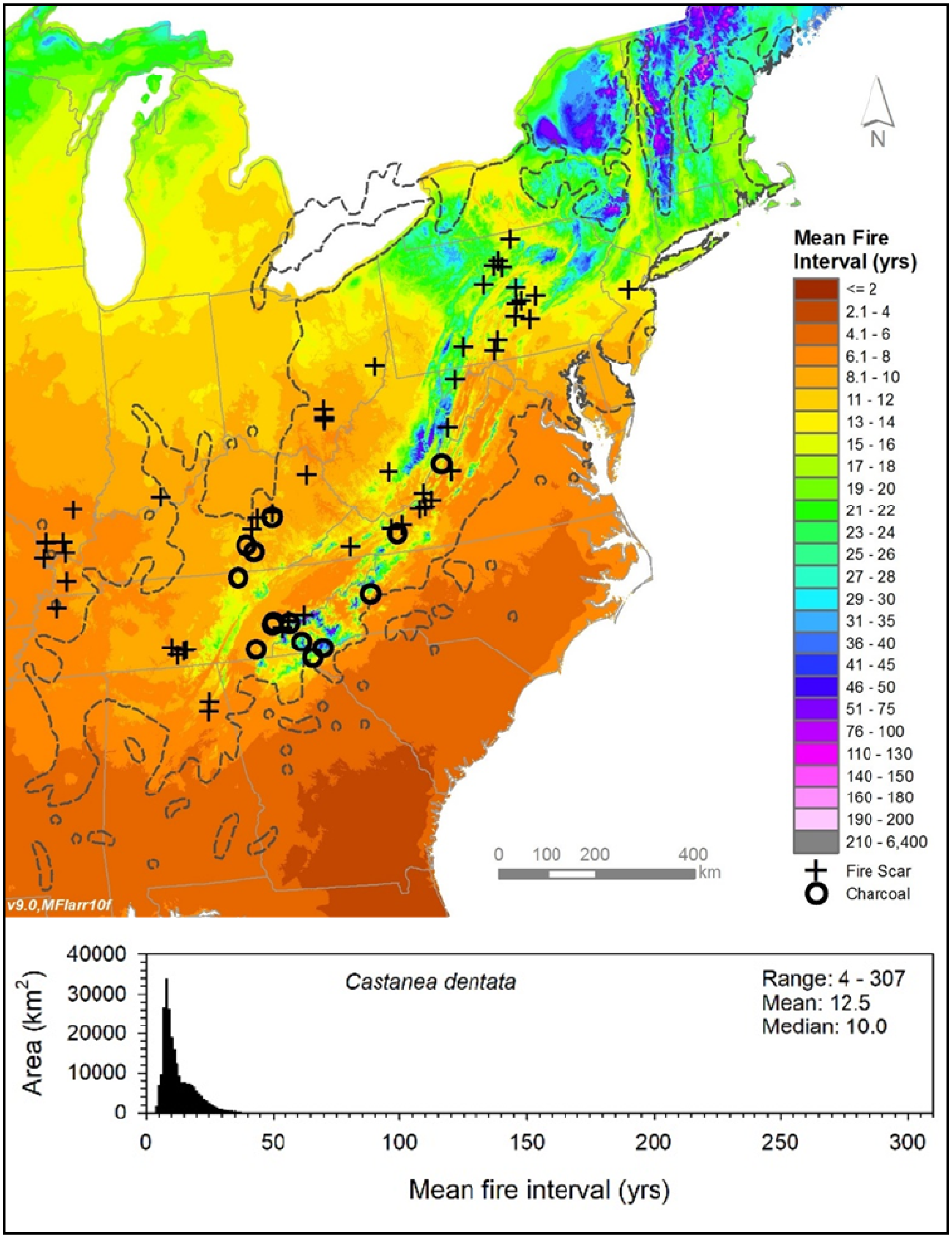

Fig. 1. Top: Map of historical mean fire intervals (MFIs) based on the Physical Chemistry Fire Frequency Model (Guyette et al. 2012) within the historical range of American chestnut (*Castanea dentata*; dark gray dashed line from Little 1977). Map includes locations of paleofire datasets from fire scars and charcoal (adapted from Stambaugh et al. 2015). Bottom: Histogram of area of MFIs within the historical range of American chestnut.

