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ARTICLE

Methods, Tools, and Technologies

Beyond blight: Phytophthora root rot under climate change limits populations of reintroduced American chestnut

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Abstract

American chestnut (*Castanea dentata*) was functionally extirpated from eastern US forests by chestnut blight, caused by a fungus from Asia. As efforts to produce blight-resistant American chestnut germplasm advance, approaches to reintroduce chestnut throughout its former range are being developed. However, chestnut is also quite susceptible to a root disease in the southern half of its former range, and the pathogen that causes the disease (*Phytophthora cinnamomi*) is expected to move northward as climate warms. Genetic resistance to root rot appears to vary among individual chestnut trees, and the prevalence of resistance is highly uncertain. Because restoration of a self-sustaining chestnut population is ultimately a landscape-scale problem, we used a process-based forest landscape model (LANDIS-II) to conduct experiments to quantify the effects of root rot on the effectiveness of chestnut population restoration efforts in the center of the former range of chestnut under various climate scenarios. We developed a new LANDIS-II extension to simulate root rot-induced tree mortality as a function of temperature and soil moisture. We conducted a factorial simulation experiment with climate and resistance to root rot as factors and found that root rot greatly reduced chestnut biomass on the landscape, even when resistance to root rot infection was at the highest levels currently observed in published studies. Warming climate enhanced the virulence of the pathogen and resulted in a greater reduction in chestnut biomass. Results indicate that root rot has the potential to seriously hamper chestnut restoration efforts if resistance of chestnut is not enhanced through breeding and biotechnology, suggesting restoration efforts will be more successful if targeted to latitudes, elevations, and site conditions where root rot is not expected to be present well into the future, including areas north of the historical chestnut range (Canada). These results demonstrate the vital importance of incorporating root rot resistance into the larger blight resistance breeding program.

KEYWORDS

American chestnut restoration, *Castanea dentata*, climate change, elevated CO_2, LANDIS-II, *Phytophthora cinnamomi*, PnET-Succession, root rot disease

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INTRODUCTION

American chestnut (*Castanea dentata* [Marsh.] Bork.) was an abundant species in many eastern US forests (Ellison et al., 2005) prior to its functional extinction by two invasive pathogens. Mortality of chestnut in the southern United States was first reported in the mid-19th century and is now attributed to infection by the root pathogen *Phytophthora cinnamomi* Rands (Anagnostakis, 2001). Chestnut blight, caused by *Cryphonectria parasitica* (Murr.) Barr. was likely introduced to the United States in the late 19th century and killed most large American chestnuts throughout the species' range by the 1950s. Today, only 10% of the preblight chestnut population remains, with most survivors found in small-size classes (<2.5 cm diameter breast height (DBH); Dalgleish et al., 2016), likely sprouts originating from blight-killed trees (Paillet, 1984). Extensive efforts have gone into developing American chestnut populations that are resistant to chestnut blight disease (Anagnostakis, 2012; Steiner et al., 2017). The principal strategy of The American Chestnut Foundation (TACF) has involved hybridizing American chestnuts with blight-resistant chestnut species (primarily Chinese chestnut, *Castanea mollissima* Blume.), followed by repeated backcrossing and intercrossing to recover American chestnut traits (Anagnostakis, 2012; Hebard, 2005). Recent genomic selection analysis has demonstrated the improbability of producing a highly blight-resistant chestnut with a genome that is predominantly American through backcross breeding (Westbrook, Zhang, et al., 2020b). Given this finding, TACF has developed plans to incorporate the use of transgenic techniques (inserting an oxalate-oxidase-encoding gene from wheat, e.g., Zhang et al., 2013) into their breeding program (Westbrook, Holliday, et al., 2020a). TACF's chestnut breeding program had not, until recently, incorporated resistance to *Phytophthora* root rot. Fortunately, some root rot resistance has been captured in families originating from one of the main sources of blight resistance used in the breeding program (Westbrook et al., 2019), and TACF now plans to cross individuals from those families with transgenic blight-resistant chestnut to combine resistance to both pathogens. Once genetically diverse populations of disease-resistant American chestnuts are produced, offspring of these trees will be reintroduced throughout its former range, with the hope of restoring the ecological, economic, and social benefits the species once provided (Jacobs et al., 2013).

There are many uncertainties associated with such an undertaking. Chestnut must be capable of successfully competing with established cohorts of other species in order to achieve a self-sustaining population. Chestnut must also be able to adapt to the novel abiotic (e.g., climate, CO_2) and biotic (e.g., insect pests, exotic species) conditions that are becoming quite different than they were when the species was dominant. Gustafson et al. (2018) used a forest landscape model (LANDIS-II) to project the efficacy of various climate and chestnut restoration scenarios in western Maryland (USA) by mechanistically accounting for temperature and elevated CO_2 effects on growth (and competition) and for natural and anthropogenic disturbances. They found that with aggressive restoration efforts, chestnut can again become an important component of forested ecosystems in the Appalachian Mountains. However, one critique of that study was the omission of the effects of *Phytophthora* root rot.

American chestnut is quite susceptible to the root disease (root rot) caused by *P. cinnamomi* and chestnut is thought to have suffered extensive mortality from root rot in the southern half of its former range prior to the arrival of chestnut blight (Anagnostakis, 2012). The pathogen infects a wide range of hosts, with pathogenic activity increased by warm wet soils, but it is limited in soils that freeze deeply in winter (Sinclair & Lyon, 2005). Because the pathogen currently occurs in North America only below 40°N latitude due to cold limitation, it is expected to move northward (and upward) as conditions warm (Burgess et al., 2017; McConnell & Balci, 2014). Restoration plantings north of 40°N latitude currently do not need resistance to *P. cinnamomi*, but as climate warms, resistance will become increasingly important throughout the former range of American chestnut. Mortality of up to 60% in plantings of American or backcross hybrid chestnut in the southern United States has been attributed to root rot infection (Clark et al., 2014; Pinchot et al., 2017; Rhoades et al., 2003). It is currently unknown what level of resistance will be needed to reach restoration goals, but resistance to the root pathogen is believed to be important for survival on some sites (Clark et al., 2019 and references within). Improving our understanding of the potential impacts of root rot and interactions with site conditions on the success of chestnut restoration plantings across the species' range is necessary for developing effective prescriptions. See Appendix S1 for additional background information.

Research related to restoration of threatened tree species generally, and American chestnut specifically, has emphasized that biotechnology is needed to overcome pests or pathogens, but understanding potential ecological barriers and responses to management are also necessary to ensure successful reintroduction (Jacobs, 2007; Jacobs et al., 2013). The majority of investigations of chestnut ecology and biology thus far reflect results of

empirical studies conducted on individual field sites, yet restoration of a self-sustaining American chestnut population is a landscape problem because restoration requires a landscape-scale planting program and the population must be resilient to multiple disturbance regimes. Furthermore, because the occurrence of an American chestnut population within its former range under the climate, pests, and disturbance regimes expected in the future is a novel combination, it is not advisable to use the past to attempt to predict the outcome of restoration efforts (Gustafson, 2013). Mechanistic forest landscape models based on first principles provide a robust tool for such a study because they are process-based (Cuddington et al., 2013) and incorporate most of the major factors (e.g., dispersal, competition, soils, climate, disturbances such as insect pests) that structure forested landscapes in time and space at landscape scale. Forest dynamics in such models are an emergent property of the interaction of the processes (including growth and competition) and the inputs (including abiotic soil and climate conditions), and produce the most reliable projections of expected future forest dynamics (Gustafson, 2013).

Following Gustafson et al. (2017, 2018), we used the physiologically mechanistic PnET-Succession forest growth simulation extension linked to process-based disturbance extensions within the LANDIS-II forest landscape model (Scheller et al., 2007) to conduct a simulation experiment to assess the outcome of American chestnut restoration efforts in the presence of the root rot pathogen. We created a new disturbance extension that simulates tree mortality caused by the root rot pathogen that accounts for the presence of suitable hosts, soil moisture and temperature, and the observation that some individuals of an infected cohort exhibit long-term survival (Perkins et al., 2019). We focused on the center of the former chestnut range, which coincides with the northern edge of the range of the root rot pathogen. We experimentally modified climate inputs to produce (1) a no root rot scenario representing the cold-protected northern part of chestnut range, (2) a current climate root rot scenario for the study areas, and (3) a hotter root rot scenario representing both the southern part of chestnut range today and one potential climate future of the study areas.

Our objectives were to (1) quantify the impact of root rot on chestnut biomass as restoration activities proceed, (2) assess whether root rot has the potential to completely thwart chestnut restoration efforts in the studied region, (3) explore how much disease resistance would be required to make chestnut restoration feasible, and (4) determine whether the results suggest management strategies that might help mitigate the negative effect of root rot on restoration efforts.

