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The implications of American chestnut reintroduction on landscape dynamics and carbon storage

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Abstract. In the eastern United States, American chestnut (*Castanea dentata*) was historically a major component of forest communities, but was functionally extirpated in the early 20th century by an introduced pathogen, chestnut blight (*Cryphonectria parasitica*). Because chestnut is fast-growing, long-lived, and resistant to decay, restoration of American chestnut using blight-resistant stock could have the potential to increase carbon sequestration or storage in forested landscapes. However, carbon dynamics are also affected by interspecific competition, succession, natural disturbance, and forest management activities, and it is unknown how chestnut restoration might interact with these other processes. We used the PnET-Succession extension of the LANDIS-II forest landscape model to study the implications of chestnut restoration on forest composition and carbon storage in the context of other disturbances, including timber harvest and insect pest outbreaks. Our results imply that it could take a millennium or more for chestnut to fully occupy landscapes without aggressive restoration efforts. When successful, chestnut restoration activities displaced other species approximately in proportion to their abundance on the landscape, rather than replacing a single species or genus (e.g., *Quercus*). Insect pests increased the rate of chestnut colonization by reducing the abundance of competitors, and also had a dominant effect on carbon dynamics. Although chestnut is fast-growing, moderately shade-tolerant, and decomposes very slowly, our results suggest that it can only modestly increase the carbon storage potential of eastern forests. However, our results also demonstrate that compositional changes in forest communities can have noticeable effects on biomass accumulation, even with the large uncertainties introduced by invasive pests.

Key words: American chestnut; carbon cycling; carbon sequestration and storage; forest landscape management; forest landscape modeling; forest restoration; insect pests; LANDIS-II.

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Introduction

Carbon sequestration is an important ecosystem service provided by forests globally and represents a driving motivation for reforestation and conservation efforts worldwide. However, the potential for carbon sequestration in many forested regions may be limited by competing land uses (Drummond and Loveland 2010), transitions in forest age structure (Xu et al. 2016), and disturbance processes that in many cases are accelerated by human activities (e.g., Lovett et al. 2016). In the eastern United States, for example, native and exotic insect pests such as forest tent

caterpillar (FTC; *Malacosoma disstria*), gypsy moth (GM; *Lymantria dispar*), and hemlock wooly adelgid (HWA; *Adelges tsugae*), as well as imminent potential invasions by the emerald ash borer (EAB; *Agrilus planipennis*) and Asian long-horned beetle (ALB; *Anoplophora glabripennis*), may fundamentally change the ability of these forests to continue serving as a regional carbon sink (Flower and Gonzalez-Meler 2015).

Assuming that the amount of forested land will remain relatively stable, it is reasonable to hypothesize that future carbon dynamics will depend, at least in part, on the mix of tree species that occupy those forests. Tree species vary widely in their growth rates under given environmental conditions and in the decay resistance of their wood (Loehle 1988, Weedon et al. 2009, Russell et al. 2014), which can affect the rate of carbon uptake and time of storage. However, predicting the consequences of compositional change is not a trivial task because in addition to species' establishment and growth rates, potential size, spacing, and life span, carbon dynamics also depend on disturbance rates and intensities.

Prior to the 20th century, American chestnut (*Castanea dentata*) was a major component of forest ecosystems in much of the eastern United States (Fig. 1; Ellison et al. 2005). Mature individuals reached up to 30 m in height and 3 m in diameter (Emerson 1846, Hough 1878, Ashe 1911, Buttrick 1915), and sometimes represented 40–45% of the forest canopy (Keever 1953). In the early 19th century, a root disease, caused by *Phytophthora cinnamomi* Rands, caused a wave of chestnut mortality (Anagnostakis 2012). From about 1900 to 1950, however, American chestnut became extirpated as a canopy tree by an invasive fungal pathogen, the chestnut blight (*Cryphonectria parasitica*), introduced on imported Asian chestnut trees. Although chestnut trees can re-sprout from their roots, the blight invariably kills these sprouts before they reach reproductive maturity (Paillet