American chestnut prior to Euro-American settlement. The Physical Chemistry Fire Frequency Model (PC2FM) was calibrated and validated using historical fire scar records and is widely used to estimate pre-European settlement mean fire return intervals (MFIs) for the conterminous United States (Guyette et al. 2012), including within the range of American chestnut. When PC2FM MFIs are summarized for the entire natural range of American chestnut, 88% of the area had an MFI of ≤ 20 yr (Fig. 1), suggesting that many forests containing American chestnut historically experienced frequent fire. While PC2FM estimates provide a coarse-scale (1 km) perspective of historical fire regimes in the former American chestnut range that incorporates variation along elevational and latitudinal gradients, it may not capture finer-scale variation (e.g., slope aspect, topographic roughness) that represent fire refugia or areas with longer fire return intervals. For instance, lower fire activity of southern Appalachian mesic cove forests that contained American chestnut may not be adequately depicted with this model (e.g., Lorimer 1980). Conversely, other studies have found consistent levels of historic fire activity between xeric and mesic sites containing American chestnut (e.g., Fesenmyer and Christensen 2010).

The veracity of broadscale characterization of the historical fire return intervals derived from PC2FM remains uncertain, but these estimates correspond well to existing finer-scale fire scar studies in portions of the American chestnut range that suggest a past dominance of high frequency fire (i.e., multiple fires per decade). Over the past few decades, there have been 18 published fire scar studies across over 30 sites that were located within the historic range of American chestnut (Fig. 1; Stambaugh et al. 2015, Lafon et al. 2017). Across all fire scar study sites, the MFIs ranged between 1.9 and 19.5 yr (Shumway et al. 2001, McEwan et al. 2011, Brose et al. 2013, Flatley et al. 2013, Aldrich et al. 2014). Direct studies that examine fire scars on American chestnut have not been conducted and are unlikely due to the century of decay since the chestnut blight outbreak began in the early 1900s. However, the species examined in the fire scar studies summarized by Lafon et al. (2017) were historically common associates of American chestnut (Braun 1950). In some of the fire scar studies that indicate frequent fire, authors have noted that the study area previously contained mature trees or contained resprouts of American chestnut, with only few studies directly stating that the species had not been previously or currently present (McEwan et al. 2007, Hutchinson et al. 2008, Brose et al. 2013). Still, most of the existing fire scar studies in the former range of American chestnut were primarily from more xeric sites containing pine and oak. Pine-dominated (mostly *P. rigida*, *P. resinosa*, and *P. pungens*) sites had an average MFI of 5.9 while mixed-oak (mostly *Q. alba*, *Q. montana*, *Q. velutina*, and *Q. rubra*) sites had a slightly longer MFI of 7.4 yr (based on studies presented in Lafon et al. 2017). These frequent historical fire return interval estimates also coincide with evidence from historical stand data indicating that many eastern U.S. forests within the American chestnut range were once much more open (Hanberry and Nowacki 2016, Hanberry et al. 2020*b*). Still, the absence of direct proof is not the proof of absence of fire in American chestnut forests. Very mesic sites, such as cove forests, undoubtedly had longer fire return intervals but the degree of difference from xeric sites is unknown, though often speculated.

There is more direct evidence of fire in American chestnut forests based on charcoal and pollen analysis from soil and sediment studies. Numerous studies indicate that prior to Euro-American settlement, fire was prevalent in most locations within the former American chestnut range (e.g., Clark and Royall 1996, Lynch and Clark 2002). In some instances, periods of higher fire activity based on charcoal accumulation coincided with increases in American chestnut pollen abundance (Delcourt and Delcourt 1998, Lynch and Clark 2002). A soil charcoal study in the southern portion of the American chestnut range showed similar charcoal age distribution patterns along a topographic gradient indicating that fire was not limited to the xeric upper slope and ridgetop forests but extended downslope to mesic forests (Fesenmyer and Christensen 2010). Additionally, each of the sites along the topographic gradient in the Fesenmyer and Christensen (2010) study contained soil charcoal that was derived from the burning of American chestnut based on microscopic analysis of the wood anatomy (Underwood 2013).