METHODS

Study area

The study was focused on western Maryland (USA), located near the center of the former range of American chestnut (Figure 1), and the focus area of our previous chestnut modeling experiments (Gustafson et al., 2017, 2018). Two state forests are in close proximity but are located in two distinct physiographic provinces. The Savage River State Forest (SRSF) is located on the Appalachian Plateau and receives relatively abundant rainfall (114–140 cm/year; Brown & Brown, 1984). Geomorphology of the plateau consists of steep and dissected ravines or undulating terrain on broad ridgetops underlain by sandstone and shale, with elevation ranging from 375–900 m (Stone & Matthews, 1974). The SRSF is dominated by northern red oak (*Quercus rubra*), with sugar maple (*Acer saccharum*) codominant on mesic slope positions, chestnut oak (*Q. prinus*) codominant on drier slope positions, and red maple common in the understory. The Green Ridge State Forest (GRSF) is located approximately 40 km east of SRSF in the Ridge and Valley physiographic province. Elevation ranges from 140 to 600 m, and because it is in a rain shadow of the Appalachian Plateau, this area receives the lowest annual rainfall in Maryland (76–88 cm/year; Brown & Brown, 1984). Topography is characterized by strongly folded and faulted sedimentary bedrock forming long, narrow, and parallel ridges with deep intervening valleys oriented in a northeast–southwest direction (Stone & Matthews, 1974). The shallow and well-drained soils of GRSF are more xeric, with forests dominated by upland oaks, with pines common on the driest slopes (Jr Hicks & Mudrick, 1994). The SRSF and surrounding lands formed a 64,128-ha simulation landscape, and the GRSF simulation landscape was 52,790 ha in size. Ecoregions ($N = 44$ in SRSF and 134 in GRSF) that represent relatively homogeneous areas in terms of climate (temperature and precipitation) and soil conditions (soil texture, slope, and aspect) were mapped by binning combinations of climate and soils (SSURGO; Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture, 2013). Ecoregion properties can be found in the LANDIS-II input files in the Forest Service Research Data Archive at https://doi.org/10.2737/JS-2021-001.

Model used

The simulation experiment was conducted using LANDIS-II (Scheller et al., 2007), a forest landscape modeling platform using extensions (plug-ins) to mechanistically

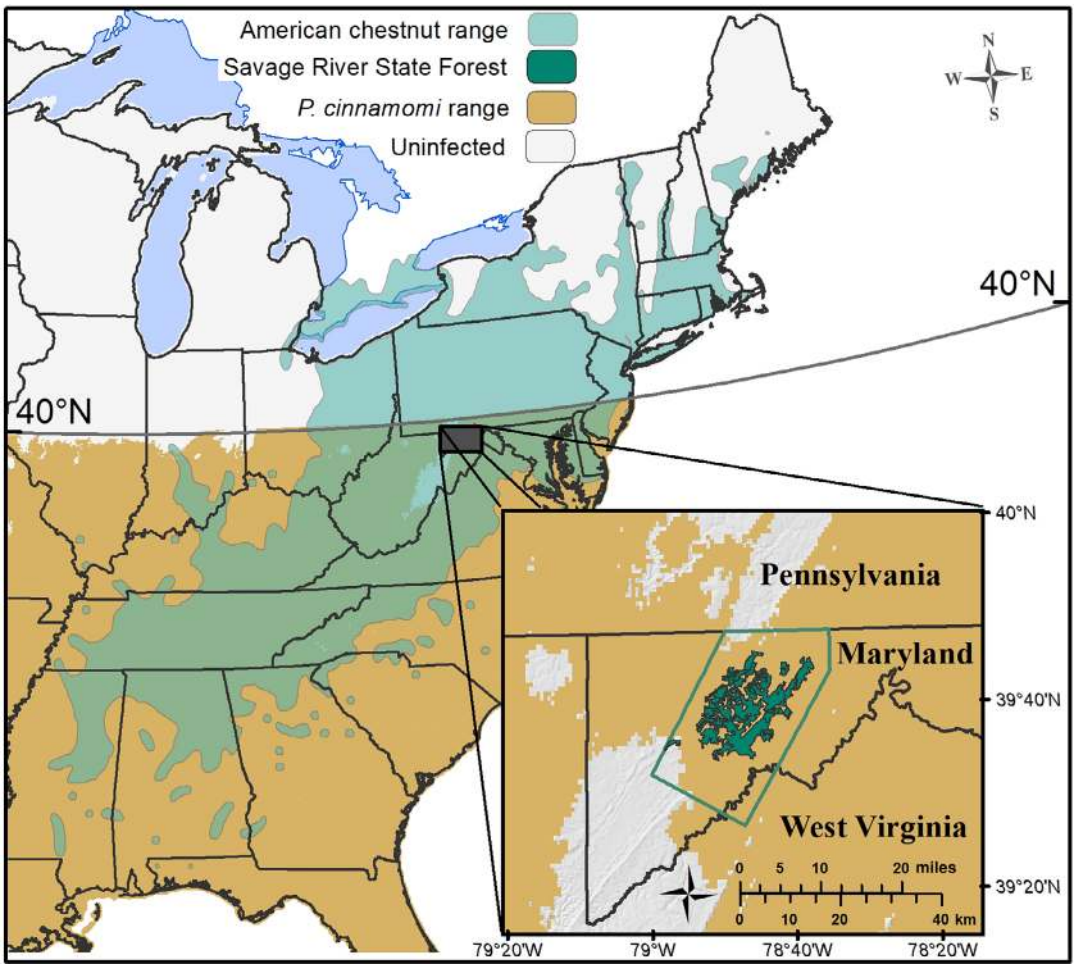


FIGURE 1 Location of the study sites relative to the former range of American chestnut and the approximate range of *Phytophthora cinnamomi*, estimated using USDA plant hardiness zones and a northern limit of 40°N latitude

simulate forest growth and disturbance (e.g., insect outbreaks and timber harvesting). LANDIS-II models species cohorts rather than individual trees, representing space as a grid of cells (30-m resolution in this study), each containing an independently dynamic collection of species cohorts. Each ecological process is encapsulated by an independent extension that modifies cohort biomass conditionally based on abiotic and vegetation conditions on the cell and input parameters. Cohort biomass drops to zero when all individuals die or are destroyed, and cohort biomass can be reduced to represent the loss of some individuals. Interactions among climate, growth, succession, and disturbance are not specified a priori, but emerge out of the cumulative effects of the independently simulated processes.

We used the PnET-Succession extension (v3.5; De Bruijn et al., 2014) to simulate growth processes (seed dispersal and establishment, growth, competition, senescence) because its mechanistic use of physiological first principles is best suited to model novel situations such as climate change and the introduction of new species. Note that this is a newer version than used by Gustafson et al. (2017, 2018), having modified algorithms for cohort establishment and temperature effects on photosynthesis. PnET-Succession models growth as a competition of cohorts for light and water, and cohorts die when their respiration exceeds net photosynthesis sufficiently to exhaust their carbon reserves. As soil water availability decreases, photosynthesis decreases. Available soil water is determined by precipitation, loss to evaporation and runoff, soil porosity, and consumption by cohorts. When water is adequate, the rate of photosynthesis for a given species cohort increases with light available to the cohort (dependent on canopy position and leaf area), atmospheric CO_2 concentration and foliar N, and decreases with age and departure from optimal temperature. Temperature also affects vapor pressure deficit, respiration and evapotranspiration rates. Thus, growth rates vary monthly by species and cohort as a function of precipitation and temperature (including extreme months),

directly affecting competition and ultimately successional outcomes. A detailed model description can be found in Gustafson and Miranda (2020).

We used the PnET-Succession tree species life history and physiological parameters found in Gustafson et al. (2018) (see Appendix S2), modifying the establishment and temperature parameters to produce behavior from the newer version of the model that is similar to that in the prior study, making our results generally comparable with that study. Chestnut restoration activities (see Experimental Design section) were simulated using the Biomass Harvest extension (v4.3; Gustafson et al., 2000). Background disturbance by insects was simulated for all factor combinations. Two established insect pests (gypsy moth [*Lymantria dispar*] and forest tent caterpillar [*Malacosoma disstria*]) were simulated using the Biomass Insects extension (Foster, 2011), and two recently introduced insect pests (emerald ash borer [*Agrilus planipennis*] and hemlock wooly adelgid [*Adelges tsugae*]) were simulated using the Biological Disturbance Agent (BDA) extension (v3.0; Sturtevant et al., 2004; Sturtevant et al., 2017). See Appendices S1 and S2 for further details.