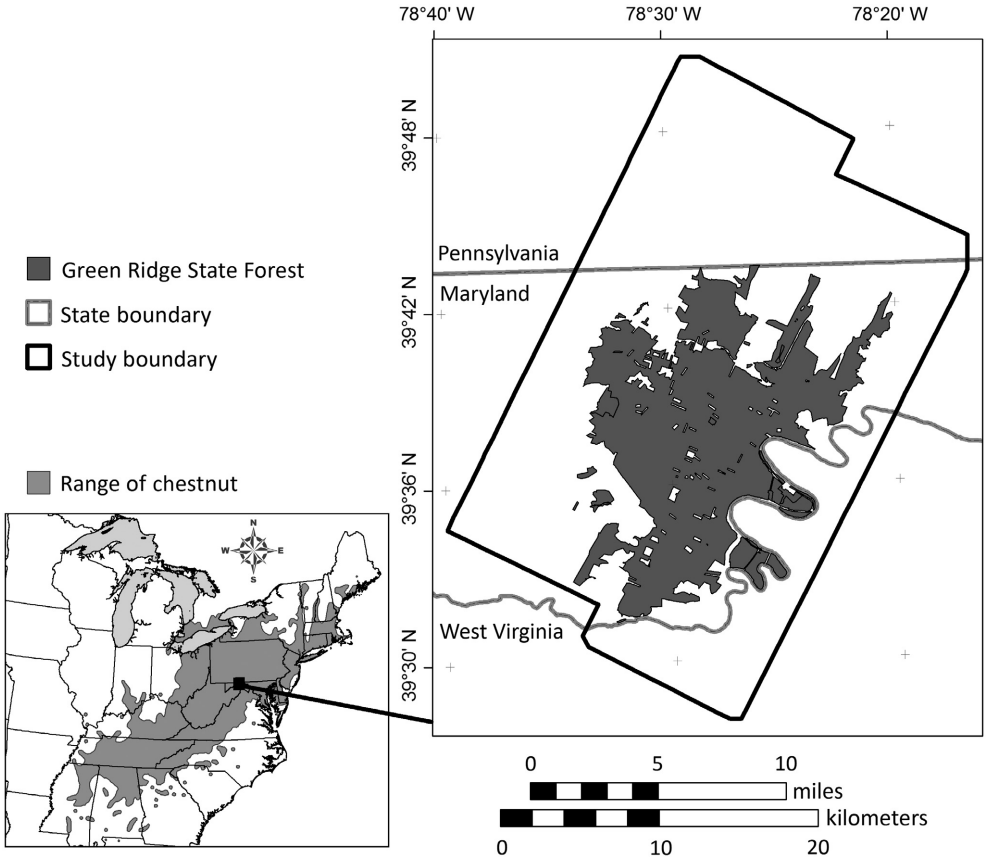


Fig. 1. Location of the study area in relation to the historic range of the American chestnut (*Castanea dentata*).

2002). A backcross hybrid chestnut for reintroduction that is genomically 94% American chestnut has been produced through breeding with blight-resistant Chinese chestnut (*Castanea mollissima*) (Burnham et al. 1986). The hybrid is morphologically indistinguishable from pure American chestnut for a host of physiological and morphological traits (Diskin et al. 2006, Knapp et al. 2014), although it may differ from purebred chestnuts at other functional traits (Blythe et al. 2015), and additional generations of breeding will be needed to ensure blight resistance (Steiner et al. 2017). Using transgenic techniques, other researchers have introduced two wheat genes into the chestnut genome, resulting in trees that contain the entire American chestnut genome and exhibit enhanced resistance to blight (Jacobs et al. 2013, Zhang et al. 2013, Clark et al. 2014, Steiner et al. 2017). Given these advances, the restoration of American chestnut to eastern forests of the United States is within practical reach (Jacobs et al. 2013, Clark et al. 2014, Steiner et al. 2017).

Because American chestnut is fast-growing, long-lived, and resistant to decay (Youngs 2000, Ellison et al. 2005, De Bruijn et al. 2014*a*), its restoration could result in increased carbon sequestration and storage in the form of living and dead trees and durable wood products. Recent research on American chestnut ecology and silvics (i.e., growth, competitiveness, ecophysiology) in blight-free plantations has found superior growth compared to co-occurring species (Jacobs and Severeid 2004, McEwan et al. 2006). In fact, it appears that they store as much carbon in their boles as do other fast-growing species used for forestry plantations in southwest Wisconsin (Jacobs et al. 2009). Given relatively low decay rate of chestnut wood (De Bruijn et al. 2014*a*), this carbon also would be expected to remain in storage for a longer period. However, the potential for American chestnut to influence carbon dynamics at landscape scales remains uncertain because interacting factors such as competitors and relative resilience to the dominant disturbances influence these dynamics, and because we do not know how well American chestnut will be able to establish itself in contemporary forests.

Regardless of any effort to restore American chestnut, insect outbreaks will play a dominant role in the carbon dynamics of eastern forests for the foreseeable future (Flower and Gonzalez-Meler 2015). These pests may positively or negatively affect chestnut restoration, depending on susceptibility of chestnut and its competitors. Native insect pests such as FTC can decrease productivity and increase stress of host tree species, reducing competitive ability and potentially resulting in mortality (Hicke et al. 2012). Several exotic insect pests have also come to the eastern forests in the past century. Gypsy moth, known to defoliate chestnut (Rieske et al. 2003), and HWA are now widely established throughout the region (USDA Forest Service 2016*a*, *b*). Other pests are expected to become increasingly prevalent. For example, the EAB (*Ag. planipennis*) is rapidly colonizing sites throughout the eastern United States since its discovery in the Midwestern United States in 2002, and it has the potential to kill virtually all of the ash trees in the entire region in a relatively short time. Similarly, the ALB (*An. glabripennis*) has been discovered in the northeastern United States, and like EAB, susceptible hosts within its introduced area appear to have virtually no defense against its attack (Dodds and Orwig 2011).

