



Rethinking restoration targets for American chestnut using species distribution modeling

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Abstract

Given the scale and speed of contemporary environmental changes, intensive conservation interventions are increasingly being proposed that would assist the evolution of adaptive traits in threatened species. The ambition of these projects is tempered by a number of concerns, including the potential maladaptation of manipulated organisms for contemporary and future climatic conditions in their historical ranges. Following the guidelines of the International Union for the Conservation of Nature, we use a species distribution model (SDM) to consider the potential impact of climate change on the distribution and quantity of suitable habitat for American chestnut (*Castanea dentata*), a functionally extinct forest species that has been the focus of various restoration efforts for over 100 years. Consistent with other SDMs for North American trees, our model shows contraction of climatically suitable habitat for American chestnut within the species' historical range and the expansion of climatically suitable habitat in regions to the north of it by 2080. These broad changes have significant implications for restoration practice. In particular, they highlight the importance of germplasm conservation, local adaptation, and addressing knowledge gaps about the interspecific interactions of American chestnut. More generally, this model demonstrates that the goals of assisted evolution projects, which often aim to maintain species in their native ranges, need to account for the uncertainty and novelty of future environmental conditions.

Keywords Assisted evolution · Climate change · Forest biotechnology · Maxent · Niche model · Range shift

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Introduction

The scale and speed of contemporary environmental changes challenge the adaptive limits of many organisms; they do not have enough plasticity to deal with new threats, dispersal capacity to escape them, or time to adapt to them evolutionarily (Merilä and Hendry 2014). Ongoing climatic change, widespread land conversion, unprecedented biotic rearrangement, and environmental pollution continue to precipitate dramatic declines in global biodiversity (Ceballos et al. 2017; Pimm et al. 2014). In this context, intensive conservation interventions have been proposed—and in some cases, are being implemented—to help species keep pace with new abiotic or biotic conditions. For decades, efforts have been focused on translocations (Seddon 2010) and assisted colonization (Hoegh-Guldberg et al. 2008)—strategies that help organisms evade new pressures by relocating them to suitable habitat outside of their native ranges. More recently, attention has turned to strategies, collectively referred to as (*human-*) *assisted evolution*, that would allow threatened plant or animal populations to remain in place by expediting their adaptation to new climates, pathogens, or other environmental stressors (Johnson et al. 2016; Jones and Monaco 2009; Thomas et al. 2013; van Oppen et al. 2015). Though diverse in target species and approach (e.g. Novak et al. 2018; van Oppen et al. 2014), most assisted evolution projects have a shared goal: establishing self-sustaining, wild populations with evolutionary potential, distributed within or throughout their historical native ranges.

While assisted evolution techniques can be used to introduce a particular—and often singular—adaptive trait in a population, simultaneous changes in land use, climate, and ecosystem structure since the decline of the species may present multiple challenges to its long-term restoration. Because climatic conditions pose significant constraints on species distributions (MacKey and Lindenmayer 2001; Woodward and Williams 1987), and given the nature of climate change projections over the next century (Pachauri et al. 2014), anticipating potential shifts in the distribution of climatically suitable habitat is particularly important for the appropriate and responsible reintroduction of populations that have been manipulated for conservation or ecological restoration (Falk and Millar 2016; Osborne and Seddon 2012; Tiedje et al. 1989). This is especially true for species with long lifespans, delayed reproductive maturity, and limited ability to migrate to track changes in climate. The International Union for the Conservation of Nature (IUCN) (2013) suggests the use of species distribution models (SDMs) to understand the climate requirements of all species targeted for reintroduction or translocation and to project the availability of climatically suitable habitat for those species now and in the future. SDMs have been used extensively in biodiversity conservation for a variety of applications (Franklin 2013; Rodríguez et al. 2007), including forecasting the natural movement of species in response to climate change (Bosso et al. 2017a, b; Fitzpatrick et al. 2008; Thomas et al. 2004; Williams and Blois 2018; Zhang et al. 2017); predicting the spread of invasive species (Bosso et al. 2017a, b; Katz and Zellmer 2018; Mainali et al. 2015; Petitpierre et al. 2017); identifying appropriate sites for reintroduction within native ranges (Adhikari et al. 2012; McDonald et al. 2018; Pearce and Lindenmayer 1998; Swinnen et al. 2017); planning for the conservation of rare or threatened species (Kabir et al. 2017; Spiers et al. 2018; Vitt et al. 2010; Webb et al. 2017; Yang et al. 2013); and anticipating the resurrection of extinct ones (Peers et al. 2016). These various applications demonstrate the utility of SDMs as foresight tool; they can be used to expand the timescale of conservation planning, particularly in a context of environmental uncertainty and technological novelty. More specifically, SDMs can be used to

evaluate the long-term potential for restoring species within their native ranges and to prompt consideration of the impacts of reintroducing species that may eventually be better suited for areas outside of their native ranges.

In this paper, we use species distribution modeling to consider long-term prospects for restoring populations of American chestnut (*Castanea dentata*), a hardwood tree species native to the Appalachian region of the eastern United States (Freinkel 2007; Rutkow 2012), within its historical range. Driven to functional extinction by *Cryphonectria parasitica*, or chestnut blight, in the early 20th century, the species persists primarily in the form of understory sprouts, which continue to regenerate from the intact root collars of affected trees, but rarely flower and fruit before being killed back again by blight (Paillet 2002). Various strategies to protect and restore populations of this heritage tree have now been pursued for over 100 years. In that time, groups involved in chestnut restoration have pioneered the application of new physical, chemical, biological, and even nuclear techniques to a conservation problem (Curry 2014; Freinkel 2007). Today, the project continues to push the frontier of species restoration with the development of blight-tolerant trees using a combination of backcross breeding and genetic engineering (Steiner et al. 2017). These contemporary research and restoration efforts are pursued with an explicit mission to return American chestnut to its native range and former niche (TACF 2017; SUNY-ESF 2018). However, while introgressed blight tolerance may allow populations of American chestnut to coexist with chestnut blight, it remains unclear whether current and future climatic conditions of the species' historical range will be suitable for reintroduced populations. Thus far, attention in the hybrid and transgenic chestnut programs has been focused solely on the assisted evolution of tolerance to blight; adaptation to climatic conditions will be derived from standing genetic diversity (Steiner et al. 2017). Our goal in this paper was to develop a simple, yet robust SDM that would evaluate potential long-term and large-scale shifts in the distribution of climatically suitable habitat for American chestnut in the future and to consider the significance of those shifts for chestnut restoration.