Description of the root rot disturbance extension

Many soil properties influence *P. cinnamomi* infection biology (texture, land use, drainage, waterlogging, drought, temperature, and water-holding capacity are some examples), but data to parameterize a landscape-scale model are largely unavailable, making it difficult to implement them in a landscape scale model at this time (Sinclair & Lyon, 2005 and references within). Detailed studies in three different Australian forested ecosystems with different species, topology, soils, and precipitation have shown that infections by the root rot pathogen are limited by both soil temperature and water potential (Weste & Ruppin, 1977). Cook (1973) reported optimal growth for *P. cinnamomi* at water potential of -5 bars (pressure head [ψ] $= -51$ m), and Weste and Ruppin (1977) found that soils with water potential lower than -5 bars began to limit populations, and potentials of -10 ($\psi = -102$ m) or lower reduced active populations to zero. Shea (1975) demonstrated that soil temperatures above 12°C are required for sporangial production and infection of roots by *P. cinnamomi*, while Weste and Ruppin (1977) found that *P. cinnamomi* population densities dropped to zero when the mean soil temperature was less than 10°C.

For this study, we developed a new LANDIS-II disturbance extension (Root Rot v1.0; Miranda et al., 2020; code and executable available at http://www.landis-ii.org/extensions) to simulate cohort biomass loss (representing individuals killed) caused by infestations of *P. cinnamomi* on each landscape grid cell (site). The extension is compatible with PnET-Succession because it models soil water potential and soil temperature profile as a function of soil texture and water content. The extension does not simulate dispersal of the pathogen from site to site, assuming the pathogen is ubiquitous on the landscape and can reach any site in the simulation landscape (e.g., SRSF) except when winter temperatures kill the pathogen on a site. Each site has a mutually exclusive infection status of Uninfected, Infected (asymptomatic), or Diseased (symptomatic). Trees on Diseased sites experience symptoms in the form of biomass decline (defined below) in proportion to the susceptibility of the species to the pathogen, while trees on Infected sites do not. Cells that are Infected or Diseased can revert to a status of Uninfected only when the pathogen has been killed by cold (Presence is equal to 0). Cells that are Diseased can stochastically revert to a status of Infected and will always revert to Infected if all susceptible tree hosts are eliminated. The user can optionally provide an input map giving the initial status of each cell; otherwise, all active cells are initially assumed to be Uninfected. Extension inputs (including the time step [periodicity] of the extension) are provided to the model in a text file (Table 1). In the LANDIS time steps when the extension is executed, each site is evaluated for transitions between states, with the probability of each transition determined by the presence of the pathogen (controlled by a lethal temperature variable) and a pathogen population density variable (controlled by a soil temperature variable [T_{soil}] and a soil wetness index [WI]) as described below.

P. cinnamomi appears unable to survive winters having temperatures below a threshold (Sinclair & Lyon, 2005). The user specifies this threshold (LethalTemp) for computation of the probability that the pathogen is present (pPresence):

$$\text{pPresence} = (\text{ExtremeTmin} - \text{LethalTemp})/\text{ABS}(\text{LethalTemp}), \quad (1)$$

where ExtremeTmin is the lowest minimum monthly air temperature observed across years in the time step, and p (Presence) is constrained to be between 0 and 1 (Figure 2). ExtremeTmin is estimated within the succession extension as the monthly average temperature minus three times the winter standard deviation as described in Gustafson et al. (2020). Presence is computed as a binary stochastic variable, being 1 if a uniform random number is greater than pPresence, or 0 otherwise. If Presence equals 0, the site transitions to Uninfected (U) regardless of current state. If Presence equals 1, other transitions are possible based on the pathogen population density variable.

TABLE 1 Root rot extension inputs

Input parameter	Description	Notes[a]	Value used
Species susceptibility table	Index of species susceptibility to damage when disease occurs, ranging from 0.0 to 1.0	1.0 is completely susceptible and 0.0 is unsusceptible. Secondary Susceptibility is used for cohorts that have previously experienced "D" status	See Table 2
LethalTemp	The monthly winter air temperature (°C) below which *Phytophthora cinnamomi* cannot survive	For example, −24 indicates *P. cinnamomi* unable to survive in USDA hardiness zone 5 or colder	−24
phWet[b]	The pressure head (m) threshold below which the soil is considered wet (optimal for *P. cinnamomi*)	Under wet conditions it is possible for a site to progress from U to I and from I to D	51
phDry[b]	The pressure head (m) threshold above which the soil is considered dry	Under dry conditions the site will not progress from U to I, but I sites can progress to D.	102
phMax[b]	The pressure head (m) threshold above which the soil is extremely dry	Tree stress under extremely dry conditions are optimal for a site to progress from I to D	250
minProbID	The minimum probability of infected sites converting to diseased	At moderate pressure head, the probability of D will be greater than this value	0.10
maxProbDI	The maximum probability of diseased converting to infected	At moderate pressure head, the probability of D will be less than this value	0.85
MinSoilTemp	The soil temperature (°C) below which *P. cinnamomi* becomes inactive	Soil temperature in a growing season month	10
SoilTempDepth	Soil temperature is measured at this depth (m)	Measured at 10 cm depth by Weste and Ruppin (1977). Currently hardcoded in the model.	0.1

[a]Site status is one of Uninfected (U), Infected nonsymptomatic (I), or Diseased symptomatic (D).
[b]ph (ψ) = m of pressure head, a unit of soil water potential. In PnET-Succession, ψ is tracked using absolute values. ψ equals 0 when soil is saturated and increases as water is reduced. ψ of approximately 3.37 equates to soil field capacity, and 153 equates to soil wilting point.

Population Density Index

Because the density of *P. cinnamomi* populations varies with soil wetness and soil temperature, we devised a Population Density Index (PDI) computed from state variables carried by PnET-Succession (e.g., soil texture and water potential) and extension-specific parameters (Table 1). First, a WI is computed that varies from 1.0 for water potentials greater than the phWet parameter (wetter) to 0.0 for water potentials less than phDry (drier), and interpolating linearly for water potentials between phWet and phDry (Figure 3). Soil texture has been found to further modify the soil moisture conditions influencing *P. cinnamomi* populations through differing abilities to hold water in the soil (Weste & Ruppin, 1977). Using data from Weste and Ruppin (1977, their figures 4–6), we regressed their PDI (rescaled to range 0–1) to our WI (calculated from their measured water potentials) and their soil field capacities (FC; estimated from their soil descriptions using relationships in Saxton & Rawls, 2004). The regression had an adjusted R^2 of 0.31 and p value of 0.0002, producing the following coefficients:

$$\mathrm{PDI} = 0.006711 + 0.556566 \times \mathrm{WI} + 0.013227 \times \mathrm{FC} - 0.008511 \times \mathrm{WI} \times \mathrm{FC}.$$

A minimum temperature parameter (MinSoilTemp) defines a soil temperature below which pathogen populations drop and do not cause infection. Soil temperature at depth of SoilTempDepth (T_{soil}) is estimated for each month of the growing season with the methods presented in Gustafson et al. (2020) using:

$$T_{\mathrm{soil}}(m) = T_{\mathrm{ave}} + A \times \exp\left(\frac{-\mathrm{SoilTempDepth}}{d}\right) \times \sin\left(\Omega m - \frac{\mathrm{SoilTempDepth}}{d}\right)$$

where T_{ave} is the average air temperature for month m, A is the amplitude of air temperature over the previous 12 months, d is the damping depth (meters), and Ω is the

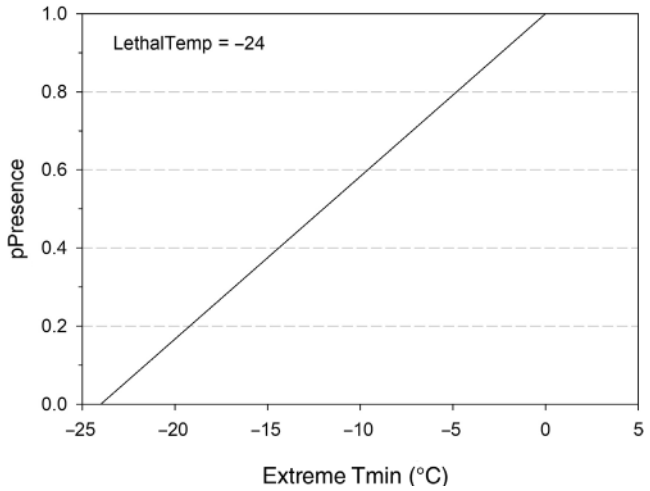


FIGURE 2 Graphical depiction of the behavior of Equation 1

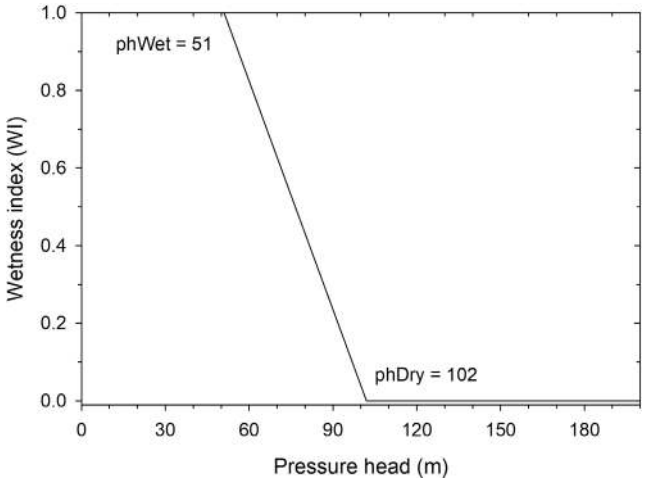


FIGURE 3 Graphical depiction of the relationship between the wetness index and soil water potential (pressure head [ψ])