Anthropogenic disturbance also affects carbon dynamics in forested areas and occurs primarily as forest management activities and extraction of commodities (timber and minerals). In eastern forests, there is an interest in maintaining the current fire-dependent vegetation mix through active management such as even-aged regeneration (i.e., clearcutting or shelterwoods) and prescribed burning (Roach and Gingrich 1968, Morrissey et al. 2008, Johnson et al. 2010). The goal of these interventions is to maintain oaks and pines by reducing competition from fast-growing, shade-tolerant competitors such as red maple. On more mesic sites, production of high-value hardwoods is a management goal. Although the effects of timber management on carbon dynamics are widely studied (Birdsey et al. 2006), it is unclear how management may impact the ability of chestnut to become abundant (Jacobs 2007, Jacobs et al. 2013).

In this study, we applied the LANDIS-II forest landscape model to gain insight into the potential effects of strategies for chestnut reintroduction, native and exotic insect pests, and their interactions on forest composition and carbon storage in the center of the former range of American chestnut. Our purpose was not to predict the outcome

of future of chestnut restoration efforts, but to evaluate whether a best-case chestnut restoration scenario might substantially increase the carbon sequestration potential of eastern forests, especially in light of current and imminent threats capable of landscape-scale damage. Specifically, we used the model to conduct a factorial simulation experiment with three levels of chestnut restoration (none, passive chestnut reintroduction, and aggressive chestnut reintroduction) and three levels of pest outbreaks (none, existing pests, and existing pests plus new invaders) to make inferences about the relative effects of each factor on forest composition and carbon sequestration. We hypothesized that although disturbances due to pest outbreaks would play the largest role in determining community composition and biomass accumulation, the introduction of chestnut to the system would increase carbon storage. In addition, we expected that, given the relatively close overlap between the niches of chestnut and oak (Keever 1953), competition from chestnut would affect oaks more than other species.

Methods

Description of study site

We conducted our study in the Ridge and Valley physiographic province of western Maryland (USA) because it is in the approximate center of the former American chestnut range (Little 1977; Fig. 1) and allowed us to capitalize on previous studies for initial conditions and disturbance parameters (Sturtevant and Seagle 2004, Foster 2011). Prior to European settlement in this region, burning with low-intensity ground fires by Native American tribes was common practice. Following colonization by Europeans, the forests of western Maryland were exploited by various mining and timber companies, leading to the replacement of its primary forest by second growth between 1880 and 1912. Fire suppression greatly reduced the incidence of fire beginning around 1930, and there was increased red maple recruitment after that time (Shumway et al. 2001). Any remaining mature chestnut trees were killed by blight between 1914 and 1950. Due to this land-use history, stands throughout our study area are almost uniformly 100–150 yr old and even-aged.

Our 144,644-ha study site is centered on the Green Ridge State Forest (GRSF) and included surrounding privately owned lands. Elevation ranges from 140 to 600 m, and the area receives the lowest annual rainfall in Maryland (76–88 cm/yr; Brown and Brown 1984). The shallow and well-drained soils of GRSF tend to be xeric, with forests dominated by upland oaks. Pine (*Pinus* spp.) is common on the driest slopes (Hicks and Mudrick 1994). Geomorphology is characterized by strongly folded and faulted sedimentary bedrock forming long, parallel, and narrow ridges with steep intervening valleys oriented in a southwest–northeast direction (Stone and Matthews 1974).

Model overview

LANDIS-II is a forest landscape disturbance and succession model that uses independent extensions (i.e., modules) to simulate forest development processes (establishment, growth, competition, and succession) and disturbances (e.g., fire, wind, insect outbreaks, and timber harvesting) at large spatial (>100,000 ha) and temporal scales (centuries; Scheller et al. 2007). The model tracks species age cohorts rather than individual trees, representing space as a grid of cells. It provides a way to formalize multiple processes that are known at site or tree scale and to project them to the landscape scale in order to simulate the dynamics of forest productivity (carbon), composition, and spatial pattern. Because LANDIS-II is a stochastic, process-based model, the patterns that it generates are emergent properties of interactions among climate, competition, and disturbance.