Over the past two decades, research has highlighted that American chestnut has multiple traits that favor persistence within frequent fire regimes. A recent study that examined the flammability of American chestnut litter indicated that the observed flame lengths and drying rates were consistent with litter of other tree species associated with forests and woodlands historically characterized by short fire return intervals (Kane et al. 2019). It is possible that the quick drying and more flammable litter may have also facilitated fire spread into more mesic sites. American chestnut was relatively long-lived and had rapid growth rates (Collins et al. 2018), allowing it to attain a tall stature and presumably a high crown base height that limits scorching and potential transition of a surface fire to a crown fire (Agee and Skinner 2005). Coupled with high litter flammability, this suite of traits has been associated with frequent fire ecosystems containing the related eastern North America oaks (*Quercus* spp.; Cavender-Bares et al. 2004, Varner et al. 2016). The fast growth rate may also indicate that American chestnut is capable of rapidly healing wounds caused by fire (as many eastern Quercus are; Hengst and Dawson 1994), potentially assuaging early concerns that fire damage increased susceptibility to pests (Russell 1987). In spite of their lower root-to-shoot ratio and moderate-to-high shade tolerance as juveniles (Wang et al. 2006, Belair et al. 2018), mature American chestnut is deeply rooted, a prolific sprouter following fire (Paillet 2002), and can quickly take advantage of overstory canopy openings resulting from disturbance (Belair et al. 2018). The combination of these characteristics suggests that American chestnut may have a higher tolerance to more frequent fire than previously appreciated.

Implications on the Loss of American Chestnut and Fire

American chestnut was once a foundation species in eastern North America due to its ability to promote stable conditions through modulating and stabilizing fundamental ecosystem processes (Ellison et al. 2005). The species' highly flammable litter may have also contributed to its role as a foundation species through its influence on the fire regime (Kane et al. 2019). Given that fire-adaptive traits, including litter flammability, have been strongly associated with historic fire regime characteristics in other species and regions (Stevens et al. 2020), it is plausible that American chestnut and other pyrophytic species that have a similar suite of traits, such as longer leaves that result in a more optimal fuel bed bulk density to facilitate drying and burning, may also promote more frequent lower intensity fire.

The absence of fire, along with other land management impacts, has resulted in substantial changes to eastern North American forest composition and structure over the last century (McEwan et al. 2011, Hanberry et al. 2020*b*). In many instances, the exclusion of fire has resulted in increased tree density and greater representation of more shade-tolerant, mesic species. These changes can alter the microclimate of a stand, further excluding fire by inhibiting fire ignition and spread predominantly through increasing fuel moisture, a positive feedback process commonly referred to as "mesophication" (Nowacki and Abrams 2008). While the primary mechanism of mesophication has focused on the removal of fire from the landscape (via fragmentation, active fire suppression, and the reduction in the use of fire as an extensive land management tool), the loss of American chestnut may represent an underappreciated driver of this process within its range (McEwan et al. 2011). Comparisons of forest composition following blight indicate that American chestnut was often replaced by more mesic, fire-sensitive species (e.g., *Acer rubrum, Liriodendron tulipifera*; Schibig et al. 2005, Elliott and Swank 2008). The loss of flammable chestnut litter may have hastened litter bed changes and the decline of fire's importance in these landscapes (Fig. 2). In areas where other pyrophytic (e.g., *Quercus alba*) species have replaced chestnut, there is likely to be less change in surface fire behavior. However, potential impacts of forest composition changes will depend upon the characteristics of the replacement species, as most of these species are unlikely to discretely classify as strict pyrophytes and mesophytes. More likely, species will reside somewhere along a continuum from strong pyrophyte to strong mesophyte based on their litter drying rates and flammability (Kreye et al. 2013, Varner et al. 2015), accretion and decomposition rates (Alexander and Arthur 2014), canopy architecture (Alexander and Arthur 2010), as well as other traits that enable species to survive surface