angular frequency of oscillation (radians per month) (Sitch et al., 2003). The damping depth (d) and angular frequency of oscillation (Ω) are calculated as follows:

$$d = \sqrt{\frac{2k}{\Omega}}, \tag{2}$$

$$\Omega = \frac{2\pi}{12}, \tag{3}$$

where k is the thermal diffusivity (in square millimeters per month) of the soil given its water content. The depth at which soil temperature is computed by the root rot extension is user-controlled.

For any growing season month with soil temperatures below MinSoilTemp, the WI value is set to 0, which causes PDI to also equal 0. Infection status transitions are based on the average PDI (PDIavg), which is calculated for each site across all growing season months within the previous succession extension time step.

Infection status transitions

The probability of U transitioning to I, p(U → I), is equal to PDIavg, which accounts for both soil moisture and soil temperature thresholds. The probability of a U site converting to D, p(U → D), is the product of the probabilities p(U → I) and p(I → D), that is, it must make both transitions:

$$p(U \rightarrow D) = p(U \rightarrow I) \times p(I \rightarrow D).$$

Cells that are Infected (I) can transition to Uninfected (U) or Diseased (D) states. The probability of I converting to U, p(I → U), is binary depending on the presence of the pathogen. If Presence equals 0, then p(I → U) = 1. If Presence equals 1, then p(I → U) = 0. This relationship assumes that the absence of the pathogen always reverts a cell to an Uninfected status, and that a cell will maintain Infected status as long as the pathogen remains present. The probability of I converting to D, p(I → D), is bimodal. The probability at pressure head values below phDry follow the value of WI as used above, except with the minimum probability constrained to be at or above the parameter minProbID. At moderate pressure head, the probability of disease development can be greater than 0, which is set by minProbID. Unlike p(U → I) above, probability p(I → D) increases from minProbID at phDry to 1 at phMax (Figure 4), reflecting observations that wet conditions favor the pathogen and dry conditions stress infected trees because infected roots are less able to uptake water. The outcome of these two processes results in greater host resistance under moderate soil wetness conditions.

p(I → D) =
  If (Ψ ≤ phDry): Maximum(WI, minProbID);
  If (Ψ > phMax): 1;
  If (phDry < Ψ ≤ phMax): m1 × ph + b1;
    m1 = (1–minProbID)/(phMax – phDry);
    b1 = minProbID – (phDry × m1),

where Ψ is the water potential in units of pressure head.

A currently diseased site (D) can transition to Uninfected (U) or Infected (I). The probability of D converting to U, p(D → U), is binary depending on the presence of the pathogen. If the Presence equals 0, then p(D → U) = 1. If Presence equals 0, then p(D → U) = 0. This relationship assumes that in the absence of the pathogen always reverts a cell to an Uninfected status.

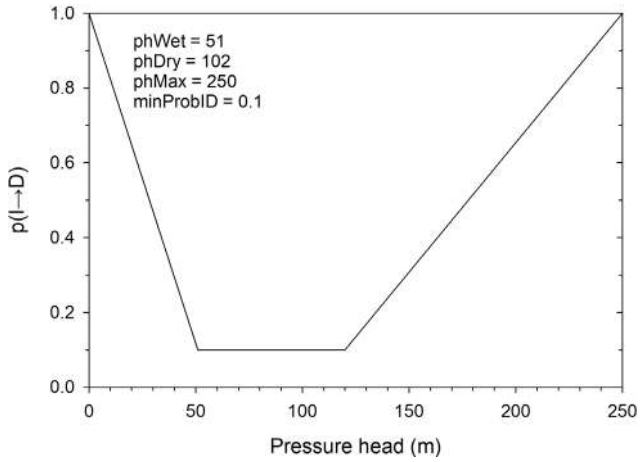


FIGURE 4 Example probability of transition from Infected to Diseased

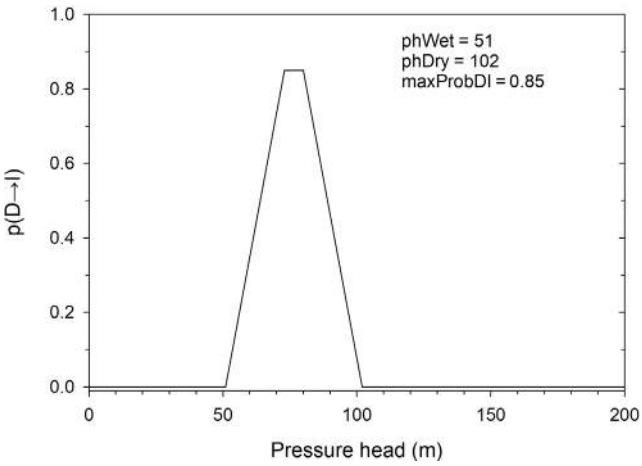


FIGURE 5 Example probability of transition from Diseased to Infected

A D site converts to I if no cohorts with susceptibility >0 are present, or with probability p(D → I) when pressure head is between phWet and phDry. The probability increases toward the midpoint between phWet and phDry. Maximum probability is capped at a user-defined parameter (maxProbDI) (Figure 5).

$p(D \rightarrow I) =$
If all Susceptibility(i) = 0: 1;
If ($\Psi <$ phWet): 0;
If ($\Psi >$ phDry): 0;
If ($\Psi \leq$ (phDry − phWet)/2): $m2 \times \Psi + b2$;
$m2 = 1/((\text{phDry} - \text{phWet})/2 - \text{phWet})$;
$b2 = -1 \times \text{phWet} \times m2$;
If ($\Psi >$ (phDry − phWet)/2), $m3 \times \Psi + b3$;
$m3 = 1/((\text{phDry} - \text{phWet})/2 - \text{phDry})$;
$b3 = -1 \times \text{phDry} \times m3$.

For any site with a status of Diseased (D), the extension removes a proportion of cohort biomass equal to the susceptibility of the species (regardless of cohort age or biomass), representing the death of that proportion of individual trees. Some individuals of otherwise susceptible species may have a natural resistance to the pathogen, and we assume that growth of resistant individuals will not be reduced by *P. cinnamomi* infection. The survival of individuals resistant to root rot is modeled by reducing the future susceptibility of such cohorts to a user-defined, species-specific level once they have previously experienced root rot mortality. For any cohorts that have previously experienced a status of Diseased, when their site reaches Diseased status again, the extension removes the proportion of cohort biomass specified by the parameter Secondary Susceptibility. The extension writes a record of its activity at each time step to both an event log and a summary log. If requested, the extension will output maps at each time step of the tree biomass killed from the disease on each site and TimeofLastDisease, reflecting the year each site was most recently damaged by the disease.

Experimental design

The study was conducted as a factorial simulation experiment on each study area, with the climate factor having two levels (historical and RCP 8.5), and a root rot susceptibility factor having four levels representing degrees of susceptibility to the pathogen. We selected two study areas that differed in rainfall (higher vs. lower) and predominant soil types (mesic vs. xeric) to assess the generality of simulated root rot effects across ecological provinces, which functioned as a third factor with two levels (wet vs. dry). We used a clearcut-and-plant chestnut restoration strategy in all simulations, which was the most aggressive restoration strategy implemented by Gustafson et al. (2018) and has been recommended as an approach to effectively restore chestnut to the landscape (Jacobs, 2007; Jacobs et al., 2013). We simulated a generic "business as usual" timber harvest regime, and the restoration strategy planted chestnut throughout harvested stands (mean size = 9 ha) that received a silvicultural clearcut treatment, and controlled competing regeneration for 1 year. We also simulated four insect pests (Gypsy Moth, Forest Tent Caterpillar, Emerald Ash Borer, Hemlock Wooly Adelgid) as a background disturbance, held constant across treatments. Each factorial combination (climate, pathogen pressure) was simulated at a monthly time step for 200 years. Because variability between runs was low, three replicates were sufficient to estimate treatment effects with limited uncertainty.