We used the LANDIS-II PnET-Succession extension (De Bruijn et al. 2014*b*) to simulate the local-scale processes of cohort establishment, growth, competition, and mortality. PnET-Succession uses first principles to simulate growth and competition as a function of available light and water (De Bruijn et al. 2014*b*, Gustafson et al. 2015), and is ideally suited to model reintroduction of a species that is not well studied as a dominant component in contemporary ecosystems. Specifically, growth rates are calculated as a function of species-cohort photosynthesis, which in turn depends on light and soil water availability to the cohort. Total water availability is determined by precipitation inputs, loss to evaporation and runoff, soil porosity, and consumption by species cohorts. Soil texture determines the maximum available water

capacity, calculated as the difference between field capacity and wilting point (Saxton and Rawls 2004). Within each cell, cohort biomass determines the priority of access to soil moisture as well as to radiation. When water is adequate, the rate of photosynthesis for a given cohort increases with light that is available to the cohort (dependent on canopy position and leaf area), atmospheric CO_2 concentration, and foliar N, but decreases negative exponentially with age and departure from optimal temperature. As soil water potential decreases, photosynthesis also decreases. Cohorts may die at any time if their respiration requirements exceed their productivity. Thus, in PnET-Succession, growth rates vary monthly by both species and cohort as a function of weather and canopy position, and these fluctuations directly affect competition and ultimately, successional outcomes.

The PnET-Succession model allocates net photosynthetic production to four pools: foliage, wood, roots, and non-structural carbon reserves. Biomass is moved to litter and woody dead pools to represent breakage and individual stem mortality (including by disturbance), and then, these pools decay exponentially. As in previous LANDIS-II succession extensions, PnET-Succession models the decay of dead material by applying a single, average decay rate to each pool. We re-calculated dead pool sizes post hoc to account for species-specific decay rates as described in Appendix S1. A more detailed description of the model can be found in De Bruijn et al. (2014*b*) and Gustafson et al. (2016). The performance of PnET-Succession has been verified in several studies; its ability to match empirical observations of physiology and growth is quite robust (De Bruijn et al. 2014*b*, Gustafson et al. 2015, 2016, Duveneck et al. 2016).

PnET-succession parameters

LANDIS-II simulates growth, competition, dispersal, and establishment as a function of the life history attributes of tree species (Appendix S2: Table S1). The PnET-Succession extension uses primarily empirical parameters (Appendix S2: Tables S2, S3). Although most parameters are empirically measurable, the uncertainty of parameter estimates requires that in practice, the precise values of model inputs must be adjusted to calibrate the outputs to local conditions. We set most parameters based on prior studies (Sturtevant and Seagle 2004, Foster 2011), published literature (e.g., Burns and Honkala 1990), and expert judgment. Some parameters are quite generic and were held constant across species to reduce parameter variability unrelated to our experiment (Appendix S2: Table S3). The growth rate of each species was then calibrated by growing a single cohort of the species on a single cell for 140 yr and tuning one to four parameters to cause simulated biomass through time to match empirical biomass growth curves found in yield tables from various sources (e.g., Burns and Honkala 1990). Species for which no empirical growth curves exist were calibrated to the growth curve of a species with similar life form (e.g., conifer), competitive strategy (e.g., pioneer), and habitat preference (e.g., mesic soil). The main tuning parameter was foliar nitrogen because it is the main determinant of photosynthetic capacity in the model. Other tuning parameters were used to keep foliar nitrogen and leaf area within empirical limits, including SLWMax (maximum specific leaf weight) and FracFol (determines amount of foliar biomass relative to active woody biomass; Appendix S2: Table S4).

Although chestnut has not been scientifically studied as a dominant component of forest ecosystems, individual chestnut trees and stands have been studied, allowing most of the PnET-Succession parameters for this species to be empirically estimated. Jacobs et al. (2009) observed remarkable growth rates of chestnut, with trees consistently reaching diameter at breast height increments >1.5 cm/yr over at least the first two decades of development. De Bruijn et al. (2014*a*) predicted that in a hypothetic monoculture, American chestnut could maintain an annual increment of 5–7 m^3/ha for 200 yr or more. The generic parameters used for all other species were also assigned to chestnut. Based on published information (e.g., McCament and McCarthy 2005, Wang et al. 2006, Brown et al. 2014), we assigned chestnut to the moderately shade-tolerant class and the somewhat drought-intolerant class. Optimum and minimum temperatures for photosynthesis were estimated based on the extent of its former range with criteria used to establish those parameters for the other species (Gustafson et al. 2016). SLWMax was tuned to produce a leaf area index comparable to other moderately shade-tolerant species.

Based on recent and historic observations (Jacobs et al. 2009 and citations therein), chestnut growth was then calibrated by tuning FolN to achieve a growth rate between that of shade-tolerant basswood (*Tilia americana*) and shade-intolerant tulip poplar (*Liriodendron tulipifera*), which are among the fastest growing species in the region. Dispersal distance (Appendix S2: Table S1) was estimated using literature and field observations (Paillet and Rutter 1989, Steele et al. 2005, Lichti et al. 2014, Blythe et al. 2015), selecting values on the long side of the uncertainty to avoid biasing our results against the passive dispersal treatment.