Though widely used in land management, risk analysis, and ecological forecasting (Franklin 2013) and specifically recommended by the IUCN (2013) for conservation planning, SDMs have major, known limitations that are particularly problematic when modeling climatic suitability for American chestnut. Correlative SDMs, which relate the observed distribution of a species to known environmental conditions in order to determine the climate requirements of that species, assume that the population under study is at equilibrium with current climatic conditions (Pearson and Dawson 2003). In other words, the model assumes that the species is found in all or nearly all regions with a suitable climate and not found in regions with an unsuitable climate (Araújo and Pearson 2005). However, the American chestnut range was still expanding to the west when chestnut blight was introduced (Russell 1987), so areas outside of its historical, realized range may also be climatically suitable. SDMs also assume that ecological relationships will be less important than climatic conditions in controlling distribution (Pearson and Dawson 2003). While American chestnut has a large range and many occurrence records—traits that improve SDM performance (Wisz et al. 2008)—those records reflect the distribution of the species in the presence of chestnut blight and another introduced pathogen, *Phytophthora cinnamomi*, both of which have substantially dislocated it (Russell 1987). Additionally, while American chestnut is still relatively abundant in some places and a portion of its gene pool still exists (Huang et al. 1998), both sexual reproduction and dispersal are rare (Anagnostakis 2001). Consequently, the species remains both evolutionarily and biogeographically frozen in the early 1900s. As has been demonstrated for other long-lived plant species (Pearson and Dawson 2003; Woodward 1990), the current distribution of American

chestnut likely reflects both historical climate conditions and ecological relationships—patterns that complicate the application of a SDM to the species.

SDMs have, however, been used a handful of times to consider the impact of climate change on American chestnut habitat at various scales. A number of large-scale projects have modeled the influence of climate change on the future distribution of temperate forest species in the U.S., including American chestnut (Iverson et al. 2008; McKenney et al. 2007; Potter et al. 2010). Given the scope of these projects, they do not account for what is known about the history or ecology of the individual species included in their analyses. Additionally, because American chestnut is currently a minor species in eastern forests, there has been no publication of a potential future range map for the species based on these models or discussion about their significance for American chestnut restoration. Another model projected changes in the distribution and quantity of suitable habitat for American chestnut within Shenandoah National Park in response to changes in maximum temperature (Santoro 2013). While this project was focused on American chestnut restoration, the coarse resolution of the temperature data used in that study precludes a strong conclusion about the likelihood of climate-induced changes in suitable habitat on a site-level scale (Santoro 2013). Further, given large differences in how climates in the northeastern and southeastern U.S. have changed over the past century and are expected to change in the future (Kunkel et al. 2013a, b), patterns in Shenandoah cannot be extrapolated to the rest of the species' range.

The utility of previous studies for anticipating the distribution of climatic suitability for populations of hybrid or transgenic American chestnut trees is also limited due to their reliance upon soil attributes and elevation to model suitable habitat for the species (Iverson et al. 2008; Santoro 2013). While these factors have been considered key determinants of American chestnut distribution (Russell 1987; Stephenson et al. 1991), limitation of the species to high elevations and well-drained, xeric soils appears to reflect niche contraction in the presence of chestnut blight (Burke 2012) and *P. cinnamomi* (Rhoades et al. 2003). In fact, American chestnut is known to have been abundant in riparian areas in the southern Appalachians before the arrival of blight (Vandermaast and Van Lear 2002), leading to the conclusion that it may be a generalist in terms of site conditions (Jacobs 2007), particularly in the absence of *Phytophthora*, which is most virulent in poorly-drained and compacted soils (Anagnostakis 2001; Rhoades et al. 2003). In the absence of these two pathogens or given the assisted evolution of resistance to them, other elevations and soil conditions may be suitable for American chestnut. Additionally, while continental-scale climate patterns are illustrative, soil attributes vary on a much smaller scale and would be needed at a finer resolution to be meaningful for restoration decisions (Rovzar et al. 2016). Below, we present a SDM for American chestnut that addresses many of the limitations of previous studies and contends with some of the more general limitations of correlative SDMs. The resulting model, rather than predicting the exact location of suitable habitat for American chestnut in the future, is a useful starting point for considering the long-term risks and benefits of American chestnut reintroduction and challenges for the assisted evolution of this species.

Materials and methods

Species distribution modeling in Maxent

The distribution of climatically suitable habitat for American chestnut was described using maximum entropy species distribution modeling in Maxent (version 3.3.3k; Phillips et al.

2006). Maxent consistently outperforms other tools for niche modeling and is relatively easy to use (Merow et al. 2013). This machine-learning process relates known, georeferenced occurrence points for a species to environmental variables that characterize that geographic area in the same time period (Phillips et al. 2006). The model can then be used to calculate the likelihood of a species occurring in other locations or times given actual or projected environmental data. Although model output can be interpreted probabilistically with rigorous assumptions and settings, it can also be used more simply as an index of habitat suitability (Merow et al. 2013). Maxent has been used to evaluate the extinction risk posed to a variety of organisms by climate change (Pearson et al. 2014) and introduced diseases (Rödder et al. 2009), and it has been specifically discussed as a valuable tool in conservation planning for threatened plant species (Kumar and Stohlgren 2009). As a presence-only model, Maxent relies only on occurrence data to define a species' climate niche, eliminating the need for absence data, which are often unavailable or unreliable (Phillips et al. 2006). Use of this modeling approach thus partially manages the fact that observed absences of American chestnut within and beyond its native range are likely to reflect biotic interactions, rather than the climate tolerance of the species.