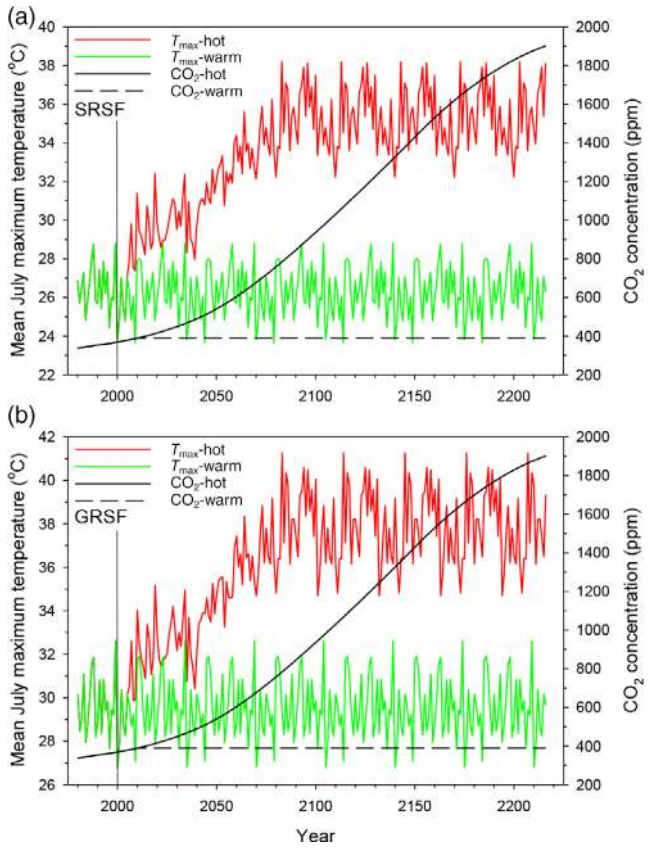


FIGURE 6 Temperature inputs for each study area. Simulations began in year 2000. (a) Savage River State Forest (SRSF); (b) Green Ridge State Forest (GRSF)

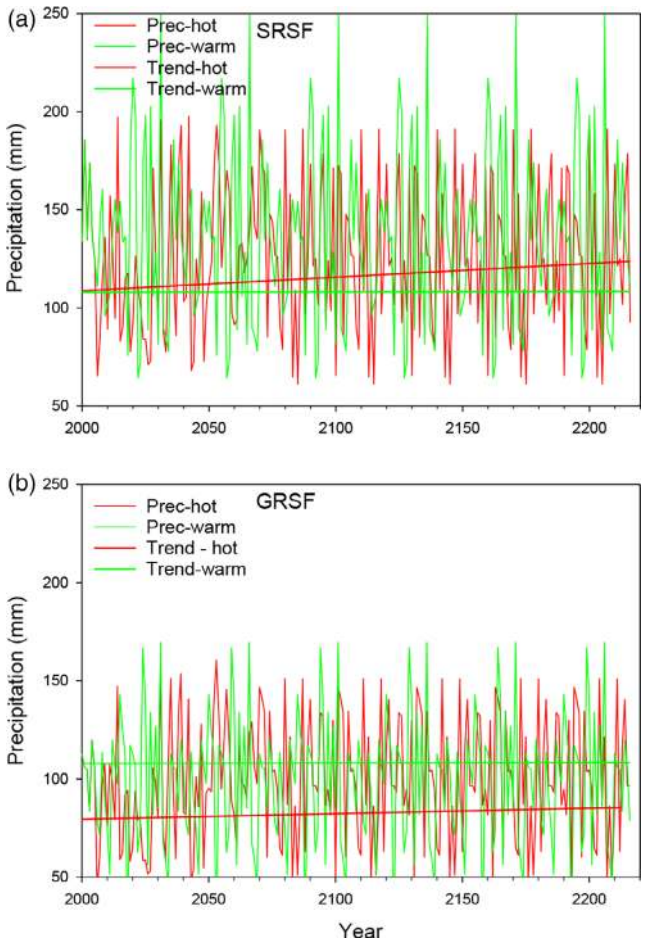


FIGURE 7 Precipitation inputs for each study area. Only July values are shown for clarity. (a) Savage River State Forest (SRSF); (b) Green Ridge State Forest (GRSF)

The "Warm" climate scenario used historical weather data (including photosynthetically active radiation, i.e., light) for an area surrounding each study area that was subset from the Daymet Daily surface weather 1-km grid for North America, 1980–2015 (Thornton et al., 2014). We used monthly averages prior to 1980 (for "spin-up" of the biomass of existing cohorts), and actual records through 2014, repeating the observations of the period 1980–2014 for 200 years to create a "Warm" weather scenario into the future. CO_2 was set at 335 ppm prior to 1980, gradually increasing to 390 ppm by 2010, and held constant after that. For the climate change "Hot" scenario, we used projections from the GFDL-CM3 GCM (RCP 8.5 emissions scenario, run = r1i1p1) centered on each study area for the period 2006–2100, repeating the last 30 years of the projections through 2216 (Figures 6 and 7). We used the extended RCP8.5 CO_2 concentrations of Meinshausen et al. (2011), with CO_2 concentration reaching 1902 ppm by 2216. The GCM data did not include photosynthetically active radiation, so we repeatedly applied the historical light data from 1980 to 2014. We also simulated a "Cold" scenario where root rot cannot survive the winter, using the "Warm" climate but turning off simulation of root rot.

The susceptibility of hybrid chestnut to root rot is estimated to be between 45% and 80% of live aboveground woody biomass in a chestnut cohort lost to an infection (Jeffers et al. 2012). Jeffers et al. (2012) reported that 83% of nonselected hybrid chestnut died within a year after inoculation by *P. cinnamomi*, while TACF has found that hybrid chestnut families selected for root rot resistance have a mortality rate of about 43% (J. Westbrook, personal communication, 2020). Because some individuals can survive infection, these survivors provide greater resistance to root rot infection on sites previously infected by the root rot pathogen. The extent of this resistance (secondary root rot susceptibility) has not yet been established empirically, but Perkins et al. (2019) found that 70% of hybrid chestnut seedlings that survived controlled inoculations also survived their first growing season after being transplanted into an orchard with a high incidence of root rot. Using the Secondary Susceptibility parameter, we simulated two secondary root rot mortality rates (10, 30%) to help understand how much resistance might be needed to allow chestnut to be restored in

TABLE 2 Species susceptibility (to root rot) values used in the simulation experiment

Species	Susceptibility	
	Primary	Secondary
Acer rubrum	0.0	0.0
Acer saccharum	0.0	0.0
Betula lenta	0.0	0.0
Carya glabra	0.0	0.0
Castanea dentata	0.80 or 0.45	0.10 or 0.30
Fagus grandifolia	0.0	0.0
Fraxinus americana	0.0	0.0
Juglans nigra	0.0	0.0
Liriodendron tulipifera	0.0	0.0
Magnolia acuminata	0.0	0.0
Nyssa sylvatica	0.0	0.0
Pinus echinata	0.0	0.0
Pinus pungens	0.0	0.0
Pinus rigida	0.0	0.0
Pinus virginiana	0.0	0.0
Pinus strobus	0.0	0.0
Prunus serotina	0.0	0.0
Quercus alba	0.05	0.03
Quercus coccinea	0.05	0.03
Quercus prinus	0.05	0.03
Quercus rubra	0.05	0.03
Quercus velutina	0.05	0.03
Robinia pseudoacacia	0.05	0.03
Sassafras albidum	0.0	0.0
Tilia americana	0.0	0.0
Tsuga canadensis	0.0	0.0
Ulmus americana	0.0	0.0

Notes: Values define the proportion of cohort biomass removed (representing the nonresistant individuals within the cohort) when "Diseased" status first occurs (primary susceptibility) and for all subsequent "Diseased" occurrences for that specific cohort (Secondary Susceptibility).

regions were root rot is found. Thus, the chestnut root rot resistance factor had four levels (two levels of Primary Susceptibility and two levels of Secondary Susceptibility) (Table 2).

Analysis approach

We evaluated simulation outputs by plotting 95% confidence intervals of chestnut biomass through time by various treatment combinations, inferring significant differences when confidence intervals did not overlap. We generally avoided conducting statistical tests as recommended by White et al. (2014) for simulation experiments, but we computed least squares means and confidence intervals using GLIMMIX in SAS v9.4. Model input parameters can be found in a Forest Service Research Data Archive at https://doi.org/10.2737/JS-2021-001.

RESULTS

The root rot extension generated spatially heterogenous distributions of infection status and root rot-induced tree biomass losses driven by soil wetness and temperature and the presence (or absence) of host tree species (e.g., Figure 8).