We evaluated the calibration of all species by comparing initial biomass projected by the model (spin-up) with continuous forest inventory (CFI) data collected on the GRSF. Although confidence intervals for the inventory data are wide, the relative abundance of all species is generally consistent between inventory measurements and spin-up projections (Appendix S2: Fig. S1). Establishment rates were calibrated by modifying (in unison) the two establishment modifier parameters that control the sensitivity of establishment to available light and water to maintain an approximately steady number of cohorts under the Current Harvest, Existing pests scenario. We verified decomposition rates by comparing simulated woody debris to empirical measures in northern hardwood forests (Harmon et al. 1986).

Disturbance extensions

Forest management practices, including harvest, prescribed burning, and planting (including chestnut), were simulated using the Biomass Harvest v3.0 extension (Gustafson et al. 2000, Scheller and Domingo 2015), which simulates species-specific removal of cohort biomass caused by forest management activities. Harvest prescriptions are applied to individual stands using prescription-specific stand ranking algorithms based on stand conditions (e.g., species and age composition) within specific management zones (e.g., ownership). Each prescription specifies how much biomass is removed from which cohorts of each species, and can optionally cause new cohorts to be established to mimic planting. Pest outbreaks were simulated using two different extensions. For GM and FTC, we used the Biomass Insects extension (v2.0; Foster 2011, Foster and Scheller 2013) that simulates landscape-level defoliation events and their cumulative effects on forest biomass growth and mortality. Temporal patterns of defoliator outbreaks are characterized as quasi-cyclic with variability in outbreak and non-outbreak periods. Spatiotemporal defoliation patterns within outbreaks are stochastically defined as a combined function of tree host patterns and the previous year's defoliation intensity designed to mimic defoliation patterns observed using remote sensing (e.g., aerial surveys, satellite imagery). Species-specific empirical relationships between cumulative annual defoliation and biomass growth reduction and mortality determine the impact of the defoliation disturbance on tree species cohorts (J. Foster, *unpublished manuscript*). For the remaining insects (HWA, EAB, ALB), we used the simpler Biological Disturbance Agent (BDA) extension (v 3.0; Sturtevant et al. 2004, 2015). Analogous to Biomass Insects, the BDA extension applies a predefined temporal outbreak pattern that can range from periodic to random to chronic. During outbreak years, the BDA extension uses host dominance within a cell and in its neighborhood to compute the probability that a cell will be attacked by a given pest, which may be optionally constrained in space by the dispersal distance of the disturbance agent. The disturbance probability score defines the intensity class that determines the likelihood of complete mortality of tree species cohorts using a susceptibility look-up table based on tree species and age. More details on these insect disturbance extensions are provided in Appendix S1, and all model input files are in Data S1.

Simulation input maps

The landscape was gridded to a cell size of 30 m and individual cells were assigned to landtypes based on soils and slope. Landtypes are spatial zones that are relatively homogeneous in terms of climate (temperature and precipitation), soil conditions (soil texture, slope, and aspect), growing conditions, and disturbance regimes. Landtype boundaries were derived from state SSURGO map unit polygons (NRCS 2013) based on soil texture classes, soil depth, and slope for each soil unit. Because of the high relief in this region, there were hundreds of combinations of soil texture, depth, and slope in the study area. We reduced the number of potential landtypes in

the study area by binning the slope and soil depth values into five quantiles each, and used the median values within each bin to assign PnET-Succession parameters. Median slope ranged from 6% to 55%, and the surface runoff parameter (PrecLossFrac) was scaled from 0% to 15% across this range. The soil texture class for each cell in a landtype was assigned based on the most abundant soil in the corresponding SSURGO polygon, and rooting depth was assigned based on median soil depth, ranging from 43 to 100 cm. This resulted in 133 distinct landtypes.

All landtypes were given the same climate, which in PnET-Succession requires inputs of monthly minimum and maximum temperature, precipitation, photosynthetically active radiation (PAR), and atmospheric CO_2 concentration. Historical weather data (including PAR) for 900 km^2 of the Ridge and Valley Province surrounding the GRSF were subset from the Daymet Daily surface weather 1-km grid for North America, 1980–2012 (Thornton et al. 2012). Because weather variability can have an important effect on competitive interactions through time, we constructed a weather stream that repeatedly applied the last 35 yr (1980–2014) of the historical weather stream for the 200 yr of all simulations. To avoid confounding the experiment, atmospheric CO_2 concentration was held constant at 390 ppm, the average measured at Mauna Loa Observatory, Hawaii, in 2010.