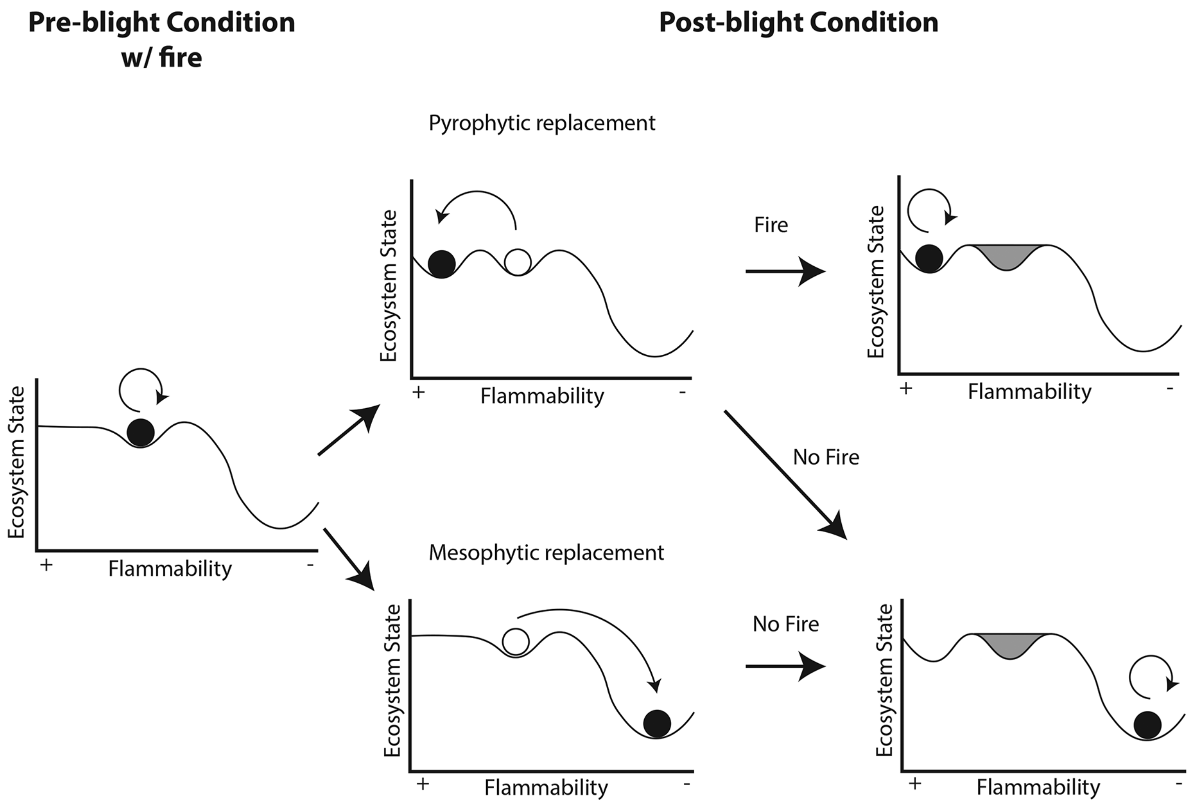

Fig. 2. A conceptual framework of potential state and transitions of American chestnut forests following chestnut blight and subsequent fire scenarios based on traits of replacement species and their impacts to litter flammability. Open circles refer to transitional states while solid circles represent stable states. Arrows reflect the direction of change or negative feedback processes of stable states. Pyrophytic replacement refers to the replacement of chestnut with species of similar or greater flammability and mesophytic replacement refers to substitution with lower flammability species. Depth of the stability wells depicted will depend upon the abundance and degree of mesophytes or pyrophytes that replaced American chestnut and whether the site is xeric or mesic. Mesic sites with a high proportion of mesophyte replacers will have deeper wells than xeric sites with pyrophyte replacers.

fires (e.g., bark, self-pruning; Jackson et al. 1999, Keeley and Zedler 1998). The degree of change in a stand will also depend on other factors, such as soil conditions and pre-invasion American chestnut density. Less productive, xeric sites would have likely experienced a lower rate of replacement of mesophytes than more mesic sites (Nowacki and Abrams 2008). The historical density of American chestnut ranged widely, but in many areas, it was clearly the dominant canopy species (Braun 1950, Mackey and Sivec 1973). These areas that historically contained a high density of American chestnut would have likely resulted in a greater rate of replacement compared to areas of lower density.

Areas for Future Research

The preponderance of evidence suggests that reconsidering the fire ecology of American chestnut is appropriate. Much of the evidence highlighted here is based on a broadscale analysis of historical fire regime modeling and history studies or deductive inference based on individual species' traits. Clearly, there are many areas for possible advancement of our understanding related to the fire ecology of American chestnut (Box 1).

Fire regime modeling (e.g., PC2FM) could be enhanced to account for finer-scale variation in mean fire return intervals through better incorporating variation associated with topography,

Box 1.

Areas for further research related to the fire history and ecology of American chestnut

Fire modeling
- develop finer-scale fire regime models to better incorporate topographic, vegetation, and ignition variables
- model fire behavior and effects under multiple scenarios with and without American chestnut

Fire history
- reconstruct remnant old-growth stands to examine recruitment and mortality patterns
- expand fire scar studies within areas that historically contained American chestnut
- extend fire scar studies to more mesic forest types adjacent to existing studies
- increased coverage of soil and sediment analysis of charcoal and pollen

Fire-adaptive traits
- quantify crown characteristics of resistant chestnut hybrids
- develop bark thickness and size relationship for remnant resprouters and resistant chestnut hybrids
- quantify other traits (e.g., forest hydrology, decomposition) of resistant chestnut hybrids and associated species
- apply a functional trait-based biogeography approach for American chestnut forests