Here, a Maxent model was trained on current occurrence data for American chestnut and climate data for North America, and then used to map the distribution of climatically suitable habitat under projected future climatic conditions. Our final model reflects the average of 10 replicate runs, using a random subsample of 25% of the occurrence records (79 points) for testing and the remainder (240 points) for training in each replicate, beginning with a random seed. Each model replicate was constructed based on 500 iterations of Maxent's optimization algorithm. As recommended by Liu et al. (2013) for presence-only models, the maximum training sensitivity plus specificity threshold was used to delimit climatically suitable habitat. All other default Maxent settings were used. The area under the receiver-operator curve (AUC) was used to determine the predictive accuracy of the model.

Occurrence records

The historical range of American chestnut is estimated to have covered over 800,000 km², extending north from Alabama to Maine and west into Kentucky, Tennessee, Indiana, and Ohio, as well as southern Ontario (Little 1977). Naturalized plantings outside of the native range have also been established in Nova Scotia, Wisconsin, Michigan, Iowa, and other U.S. states (Russell 1987). We aimed to model climate suitability across this continental range, since at that scale, climate factors tend to dominate biotic interactions in determining species distributions, and the assumptions of correlative SDMs are more likely to hold (Pearson and Dawson 2003). In an effort to capture occurrence records for American chestnut across the entire native range, we compiled georeferenced observational data publicly available from the Global Biodiversity Information Facility (www.gbif.org) and the Forest Inventory and Analysis National Program (<http://www.fia.fs.fed.us/>). These records reflect human observations of American chestnut, as well as herbarium records. Downloaded records were cleaned to remove duplicate points and exclude those to the west of the 100th meridian, which is well outside of the native range of American chestnut, resulting in a total of 611 records. As is common with many species of conservation concern, these records were concentrated in areas in which sampling effort has been greatest. In particular, early and ongoing survey and restoration efforts in Pennsylvania and North Carolina, as well as a large herbarium collection in Connecticut, resulted in clusters of occurrence records in those states. Because presence-only models and Maxent, in particular, assume

random or representative sampling, the accuracy and practical value of model output are improved when occurrence data are processed to reduce sampling bias (Kramer-Schadt et al. 2013; Yackulic et al. 2013). In order to partially correct for oversampling, we used SDMtoolbox (Brown 2014) within ArcGIS 10.4.1 to thin spatially correlated occurrences. This process thinned points clustered in regions of low climate heterogeneity, resulting in a final dataset with 319 unique occurrence points (Fig. 1).

Selection of environmental variables

We tested the importance of 19 bioclimatic variables for American chestnut distribution. In an effort to capture as much climatically suitable habitat as possible, we selected the fewest environmental variables that would provide realistic insight into the response of American chestnut to expected climatic changes. We consulted the permutation importance to evaluate the importance of the selected variables. Maxent determines the permutation importance by randomly rearranging the values of a given variable at presence and background locations and then re-assessing the ability of the model to correctly identify known occurrence locations; a large decline in model performance means that variable is important for model quality (Searcy and Shaffer 2016). Searcy and Shaffer (2016) have argued that this measure is the best reflection of the importance of environmental variables to model accuracy and may provide new insight into the ecological factors that explain species' distributions.

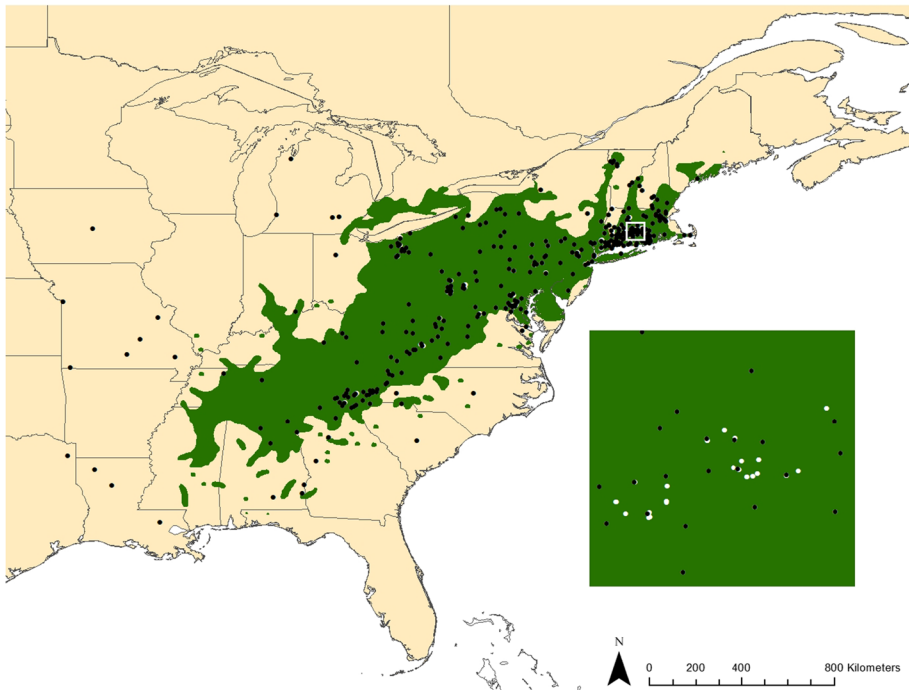


Fig. 1 Historical range of American chestnut (Little 1977) and occurrence records compiled from GBIF and FIA. White dots represent records removed during thinning. Black dots represent the 319 occurrence points used in analysis. Inset shows an example of thinning in detail