Maps of the initial conditions for the species and age cohorts present on each cell were generated from several complementary sources: 435 CFI plots measured in 1999 and 2000, age estimates from tree-ring counts collected on 183 CFI plots, maps of forest stands harvested 1960–2000, and updates to a detailed satellite image classification derived from Hyperspectral AVIRIS imagery (Foster and Townsend 2004, Foster 2011). Species cohorts observed in individual CFI plots were randomly imputed to grid cells based on class membership in the satellite forest community maps. Cohort ages were assigned from tree-rings sampled on up to three trees per plot by grouping species into dbh terciles and assigning the oldest age to the largest size-class and the youngest age to the smallest size-class. Ages were estimated for trees on the remaining CFI plots by predicting age from dbh and grouping predicted plot-level age distributions into terciles to represent age cohorts. The model computes the initial biomass for each cohort by simulating growth from the time of cohort establishment (determined by age) to the start year of simulations (i.e., 2000); this process is known as "spin-up."

The Biomass Harvest extension requires input maps of stand boundaries and management zones. Such maps were available for the state forest, but not for private land. The timberland survey (Butler 2008) for Maryland indicates that timber harvest activities do not occur on about 40% of privately owned forestland, and within the state forest, about 40% of the land has reduced rates of harvest to support objectives other than forest products. To create generic stand maps of the land surrounding the state forest, we generated a regular grid of square, 9-ha stands across the study area and superimposed the stand map of the state forest on them. Forty percent of all stands outside the timber production zones of the state forest were randomly assigned to the "unmanaged" management area and the remainder to a "managed" management area. Area harvested by the model was calibrated to match harvest rates specified in the GRSF management plan (MDNR-FS 2011).

Factorial experiment

We conducted a factorial simulation experiment to quantify the relative effects of two causal factors (pest outbreaks and chestnut restoration, each with three levels) on forest composition and carbon sequestration. Six replicates of each factorial combination were simulated for 200 yr. The "None" pest outbreak treatment had no insect outbreaks simulated, the "Existing" pest outbreak treatment included GM, HWA, FTC; and the "Imminent" outbreak pest treatment included the existing pests plus EAB and ALB. The chestnut restoration factor included a reference treatment (no chestnut restoration), in which only current forest management activities (business as usual; BAU) were simulated. All treatment combinations included the BAU activities, plus the treatment activities. To implement BAU, we used the harvest prescriptions developed by Foster (2011) for the GRSF based on the forest management plan (MDNR-FS 2011) that actively uses thinning, shelterwood cutting, and prescribed burning to enhance oak regeneration (Appendix S1). Prescribed burning in the oak emphasis prescriptions

was mimicked by including the removal of cohorts that would be killed by prescribed burning according to their age and susceptibility to fire. On sites not optimal for oak management, other prescriptions favor white pine (*Pinus strobus*), shade-intolerant species, or other hardwoods, designed to enhance diversity. The no chestnut restoration treatment is labeled as BAU henceforth. The "Passive" chestnut restoration treatment did not use widespread and continued planting, but a central north–south transect of single cells at 500-m intervals was initialized with a 20-yr-old chestnut cohort to represent a hypothetical short-term restoration effort, and unaided dispersal of chestnut was simulated from those sites. The aggressive chestnut restoration treatment also included the BAU prescriptions, with the exception that a cohort of chestnut was established (ostensibly by planting, although the model simply establishes a cohort without mechanistically simulating planting) after certain harvest activities (locust salvage and variable retention clearcut), with up to 2.5% of the study area planted per decade. Aggressive chestnut restoration by planting was simulated for 100 yr, and then, only natural regeneration was simulated for the final 100 yr. The purpose of this treatment was to simulate a best-case, possibly feasible scenario for chestnut restoration for comparison with the Passive chestnut scenario. We assumed that forest management tactics on private and other public lands are generally similar to those practiced on the state forest, and we applied the same timber harvest prescriptions to "managed" management zones both within and outside the state forest. Chestnut was never targeted for harvest, but when it was present in stands being harvested, it was harvested using similar rules as for other species, with minimum age for cutting set at 80 yr for thinning and 100 yr otherwise.

Analysis

For the purposes of our study, we selected the following response variables, which were monitored as landscape-level averages over all forested cells: area occupied by chestnut; total biomass of six species groups (Table 1); total of the living and dead biomass pools and their combined values; species and age-class diversity. Plots showing the effect of all factors through time for each response variable were produced to allow visualization of trends and their uncertainty in comparison with a reference condition (BAU-Existing).

Ideally, stochastic simulation studies should generate enough replicates that the distributions of outcomes can be compared directly across treatments (White et al. 2014). However, complex models such as LANDIS-II require long run times so that generating hundreds of replicates is impractical. We therefore used an approach similar to statistical emulation (Oakley and O'Hagan 2004) to compare treatment responses. Specifically, a Bayesian model was fit to each of the species groups in Table 1, as well as the dead woody and litter biomass variables, yielding 2000 predicted time-series for each response variable under each treatment scenario (details in Appendix S1). Our inferences are based on direct comparisons of the predictive distributions among scenarios. This methodology allowed us to obtain a reasonable estimate of simulation uncertainty from a small fraction of the number of replicates required for full simulation-based inference.

Results

Efficacy of American chestnut restoration

The area occupied by chestnut increased very slowly under the Passive restoration treatment

Table 1. Assignment of species to species groups.