Effect of temperature

In a comparison of no root rot (cold-limited) and active root rot scenarios, root rot caused a dramatic reduction in chestnut biomass on both the mesic (SRSF) and xeric (GRSF) study areas (Figure 9). The hotter climate (RCP 8.5) enhanced the virulence of the pathogen and resulted in a greater reduction in chestnut biomass as climate warmed.

Effect of root rot resistance

Decreasing levels of secondary root rot susceptibility resulted in a nonlinear positive response of chestnut biomass that was reduced by a warming climate (Figure 10). Although the highest root rot susceptibility scenario (80%–30%) severely limited chestnut abundance, it did not produce a 95% confidence interval for mean chestnut biomass over the last 50 years that included zero on either SRSF or GRSF.

Interaction of temperature and wetness

We expected that root rot would have less impact on the GRSF study area because it receives less rainfall and has more xeric soils. However, both study areas had a similar response to the treatments (Figures 9 and 10). Although soil wetness (i.e., WI) was indeed lower on the GRSF site (Figure 11), soil temperature sometimes dropped to levels that are lethal to *Phytophthora* on the SRSF site (Figure 12), and these two factors apparently offset each other on the two study areas. The interacting drivers of root rot infection produced differing infection status profiles, as seen in Figure 13 (and Figure 8). GRSF had higher levels

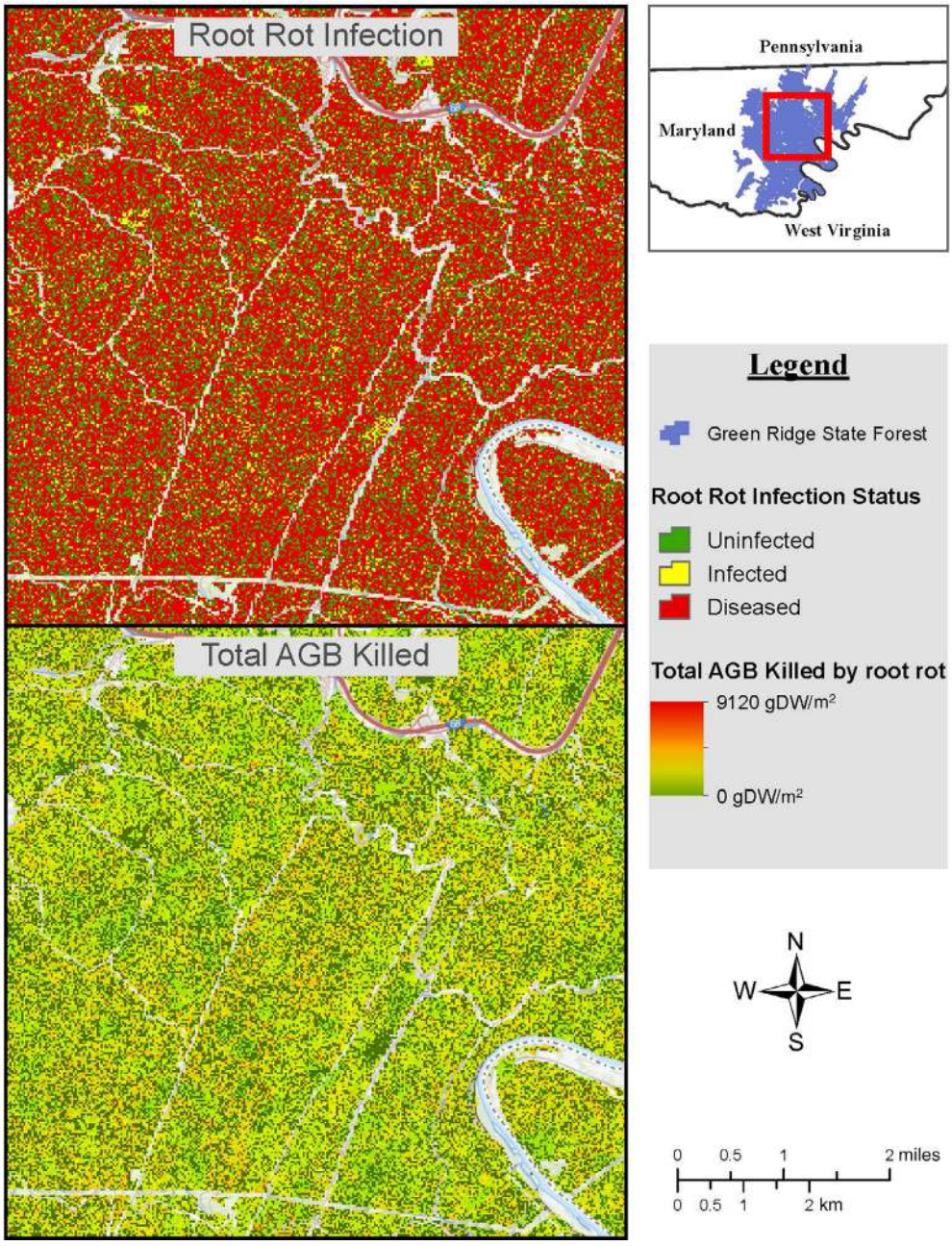


FIGURE 8 Maps of root rot infection status and infection-induced tree biomass (above-ground biomass, AGB) loss (mortality). Infection status is stochastic, driven by soil temperature and wetness, the latter driven primarily by soil texture and vegetation (transpiration) on the site. This example was generated by the Hot-45-10 factorial combination at year 50

of Infected and Diseased status compared to SRSF. Tree cohort Damage occurs only on Diseased sites, and SRSF had relatively less Damage compared to the prevalence of Diseased status than on GRSF, presumably because susceptible species occurred less frequently on Diseased sites. Similarly, GRSF had fewer sites that did not convert from Infected to Diseased than SRSF, and fewer where *Phytophthora* was absent. Note that climate change elevated infection rates on each site and reduced the number of sites where the pathogen was absent, with no sites free of *Phytophthora* on GRSF after about year 100 under climate change.

DISCUSSION

Major insights

Our results suggest that root rot has the potential to seriously hamper chestnut restoration efforts in regions

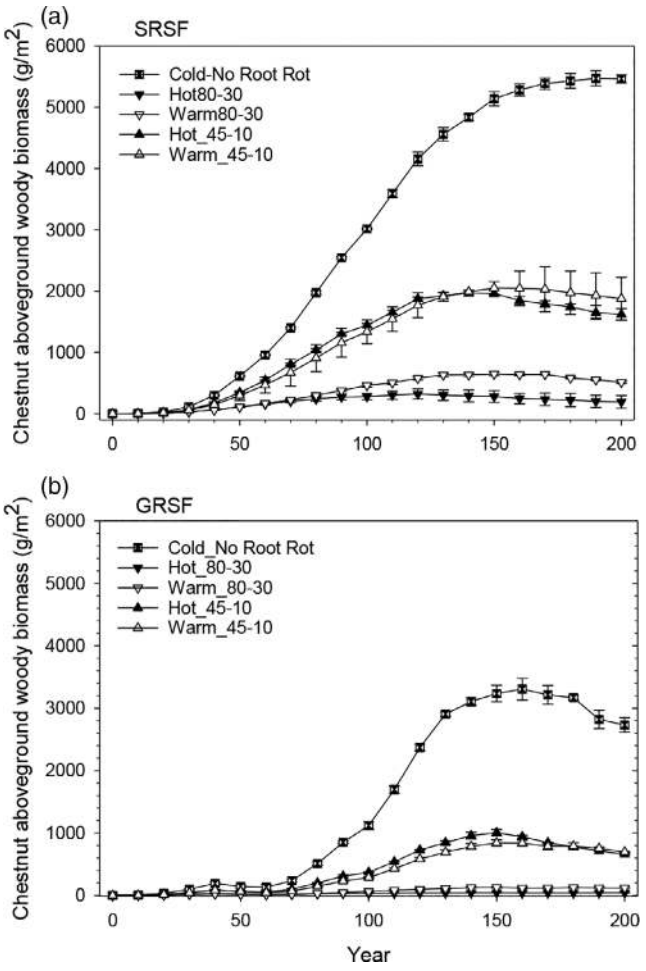


FIGURE 9 Effect of climate on the mean biomass of chestnut across the (a) Savage River State Forest (SRSF) and (b) Green Ridge State Forest (GRSF) landscapes through simulated time for selected root rot susceptibility values. Error bars show 95% confidence intervals of replicate variability