Climate data

Current climate data were obtained from WorldClim 1.4 (<http://www.worldclim.org/version1>) and reflect averages from 1960 to 1990. Downscaled future climate data were obtained from the International Centre for Tropical Agriculture (CIAT) and the CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS) (<http://ccafs-climate.org/>) (Ramirez and Jarvis 2008). In this dataset, WorldClim 1.4 data were used as the baseline and processed to produce future climate layers through 2080. Current and future data were downloaded at a resolution of 2.5 min, a resolution that balances the importance of fine-scale climate data for SDM sensitivity to the microclimates that shape species distributions (Franklin et al. 2013; Rovzar et al. 2016; Seo et al. 2009) with the continental scale of the American chestnut range and our model. The selected bioclimatic variables were projected into the future (to 2030, 2050, and 2080) on the basis of 11 different global circulation models (GCMs) for two different representative concentration pathways (rcp): rcp 4.5 and rcp 8.5. Various GCMs have been developed by parties worldwide and embed different mathematical assumptions about the impact of carbon forcing on the atmosphere and oceans, as well as terrestrial and icy surfaces (Pachauri et al. 2014). Existing SDMs for American chestnut have used one or a few GCMs to project future climate conditions. Our choice to average distribution models based on a large number of GCMs acknowledges the high level of uncertainty inherent in climate modeling and accounts for large differences between individual climate models (Beaumont et al. 2008). Rcp 4.5 and rcp 8.5 are two of the greenhouse gas concentration trajectories adopted by the International Panel on Climate Change (IPCC) in its Fifth Assessment Report (Pachauri et al. 2014). These scenarios reflect a likely best- and worst-case scenario for greenhouse gas concentrations over the next century, with emissions peaking around 2040 in rcp 4.5 and continuing to increase throughout the 21st century in rcp 8.5 (Pachauri et al. 2014). Here, Maxent projections based on 11 different GCMs were averaged together for each future time period and rcp, resulting in six scenarios of climate suitability in the future (under rcp 4.5 and 8.5 in 2030, 2050, and 2080).

Calculating changes in the area of climatically suitable habitat

In order to calculate changes in the total area of climatically suitable habitat for American chestnut under future climate scenarios, the raster maps produced in the previous steps were transformed from the WGS 1984 geographic coordinate system (measured in angular degrees) to the North America Albers equal area conic projection (measured in linear meters). Then, the continuous probability values of those maps were converted into binary values representing only suitable or unsuitable habitat using SDMtoolbox (Brown 2014). The maximum training sensitivity plus specificity threshold was used to delimit climatically suitable habitat in the binary maps. For our model, this was one of the most inclusive thresholds, meaning it maximized the amount of potential habitat.

Results

The Maxent model

Our Maxent model was constructed using the four bioclimatic variables that were least correlated with each other (determined by Pearson correlation coefficients) and most

explanatory of current American chestnut distribution. These included mean annual temperature (Bio1), temperature seasonality (Bio4), annual precipitation (Bio12), and precipitation seasonality (Bio15) (Table 1). The model's validation AUC was 0.949, with a standard deviation of 0.005, indicating strong and consistent model fit across the 10 replicates. Qualitatively, our model of the current distribution of climatically suitable habitat for American chestnut is consistent with the historical range of the species as described by Little (1977) (Fig. 2).

Projected distribution of climatically suitable habitat

The following maps (Fig. 3a–f) show the above species distribution model for American chestnut projected to 2030, 2050, and 2080 under the assumptions of the Pachauri et al. (2014) rcp 4.5 and rcp 8.5 scenarios. Each figure represents the average of projections based on 11 independent climate models (GCMs). In general, these figures consistently show contraction of climatically suitable habitat within the historical range of American chestnut in the U.S. and expansion of suitable habitat beyond the native range into southern and eastern Canada. Most of the climatically suitable habitat identified to the west of the species' native range becomes unsuitable in these projections. These maps also show non-linearity in the relationship between climate change projections and the distribution of climatic suitability for American chestnut. Rather than a constant increase or decline in suitable habitat over time, this model projects fluctuations in the quantity of suitable habitat and the continual emergence of new habitat in some regions as it is lost from others. Projections based on rcp 8.5 show more drastic changes within the native range of American chestnut, with more extreme loss of suitable habitat by 2080. This scenario indicates that by 2080, climatically suitable habitat within the historical range will be primarily limited to fragments of the Appalachian core in the south and smaller portions of the mid-Atlantic and northeast. Models based on both rcp 4.5 and 8.5 project substantial expansion of climatic suitability for American chestnut in Ontario and Quebec by 2080, as well as in New Brunswick, Nova Scotia, and Newfoundland.

Projected changes in the area of climatically suitable habitat

In our model, over 1.1 million km² in the U.S. and Canada are currently considered climatically suitable for American chestnut. Importantly, this area, which is larger than previous estimates of the extent of the native range of American chestnut, includes all regions that are climatically suitable, whether or not they are suitable for American chestnut in terms of other abiotic or biotic conditions, including topography and land use. Additionally, this value depends heavily on the threshold selected to define climatic suitability; use of a

Table 1 Environmental variables used in analysis and their contribution to the Maxent model

| Variable | | Importance in model (permutation importance) |
|---------------------------|---------|----------------------------------------------|
| Annual mean temperature | (Bio1) | 49.5 |
| Temperature seasonality | (Bio4) | 5.8 |
| Annual precipitation | (Bio12) | 4.2 |
| Precipitation seasonality | (Bio15) | 40.6 |