Species group	Species
Maples	*Acer rubrum, Acer saccharum*
Oaks	*Quercus alba, Quercus coccinea, Quercus prinus, Quercus rubra, Quercus velutina*
Pines	*Pinus echinata, Pinus pungens, Pinus rigida, Pinus virginiana, Pinus strobus*
Pioneers	*Juglans nigra, Liriodendron tulipifera, Fraxinus americana, Magnolia acuminata, Prunus serotina, Robinia pseudoacacia, Sassafras albidum*
Late seral	*Carya glabra, Nyssa sylvatica, Tilia americana, Ulmus americana, Tsuga canadensis*
Chestnut	*Castanea dentata*

(Fig. 2), and although the mean overall biomass of chestnut on the landscape under Passive restoration did appear to increase exponentially (Fig. 3, Appendix S2: Fig. S10), the species would probably take a millennium or more to fully occupy the landscape at the simulated rate of expansion (Fig. 4). Both the area occupied by chestnut and its biomass expanded much more rapidly under the Aggressive restoration treatment (Figs. 3, 4), achieving an average biomass >2 kg/m^2 by year 100 in most cases (this level is similar to the average biomass of maples at year 0). However, the area occupied by chestnut on the landscape increased slowly after the cessation of planting at year 100 (Fig. 4). Prior to year 50, the area occupied by chestnut increased at a similar, rapid rate in all three Aggressive scenarios. However, the Aggressive-None treatment yielded a greatest area of occupation by chestnut through the period from 50 to 150 yr (Fig. 4), but at the end of 200 yr, the area occupied by chestnut was highest under the Aggressive-Imminent scenario.

The interaction between chestnut restoration treatments and pest outbreaks also affected chestnut restoration success (Fig. 3). Under the Aggressive restoration treatment, there were no discernable differences in chestnut biomass under the Existing and Imminent pest treatments. On average, biomass under the No pests treatment was greater than under the other two treatments, but the effect peaked near year 150 and appeared to be declining by the end of the simulated timeline. In contrast, biomass under Passive management expanded at its slowest rate under No pests, and the rate under the Imminent treatment was marginally faster than under the Existing treatment.

Other compositional changes

At present, oaks represent the largest species group in the study area by biomass, with a total average biomass of approximately 15 kg/m^2 at year 0. Pines are the second most abundant group (3 kg/m^2), followed by maples (1.9 kg/m^2), late seral species (1.8 kg/m^2), and pioneers (1 kg/m^2). Although uncertainties are large, oaks show a steady, approximately linear decline in biomass over 200 yr under the current disturbance regime (Fig. 5F). Pines show an even more precipitous decline, and late seral species also decline, but

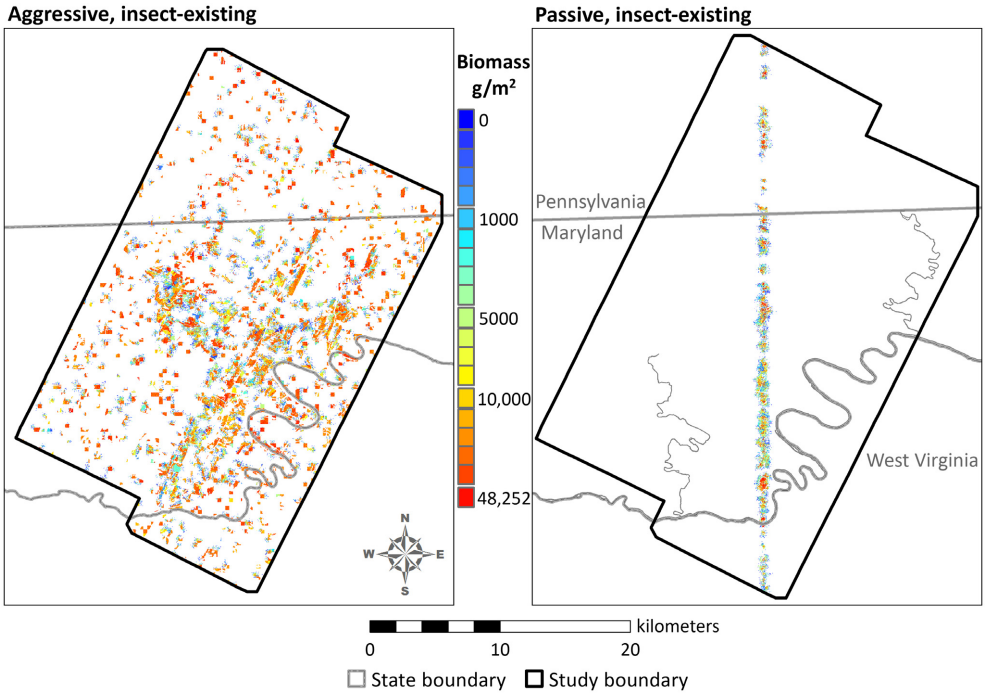


Fig. 2. Spatial distribution of chestnut biomass at year 200 under the Aggressive-Existing and Passive-Existing scenario.