Fire effects
- examine the interactions of fire on chestnut blight and blight resistance
- establish experimental burns to measure fire behavior of chestnut litter and associated species
- monitor fire damage and survival of resistant chestnut hybrids following prescribed burns
- measure the resprouting response of resistant chestnut hybrids and associated species following prescribed burns

vegetation types, and ignition patterns. Other models could be developed that simulate fire behavior and effects under a range of forest conditions to examine the potential role of American chestnut loss and its replacement by associated pyrophytes and mesophytes. Advances in computational fluid dynamic fire behavior modeling (e.g., FIRETEC; Linn et al. 2002) in combination with forest growth models (e.g., Forest Vegetation Simulator; Dixon 2002) or other modeling frameworks (e.g., LANDIS II) may provide valuable insight into modeling a range of scenarios that represent varying degrees of replacement by pyrophytes and mesophytes.

The opportunity to directly examine fire scar evidence was lost many decades ago by the functional extinction of this species, although some alternative avenues of investigation could still be pursued. One approach could include the reconstruction of American chestnut forest stand dynamics in areas that are known to contain many dead and resprouting remnant trees (M. Stambaugh, *personal observation*). Fire history studies could also be conducted on these sites when they co-occur with remnant pine and oak that have preserved fire scars and growth rates (i.e., stand density conditions) that extend prior to Euro-American settlement. Additional fire scar studies that extend to historically more mesic forest sites, such as cove forests, are also needed to better account for a more complete understanding of the variation in fire return intervals within the American chestnut range. Ideally, new fire scar studies could be conducted along topographic gradients that extend from existing studies. Broadening the range of soil and sediment charcoal studies throughout the former American chestnut range would also provide helpful insights on the historical role of fire.

Further research about the fire-adaptive traits of American chestnut and its associated species is needed. While American chestnut is functionally extinct with no mature trees likely remaining across its former range, the development of blight-resistant American chestnut may provide some opportunities to study fire-adaptive traits that otherwise would not be possible. Both the back-crossed hybrid and transgenic chestnuts are genetically similar to American chestnut with traits that likely reflect the species. Given that the back-crossed hybrid chestnut has been extensively planted as part of long-term experiments, orchards, and other outplantings in many locations over many decades (American Chestnut Foundation 2019), there are ample opportunities to examine bark (e.g., thickness, accumulation rates) and crown (e.g., crown lacunarity and bulk density, self-pruning) traits across a range of conditions and size classes.

The fire ecology of many of the species that have replaced American chestnut following its loss are also not well understood. For instance, litter drying and flammability traits of many species that co-occur with American chestnut have not been examined (e.g., *Q. montana*, *Carya glabra*) and limit our ability to estimate potential changes to surface fuels and resultant fire behavior. Given the wide range of possible shifts in composition following the loss of American chestnut, it is necessary to better understand the relevant traits of replacement species. Compiling fire-adaptive traits of American chestnut and its associated species would also allow for the development of a functional trait biogeography, similar to an approach used for western U.S. conifer forests (Stevens et al. 2020). This biogeography could then be used to estimate the potential fire regime effects from American chestnut loss and replacement by other species.

Investigations of fire interactions with blight and blight resistance are clear priorities, although the availability of blight-resistant hybrids or transgenic chestnuts provides an opportunity to directly examine interactions with fire. One approach could be to conduct experimental prescribed fire treatments on older hybrid stands. Specifically, quantifying fire injury (e.g., crown scorch, bole char, cambial kill), mortality (topkill and true mortality), growth rates, and resprouting responses would provide important information on the fire ecology of American chestnut and inform management interventions needed to hasten the restoration of American chestnut ecosystems.

Conclusion

The American chestnut was a foundation species that spanned a large portion of the eastern United States and provided numerous ecosystem services. The functional extinction of this species has had numerous ecological impacts across much of its historic range and likely influenced fire in these regions as well. But the loss of American chestnut has constrained our ability to understand its fire ecology. Despite these challenges, direct and indirect evidence across multiple lines of inquiry reinforces the notion that many woodlands and forests that once contained American chestnut likely experienced frequent fire. Given the ubiquity of evidence of frequent fire and the capacity of American chestnut to withstand low intensity fires based on its fire-adaptive traits, it is difficult to imagine that fire did not serve as a substantial ecological process in many of these ecosystems.

Advances in our understanding about the fire ecology of American chestnut continue and there are numerous ways to expand this work. The substantial progress made in developing pathogen resistance in American chestnut holds promise for reintroducing the species, but it also can provide important insights into the fire ecology of this species and its associated ecosystems. Much work is left to be done and, ultimately, will be needed to facilitate the recovery of this iconic species.

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