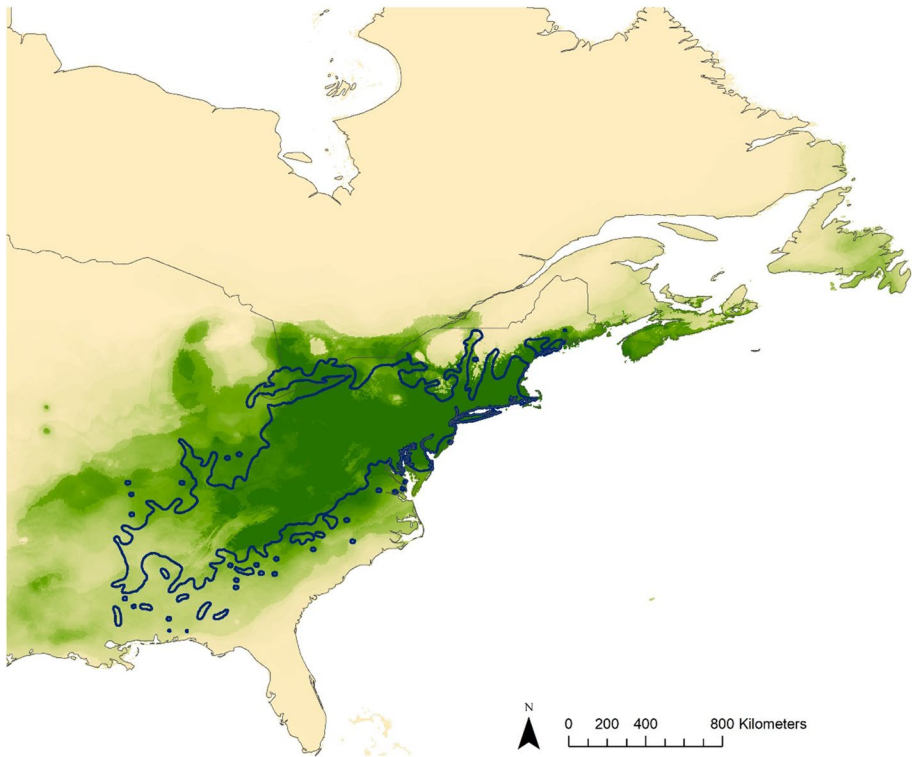


Fig. 2 Species distribution model for American chestnut trained on contemporary occurrence and climate data. Darker regions indicate the most suitable habitat. Outline of historical species range (Little 1977) also shown

less inclusive threshold would reduce the total area of suitable habitat. Because the same threshold was consistently used to define suitable habitat for each time period, percent differences may be more reliably illustrative of changes in habitat availability over time than estimates of absolute area. The total area of climatically suitable habitat for American chestnut is generally expected to decline over time as the amount of habitat being lost from currently suitable regions exceeds the amount of habitat being gained in new regions (Table 2). However, our model projects a small, but notable increase in total area of climatic suitability for the species by 2080 under rcp 8.5. In general, American chestnut is expected to fare better under rcp 8.5 than rcp 4.5 in terms of total available habitat, primarily due to the substantial expansion of climate suitability north of its native range in this scenario. Under both rcp 4.5 and rcp 8.5, the area of climatically suitable habitat is expected to decline most significantly in the short-term and then increase somewhat as gains in suitable habitat compensate for losses.

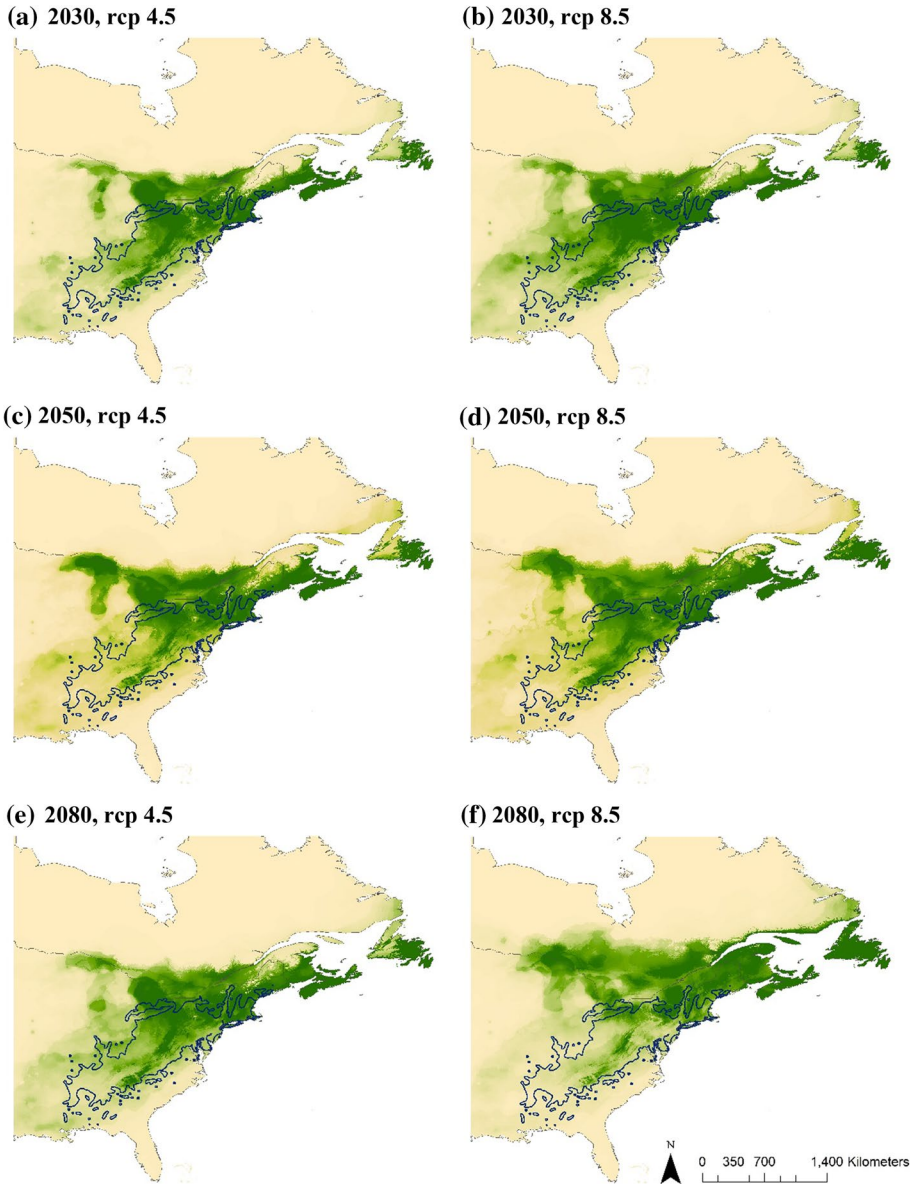


Fig. 3 a–f Future projections of species distribution model for American chestnut. Model was projected to 2030 (2a and 2b), 2050 (2c and 2d), and 2080 (2e and 2f) under the assumptions of rcp 4.5 (2a, c, e) and rcp 8.5 (2b, d, f). Darker regions indicate the most suitable habitat. Outline of historical species range (Little 1977) also shown

Discussion

Efforts to establish blight-tolerant American chestnut trees in the species' native range and former niche in Appalachian forests may be one of the first range-wide experiments