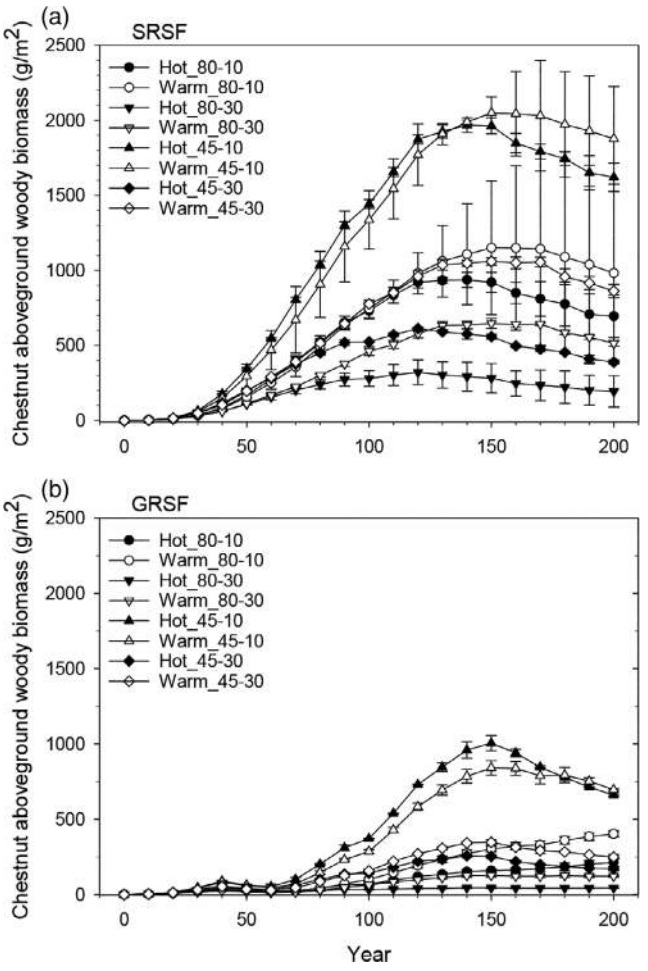


FIGURE 10 Effect of primary and secondary root rot susceptibility and climate on the mean biomass of chestnut across the (a) Savage River State Forest (SRSF) and (b) Green Ridge State Forest (GRSF) landscapes through simulated time. Error bars show 95% confidence intervals of replicate variability

where *P. cinnamomi* is common or likely to become so with climate change. There is considerable uncertainty about the susceptibility of chestnut to *P. cinnamomi*, but even an optimistic selection-induced reduction of susceptibility of chestnut to root rot to 10% does not allow chestnut to regain anything approaching its former abundance on the landscape, despite the aggressive restoration efforts (clearcut and plant) we simulated. This suggests that restoration efforts will be more successful if targeted to latitudes, elevations, and site conditions where root rot is not expected to be present well into the future, or that resistance to root rot must be increased substantially in chestnut germplasm developed for reintroduction.

Gustafson et al. (2018) used LANDIS-II to assess the effect of various chestnut restoration strategies on these same study areas under three climate futures, and they found that aggressive restoration (planting in recent clear cuts) has potential to return chestnut to a respectable level

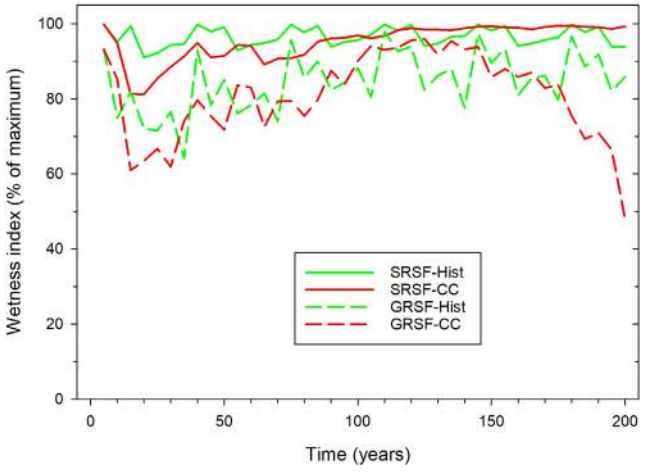


FIGURE 11 The effect of climate and study area (climate and soil) on mean soil wetness through time. "Hist" is historical and "CC" is climate change scenario. GRSF, Green Ridge State Forest; SRSF, Savage River State Forest

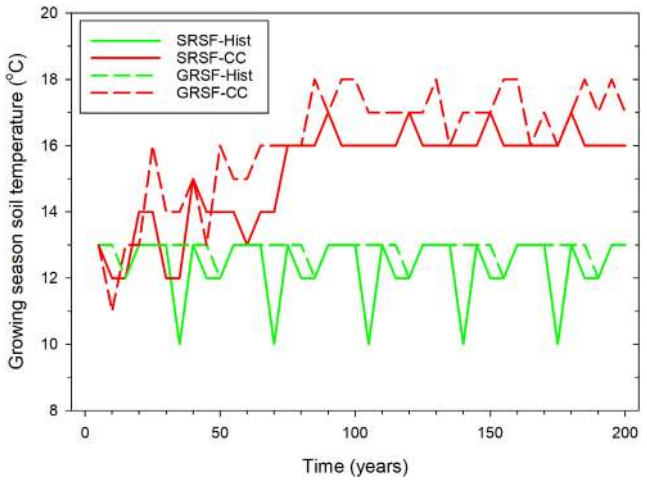


FIGURE 12 The effect of climate and study area (climate and soil) on mean soil temperature through time. "Hist" is historical and "CC" is climate change scenario. GRSF, Green Ridge State Forest; SRSF, Savage River State Forest

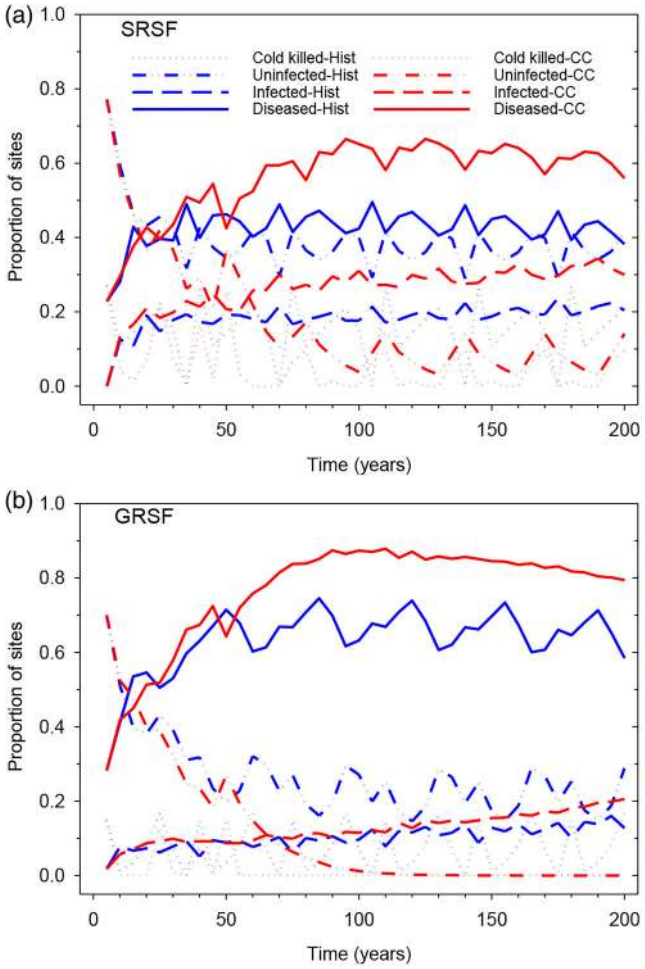


FIGURE 13 Proportion of sites having each root rot infection status through time for each study area. Note that Damage stochastically occurs only on Diseased sites according to species-specific susceptibility to root rot; the proportion of Uninfected, Infected, and Diseased sites sums to 1.0; cold-killed sites are a subset of uninfected sites. Standard deviations are generally less than the width of the lines. "Hist" is historical and "CC" is climate change scenario. (a) Savage River State Forest (SRSF); (b) Green Ridge State Forest (GRSF)

of abundance, as empirical studies have demonstrated (Gauthier et al., 2013; Jacobs & Severeid, 2004). However, they did not simulate root rot, assuming that root rot infections could be managed near the northern edge of *P. cinnamomi* range. The results generated in this paper suggest that the results of Gustafson et al. (2018) may have applicability to the northernmost portion of former chestnut range, but that prospects for the rest of the range are not encouraging unless root rot infections can be mitigated.