Table 2 Projected changes in the total area of suitable habitat for American chestnut

| | Total km ² | Habitat difference (relative to current) | | Habitat lost (relative to current) | | Habitat gained (relative to current) | |
|---------|-----------------------|------------------------------------------|--------|------------------------------------|------|--------------------------------------|------|
| | | km ² | % | km ² | % | km ² | % |
| Current | 1,178,293 | | | | | | |
| rcp 4.5 | | | | | | | |
| 2030 | 870,220 | − 308,073 | − 26.1 | 609,176 | 51.7 | 322,792 | 27.4 |
| 2050 | 1,031,081 | − 147,212 | − 13.6 | 661,639 | 56.2 | 536,116 | 45.5 |
| 2080 | 984,965 | − 193,328 | − 17.3 | 609,844 | 51.8 | 438,205 | 37.2 |
| rcp 8.5 | | | | | | | |
| 2030 | 1,086,082 | − 92,211 | − 10.6 | 434,910 | 36.9 | 364,388 | 30.9 |
| 2050 | 1,115,186 | − 63,107 | − 6.1 | 614,654 | 52.2 | 573,236 | 48.6 |
| 2080 | 1,206,818 | 28,525 | 2.9 | 870,086 | 73.8 | 920,300 | 78.1 |

Calculations of total area of climatically suitable habitat for American chestnut are based on thresholded, binary output under current and future climatic conditions. Table shows differences between the current area of suitable habitat and the area of suitable habitat projected to be available under rcp 4.5 and rcp 8.5 in each future time period, as well as net gains and losses in suitable habitat relative to current conditions

in assisted evolution for conservation purposes (Schlaepfer et al. 2005; van Oppen et al. 2015), especially for plants and certainly using biotechnology. In advance of this and other assisted evolution projects, SDMs are a valuable tool for visualizing the potential impacts of these efforts across long-term time horizons. SDMs are, however, characterized by well-known limitations, and we insist, with Millar et al. (2007, pp. 2145–2146), that “[a] healthy skepticism leads us to use models to help organize our thinking, game different scenarios, and gain qualitative insight on the range of magnitudes and direction of possible future changes without committing to them as forecasts.” Our model has managed some of the limitations of SDMs and previous models of the impact of climate change on American chestnut habitat by (1) using presence-only modeling; (2) relying on occurrence data that has been thinned to correct for nonrandom sampling; (3) modeling climatic suitability on a continental scale; (4) limiting environmental variables to temperature and precipitation factors; and (5) averaging a large number of global climate models to project the climate suitability of the historical American chestnut range in the future.

Modeling climatic suitability for American chestnut

Our Maxent model of the climatic suitability of American chestnut was constructed using annual mean temperature, temperature seasonality, annual precipitation, and precipitation seasonality. Based on both historical observations and contemporary silvicultural studies, the distribution of American chestnut is known to be delimited by temperature, particularly low temperatures. Historically, American chestnut was confined in terms of both latitude and elevation by sensitivity to frost, with densities and altitudinal limits declining in the northern portions of its range (Russell 1987). Contemporary research has also demonstrated the sensitivity of American chestnut seeds, shoots, and leaves to frost damage in the northeastern U.S. (Gurney et al. 2011; Saielli et al. 2012; Schaberg et al. 2017). Relatively little has been published about the relationship between American chestnut distribution and precipitation (Jacobs 2007), but American chestnut growth is known to be limited

in very wet and very dry soils (Russell 1987), so the importance of precipitation variables in our model may reflect sensitivity to both drought and saturation. Experimental studies have demonstrated physiological adaptation to water stress in American chestnut (Abrams et al. 1990; Bauerle et al. 2006); however, observed declines in the abundance of chestnut sprouts in both southwestern Virginia (Parker et al. 1993) and western North Carolina (Elliot and Swank 2008) have been partially attributed to severe drought conditions. Precipitation seasonality may also influence the distribution of American chestnut due to the impact of *Phytophthora*, as a waterborne pathogen, on American chestnut populations in areas subject to extended periods of soil saturation (Crandall et al. 1945; Rhoades et al. 2003).

Our model of climatic suitability captures much of the historical range of American chestnut used as a baseline in both research and restoration planning, with some notable exceptions. The absence of suitable habitat in the southwestern part of the historical range in our model likely reflects permanent constriction of the American chestnut range in areas in which *P. cinnamomi* infection is widespread. *P. cinnamomi*, unlike chestnut blight, causes root rot and complete mortality in American chestnut trees (Crandall et al. 1945). *Phytophthora* infection eliminated American chestnut from previously suitable areas in Florida, Alabama, and the Piedmont of North Carolina before the 19th century and has continued to constrict the distribution of the species in other warm and low-elevation regions of its native range (Anagnostakis 2001). Our model also shows the availability of climatically suitable habitat outside of the historical native range, especially to the west. The range of American chestnut was still expanding westward when chestnut blight was introduced (Russell 1987); this habitat thus likely reflects portions of the fundamental niche of American chestnut that had not yet been colonized.

Projecting this model to future climate scenarios provides a long-term and broad perspective on the ways in which the distribution of climatic suitability for American chestnut may shift in response to global climate change over much of the next century. Depending on how regional climates respond to carbon forcing, significant portions of the historical range may become climatically unsuitable for American chestnut over the next 60 years. Just on the basis of climate, the species could become confined to less than half of the area that is currently suitable for it. This model thus indicates that enduring restoration of blight-tolerant American chestnut throughout the native range of the species is likely not a tenable goal. New habitat for American chestnut is expected to open in much of southern Canada, however. Under rcp 8.5, these gains are substantial enough to offset losses in the native range and result in an overall increase in the area of climatically suitable habitat for the species. These patterns are generally consistent with those seen in other models for American chestnut habitat described previously. In particular, models based on high-emissions scenarios consistently show virtual elimination of the most suitable habitat for American chestnut from its historical range by 2100 and significant expansion of suitable habitat in Canada. Iverson et al. (2008) also found a complex relationship between habitat availability and climate change for American chestnut, with the total area of suitable habitat for the species expected to increase over time under a low emissions scenario, but decline under a high emissions scenario (Iverson et al. 2008). Iverson et al. (2008) concluded that many North American tree species may experience net gains in climatically suitable habitat under climate change (Iverson et al. 2008), and our model likewise indicates that American chestnut may experience net gains in climatically suitable habitat under rcp 8.5.

Implications for the American chestnut restoration

The SDM presented here is not intended to predict the specific location of suitable habitat for American chestnut in the future. It does, however, provide a visual tool for considering the ways in which climate change may mediate the feasibility and desirability of intervening in the natural history of American chestnut and attempting to reintroduce this species throughout its historical range. Insofar as this model prompts scientists, conservationists, philanthropists, regulators, and others involved in American chestnut restoration to consider the potential long-term implications of their efforts, it can facilitate the kind of future-oriented conservation and restoration planning that is increasingly called for from both natural and social scientists (Choi 2007; Willis and Birks 2006; Wyborn et al. 2016). Two broad patterns are illuminated by the present model that carry important implications for restoration practice: first, American chestnut is likely to lose climatically suitable habitat throughout its historical range in the eastern U.S. within this century, and, second, it is likely to gain new habitat in southern and eastern Canada.

The potential loss of climatically suitable habitat for American chestnut in its historical range is significant for reintroduction plans that depend on open crosses between backcross or transgenic trees and surviving wild trees. Rescuing the genetic diversity contained in wild sprouts is important for the future adaptive capacity of American chestnut, as the restoration programs of TACF and especially SUNY-ESF are based on a limited number of parental trees (Steiner et al. 2017). Our model suggests that wild trees in much of the native range may be at risk for climate-related extirpation in coming decades. TACF actively works to preserve the genetic backgrounds of surviving trees, primarily through the efforts of 16 state and multi-state chapters across the historical range of American chestnut. Chapter volunteers locate and collect germplasm from surviving trees in their areas and backcross hybrid material produced by the national organization in Meadowview, VA to these native trees (Steiner et al. 2017), creating a “living repository” of genetic diversity (Alexander et al. 2005). TACF has also established a number of germplasm conservation orchards into which wild American chestnut trees are transferred for both ease of access and improved growing conditions. To date, the majority of these orchards are in Pennsylvania—an area that our model suggests is likely to remain climatically suitable for American chestnut in the future. However, the most neutral genetic diversity and rare alleles are found in American chestnut populations in the southwestern part of the species’ range (Kubisiak and Roberds 2003; Huang et al. 1998)—an area that our model indicates may not be climatically suitable for American chestnut within the next century. Efforts in both in situ and ex situ conservation of this germplasm have been initiated (Alexander et al. 2005), and our model suggests that they should be prioritized and expanded. This work may be a valuable contribution from southern chapters situated in these areas.

The conservation of southern germplasm may also be particularly important given its adaptation to warmer climatic conditions and the apparent heritability of these adaptations in American chestnut. Genetic analyses of surviving American chestnut populations indicate that the species existed as just one metapopulation; however, genetic differentiation across altitudinal and soil gradients provides evidence of “microsite” (Steiner 2006) adaptation to local conditions, including climate (Kubisiak and Roberds 2003; Worthen et al. 2010). Silvicultural research also supports a genetic basis for regional climatic adaptation. For example, Saielli et al. (2012) found that nuts from southern American chestnut populations had lower levels of cold tolerance than those from northern populations. TACF’s state chapter structure significantly increases the level of local adaptation in the backcross

breeding program, and it may eventually provide an important source of locally-adapted material that can be fertilized with pollen from transgenic, blight-tolerant trees. However, local chapters largely operate within a paradigm that assumes environments to be static, rather than dynamic. Consequently, these chapters maintain relatively diverse populations of American chestnut that are well-suited to contemporary climate conditions in their regions—or, more likely, historical conditions—but may not be fit under future conditions. Jones and Monaco (2009) have argued that an emphasis on indigeneity in the selection of plant materials for ecological restoration may be misguided under novel environmental conditions. Instead, they suggest the incorporation of plants that are either already well-adapted or able to adapt to selective pressures in locations targeted for restoration. Given heritable thermal tolerance, TACF could facilitate crosses among surviving trees from different parts of the native range, as has been proposed for the genetic rescue of corals threatened by ocean warming (Dixon et al. 2015). Crossing individuals from remaining southern populations of American chestnut with surviving trees in other geographic regions may assist the evolution of thermal tolerance in the species, concurrent with the assisted evolution of blight and *Phytophthora* resistance.

The potential for substantial areas of climatically suitable habitat to open for American chestnut in areas north of its native range by the end of the century also has implications for restoration practice. Although Schwartz (2012) has suggested that projections of range expansion are more robust and useful for conservation planning than projections of range contraction, the ecological implications of that new habitat are likely to be highly uncertain. Even within its native range, relatively little is known about the ecology of wild American chestnut, particularly the nature of its interactions with other plants and wildlife (Freinkel 2007; Paillet 2002). Detailed records of the pre-blight distribution of American chestnut and associated plant species are only known to exist for one plot in Connecticut; consequently, most analyses of its dispersal and migration characteristics and its community dynamics are based on surveys conducted after the decline of American chestnut began or reconstructions using chestnut stumps (Elliott and Swank 2008). Analysis of post-blight surveys along permanent transects in Coweeta Basin, NC have shown a significant increase in floral diversity following the decline of American chestnut as one dominant species was replaced by many species (Elliott and Swank 2008). Additionally, American chestnut has demonstrated the capacity to displace indigenous plant communities in a relatively short amount of time when planted outside of its native range (Paillet and Rutter 1989). At present, American chestnut, which remains highly susceptible to blight infection and rarely reproduces sexually, is unlikely to pose a risk for forest communities north of its native range. However, the introgression of blight resistance or tolerance may reinstate its competitive advantage in the long-term, and widespread planting of either backcross or transgenic trees would provide abundant source material for dispersal. Given the potential for American chestnut to be a primarily Canadian species by the end of the century, filling current knowledge gaps about the ways in which blight-resistant American chestnut may interact with other Canadian forest species is essential for its responsible introduction.