Various strategies may help to mitigate the effects of *P. cinnamomi* in regions where the pathogen is currently or likely to become present. *P. cinnamomi* is favored by compacted soils with poor aeration and/or that tend to remain saturated (Anagnostakis, 2001; Rhoades et al., 2003, 2009), such as heavy clay soils and those highly disturbed by agriculture or mining. This suggests that sites for reintroduction should be carefully selected (e.g., nondisturbed, well-drained sites). In addition, applying optimized silvicultural management to minimize environmental stresses may help to reduce the expression of the pathogen, similar to an approach suggested for blight resistance (Griffin, 2000; Jones et al., 1980). Additional strategies may include identification of soil microbes that provide protection to roots, identification of suppressive soils and a continued focus on breeding for *P. cinnamomi* resistance (Anagnostakis, 2001; Keen & Vancov, 2010; Rhoades et al., 2003).

Assumptions

The root rot extension includes several assumptions. (1) It does not simulate dispersal of *P. cinnamomi*, a globally common invasive pathogen, and assumes that the pathogen can reach every site on the simulated landscape, although its presence can be prevented by low winter temperatures in specific ecoregions (Burgess et al., 2017). Near the northern edge of *Phytophthora* range where *P. cinnamomi* is not widespread, this assumption of *Phytophthora* ubiquity may result in greater simulated *Phytophthora* impacts than would be seen empirically. Further, PDI may be substantially reduced in ecoregions with soil types and precipitation patterns that reduce soil water, thereby mitigating the impact of *P. cinnamomi* on those sites, so this assumption should be evaluated further. For landscapes that are outside the expected future range of *P. cinnamomi*, the extension need not be invoked. (2) The

extension assumes that *P. cinnamomi* population density is controlled solely by soil moisture and soil temperature, and can be reset by extreme minimum air temperature. Because these variables do not explain all the variation in PDI in the data set used to develop the index (Weste & Ruppin, 1977), it is apparent that other factors must play some role. Further empirical study is required to elucidate other factors influencing *P. cinnamomi* infection biology to reduce this uncertainty and parameterize future models. (3) The extension does not model natural selection for root rot resistance, primarily because the LANDIS-II model cannot track the heritability of genetic properties among dispersing propagules. (4) The extension assumes chestnuts planted are resistant to the chestnut blight. Breeding, primarily by TACF, one of the principal organizations working to develop blight-resistant American chestnuts, has not yet succeeded in producing hybrid chestnuts that are both highly blight resistant and predominantly American (Steiner et al., 2017; Westbrook, Zhang, et al., 2020b). If chestnuts with intermediate rather than high levels of blight resistance are used in restoration plantings, infection by blight will likely lead to further reduced levels of chestnut biomass on the landscape than the model predicts.

Caveats

(1) Root rot susceptibility probabilities do not vary by cohort age or size; mere presence of hosts is sufficient to determine susceptibility. This was a simplifying assumption made to reduce parameter burden and complexity. (2) *P. cinnamomi* reproduces very quickly, and infections may develop when soil is saturated for as few as 24 h. For example, a single heavy rain event could be enough to convert a site from a state of U to I. Our model would be fairly insensitive to such events because the extension time step can never be less than 1 year, and temperature and precipitation inputs have a monthly resolution. However, p(U:I) would be much lower in the case of a single rain event compared to periods of prolonged wetness, so we believe that our approach produces valid projections regardless of the temporal variability of rainfall within a month. (3) We used a range of values for the primary susceptibility of chestnut to *P. cinnamomi*. The 80% rate came from 197 TACF hybrid chestnut seedling families (from generations ranging from F_1 to BC_4) screened by Jeffers et al. (2012) from 2004 to 2010 using a tub screening method and a flooding treatment to encourage root rot infection. This approach resulted in mean annual mortality for seedlings of 83%, which is possibly higher mortality than might be found in many field sites because the moisture conditions were highly conducive to root rot. The seedlings were not selected for resistance to the pathogen whereas genotypes that will be deployed in restoration efforts will likely be selected for root rot resistance and suffer reduced mortality. More recent root rot resistance data from nonselected American chestnut backcross hybrids tested using similar methods in 2018 and 2019 also supports this 20% survival rate (J. Westbrook, personal communication). The 45% susceptibility rate is the approximate mortality rate of TACF hybrid backcross families that were selected for resistance to root rot (J. Westbrook, personal communication). The 45% treatment level represents the current goal for selection of root-rot-resistant chestnut families using traditional breeding methods. As more accurate parameter estimates become available, the analyses can be rerun with revised parameters. (4) The parameters controlling *P. cinnamomi* establishment, spread, and mortality used here are not currently well defined for this system and were derived from a relevant study in Australia (Weste & Ruppin, 1977) and knowledge synthesized across several systems (González et al., 2020 and references within). As better parameter estimates become available researchers can use the model to conduct new analyses. (5) In the model, biomass is a proxy for height, and foliage is proportional to woody biomass. Because root rot reduces cohort biomass, it also reduces foliage relative to competitors and slows productivity, and the decline in chestnut biomass seen in root rot scenarios in Figures 9 and 10 is a consequence of chestnut being overtopped by competitors. In reality, individuals that survive root rot will retain their height and are unlikely to be overtopped. Therefore, it is defensible to assume that the trajectory of chestnut under root rot scenarios will not decline in the last 50 years (due to overtopping), but be similar to that of the SRSF no root rot scenario. (6) Variability among replicates is low, resulting mostly from stochasticity in access of cohorts to light and water, cohort establishment, and disturbances. Uncertainty related to model and parameter specification and future climate are much higher, but were controlled here to increase the signal from the experimental treatments.

Management implications

The northern range of root rot in the United States currently extends to southern Pennsylvania and Ohio, where it is constrained by cold winter temperatures (Balci et al., 2007). As the climate continues to warm, the pathogen is expected to spread northward. A model developed by Burgess et al. (2017) predicts that the potential distribution of root rot will expand throughout the current range of American chestnut by 2080. However, climate change

is expected to expand the suitable habitat for chestnut northward as well, perhaps beyond the expanded range of root rot. In one climate suitability model based on high emission scenarios, for example, Barnes and Delborne (2019) predicted that by 2080 there may be a significant expansion of suitable habitat for American chestnut into Canada. Areas that are located within the predicted future range of American chestnut, yet beyond the predicted northern limits of root rot, could be considered for chestnut reintroduction efforts.

The nursery trade continues to facilitate the movement of *P. cinnamomi* among plant materials (Bienapfl & Balci, 2014) and from plant material to planting sites (Beaulieu et al., 2017). Because planting stock from commercial nurseries, especially for bareroot production, can be infected by the pathogen even following soil sterilization, it may be advisable to use nurseries outside of the pathogen's current range for chestnut restoration, because even containerized nursery material can also harbor *P. cinnamomi* (Bienapfl & Balci, 2014). If nursery-grown chestnuts free of *P. cinnamomi* cannot be obtained, direct seeding may be considered when reintroducing the species to sites that are or may become susceptible to *P. cinnamomi* but are currently free of the pathogen. Direct seeding may be effective in establishing chestnut if seed predation is controlled, for example, with physical barriers (Jacobs & Severeid, 2004).

While resistance to chestnut blight has been the primary goal of chestnut breeding efforts for over 100 years, the importance of integrating resistance to root rot has long been suggested (Anagnostakis, 2001) and TACF plans to incorporate root rot resistance into their larger blight resistance breeding program. The results of our modeling demonstrate the vital importance of this plan. Our results suggest American chestnuts used in restoration plantings in areas where *P. cinnamomi* can survive will need to be nearly as resistant to root rot as Chinese chestnuts in order to persist in meaningful numbers.

CONCLUSIONS

This study highlights the usefulness of landscape-scale modeling to guide on-the-ground restoration approaches. While empirical studies have demonstrated the substantial impact of *P. cinnamomi* on small-scale chestnut plantings, this is the first study to reveal the potential severity of this impact at landscape scales—over several climate scenarios, two ecological provinces, and four resistance levels. Our results illustrate the enormous challenges this pathogen presents to the successful restoration of American chestnut and highlight the importance of increasing resistance to *P. cinnamomi* in the genome of hybrid chestnut selected for blight-resistance. Concurrent with, or at least in absence of, successful efforts to increase the resistance of chestnut to *P. cinnamomi*, our results suggest that chestnut restoration should be prioritized for regions and sites that are located within the predicted future range of American chestnut, yet beyond the expected limits of root rot. Our study explores some of the major uncertainties surrounding the interaction of *P. cinnamomi* and hybrid chestnut in a restoration setting, and therefore cannot be considered a definitive prediction of how a major restoration program might fare. However, most parameters used in our model are user-defined, and the model is freely available to researchers and practitioners (http://www.landis-ii.org/). This will allow refinement of these parameters as more data become available and enable researchers to test hypotheses concerning specific levels of resistance and specific restoration goals.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Novel code and executable files, as noted in the Methods section, are available at http://www.landis-ii.org/extensions. Model input parameters (Gustafson et al., 2021) are available from the Forest Service Research Data Archive: https://doi.org/10.2737/JS-2021-001.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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