Limitations

Statistician George Box famously noted that “all models are wrong, but some are useful” (Box 1979). He was referring to the ways in which models necessarily represent simplified versions of the systems they are used to investigate; they neglect certain dimensions

in order to generate a manageable yet meaningful approximation of the real world (Box 1979). Because it relies on just four climatic variables to define suitable habitat for American chestnut, the model presented here is, like all models, wrong. It was developed and should be interpreted with awareness of the general limitations of SDMs and their specific limitations for modeling habitat for a functionally extinct species whose present distribution is a relic of its dispersal patterns in the late 19th century and its displacement by two introduced pathogens. Two limitations are especially worth noting: first, the unavoidable conflation of biotic and abiotic constraints on the distribution of American chestnut and, second, the assumption that evolutionary processes will be negligible over the next century.

First, although Maxent is a presence-only model that reduces the importance of missing occurrence records, in this case, a prohibitive biotic condition for American chestnut—*Phytophthora* infection—has historically overlapped with specific and regional abiotic conditions—the warm temperatures and saturated soils of the Piedmont and Coastal Plain. Consequently, our model likely underestimates climatically suitable habitat in the warmer, southern portion of the species' historical range in the present, as well as any habitat represented by that climate envelope in the future. Although *P. cinnamomi* is already widespread in the U.S. under 40 degrees latitude (Balci and Bienapfl 2013), the development of root rot disease on American chestnut and other host species is thought to be limited by climatic factors, particularly low winter temperatures (Eggers et al. 2012). Under climate change, the range of *P. cinnamomi* is expected to expand and its virulence at higher latitudes and elevations is expected to increase (Bergot et al. 2004; Eggers et al. 2012). It has also been suggested that American chestnut and other trees are more susceptible to *Phytophthora* infection and root rot disease when stressed by climatic conditions (Brasier and Scott 1994; Woods 1953). Thus, without the development of American chestnut trees that are resistant to *P. cinnamomi* or otherwise protected from disease, such as through the colonization of seedlings with protective ectomycorrhizal fungi (Rhoades et al. 2003), chestnut restoration may in fact be confined to the small portion of the species' historical range depicted as suitable by our model. In fact, the area of suitable habitat may be even further reduced as warmer temperatures and more extreme precipitation events (Pachauri et al. 2014) foster *Phytophthora* infection and spread. Both TACF and the team at SUNY-ESF have recently begun to explore the potential for adding *Phytophthora* resistance to their blight-tolerant germplasm using Asian sources available in the backcross program, an additional transgene, or a cisgene from Chinese chestnut (Steiner et al. 2017). Ultimately, although the present model cannot tease apart the influence of climate and *Phytophthora*, it does show the substantial portion of the historical range that has become unsuitable for American chestnut in the presence of this pathogen (Fig. 2) and demonstrate the extent to which the introgression of *Phytophthora* resistance may increase the availability of suitable habitat for American chestnut in the future.

A second limitation emerges from the fact that SDMs are based on ecological niche theory (Pearson and Dawson 2003) and evidence that a species' niche is highly conserved over time, even in the wake of disruptive changes in climate and other environmental conditions (Wiens and Graham 2005). This allows use of the niche to understand the nature and distribution of suitable habitat for a species in the past, present, or future (Martínez-Meyer and Peterson 2006), but it also minimizes attention to evolutionary processes and the adaptive capacity of organisms (Pearson and Dawson 2003). Our model assumes that American chestnut will maintain its current niche in the future, rather than adapt to new climatic conditions, and there are reasons to both support and challenge this assumption. Based on an analysis of the bioclimatic envelopes of all chestnut species, Fei et al. (2012) concluded that the high degree of similarity in

thermal tolerances among *Castanea* species indicates strong niche conservatism within the genus over tens of millions of years. Additionally, evolutionary processes are generally expected to play a smaller role for species, like American chestnut, that are long-lived and slowly dispersed (Pearson and Dawson 2003). However, experimental evidence is mounting for contemporary evolution (Stockwell et al. 2003) and the ability of populations to adapt to rapid change when they are sufficiently large and adaptive variants are present (Bell and Gonzalez 2009). Additionally, given blight and *Phytophthora* resistance and the subsequent return of sexual reproduction, the influence of both heterozygote advantage (Stilwell et al. 2003) and obligate outcrossing due to genetic self-incompatibility (McKay 1942) in American chestnut populations may facilitate higher adaptive capacity than would otherwise be expected from the small founder populations that will be used in the reintroduction of the species.

Conclusion

A century ago, residents of the southern Appalachian mountains thought the world was dying (Davis 2006), and by some measures, it was; chestnut blight brought with it the end of a subsistence way of life that had been working for hundreds of years and a forest type that had dominated the landscape for thousands (Rutkow 2012). However, a longer-term perspective, informed by the past natural history of American chestnut, as well as scenarios of its future, reveals that American chestnut was not always a fixture in the Appalachian landscape and that it may not be possible to fully re-establish it as one. The expected long-term decline of climatically suitable habitat for American chestnut throughout its native range in the future raises important questions about the purpose and goals of its restoration, as does the potential emergence of substantial areas of new habitat outside of its historical range. As the social and ecological memory of American chestnut wane, efforts to resurrect it should reconsider what successful restoration means, given the novelty and uncertainty of contemporary and future environmental conditions (Jacobs et al. 2015; Redford et al. 2011; Hobbs et al. 2009). The American chestnut restoration program, though still untested on a landscape scale, remains one of the only examples of the use of assisted evolution techniques to facilitate the adaptation of a wild, forest species to an introduced pathogen. It is thus positioned to set a precedent for the assisted evolution of other species, particularly forest trees (Jacobs et al. 2013; Merkle et al. 2007; Steiner et al. 2017). Those involved in this project have an opportunity to establish a model for species restoration that responds to calls for a long-term perspective in biodiversity conservation (Choi 2007; Willis and Birks 2006; Wyborn et al. 2016). Simple SDMs cannot predict the response of complex biological systems to uncertain and multidimensional changes in future climates at any fine resolution; however, as we demonstrate for American chestnut, insights gleaned from them can inform both our expectations for the future of targeted species and conservation practice in the present.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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