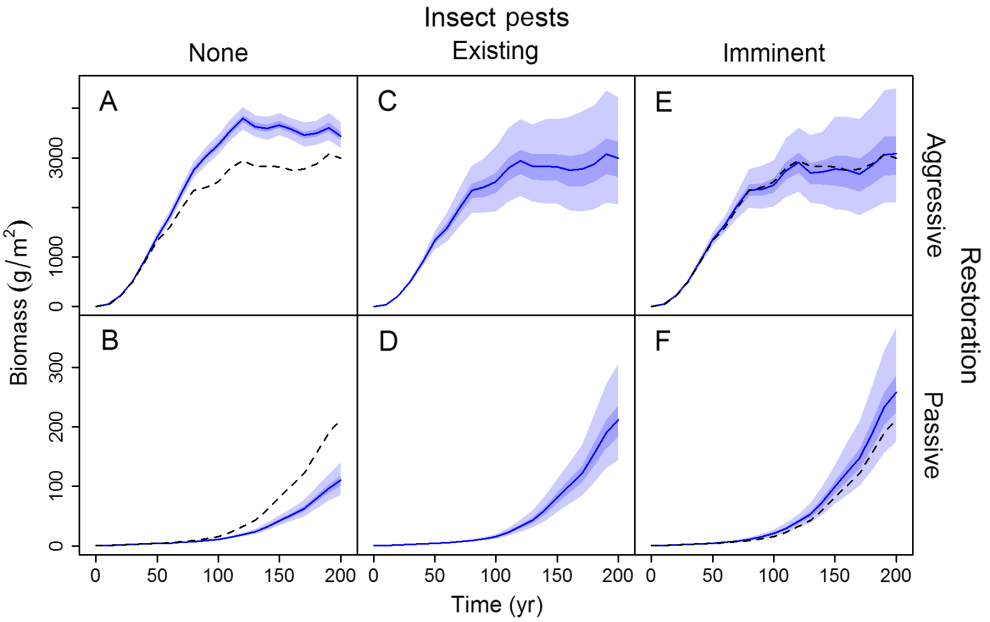


Fig. 3. Average live biomass (wood and roots) of chestnut by chestnut restoration and insect pest treatment. Solid lines show mean trends over time, and shaded areas show 95% and 50% prediction intervals. The dashed line shows the trend for the Existing Insects scenarios to enhance comparisons within each restoration treatment. Note difference in scale between upper and lower panels.

at a more moderate rate than oaks or pines (Fig. 5G). In contrast, maples expand rapidly under the current disturbance regime Fig. 5I). Pioneer species decline slightly initially, but begin to increase around year 100, likely related to age-related senescence and regeneration of existing stocks (Fig. 5J).

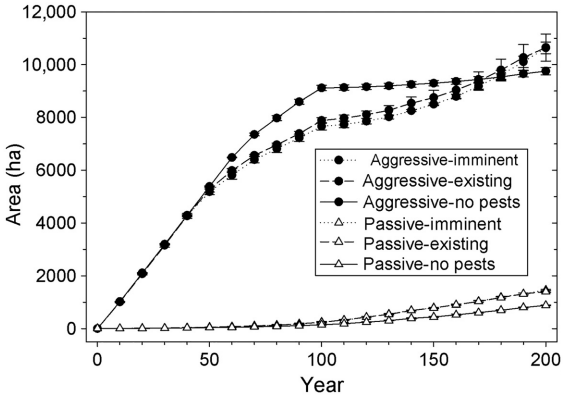


Fig. 4. Area occupied by chestnut through time by chestnut restoration treatment combination. Total forested area in the study area = 52,881 ha. Error bars show one standard deviation.

The pest outbreaks treatments substantially affected compositional trends. On average, oaks and late seral species (Appendix S2: Figs. S2, S3) fared best under the Imminent pests treatment and the Existing pests treatment resulted in slightly less biomass than the No pests treatment. These results were reversed for pines, which fared best under the No pests treatment—due almost exclusively to the steady persistence of white pine under this treatment—and the Existing pests treatment resulted in slightly less biomass than the Imminent pests treatment (Appendix S2: Fig. S4). These differences, with the exception of white pine, corresponded primarily with changes in the trajectory of maple biomass. Under the current disturbance regime, maples increased steadily, but the increase was somewhat less with No pests and much less under Imminent pests, with red maple increasing to three times the biomass of sugar maple (Appendix S2: Fig. S5). Relative to the current disturbance regime scenario, the pioneer species ultimately increased under Imminent pests and declined with No pests (Appendix S2: Fig. S6).

The chestnut restoration treatments had little effect on oaks, contrary to our expectation

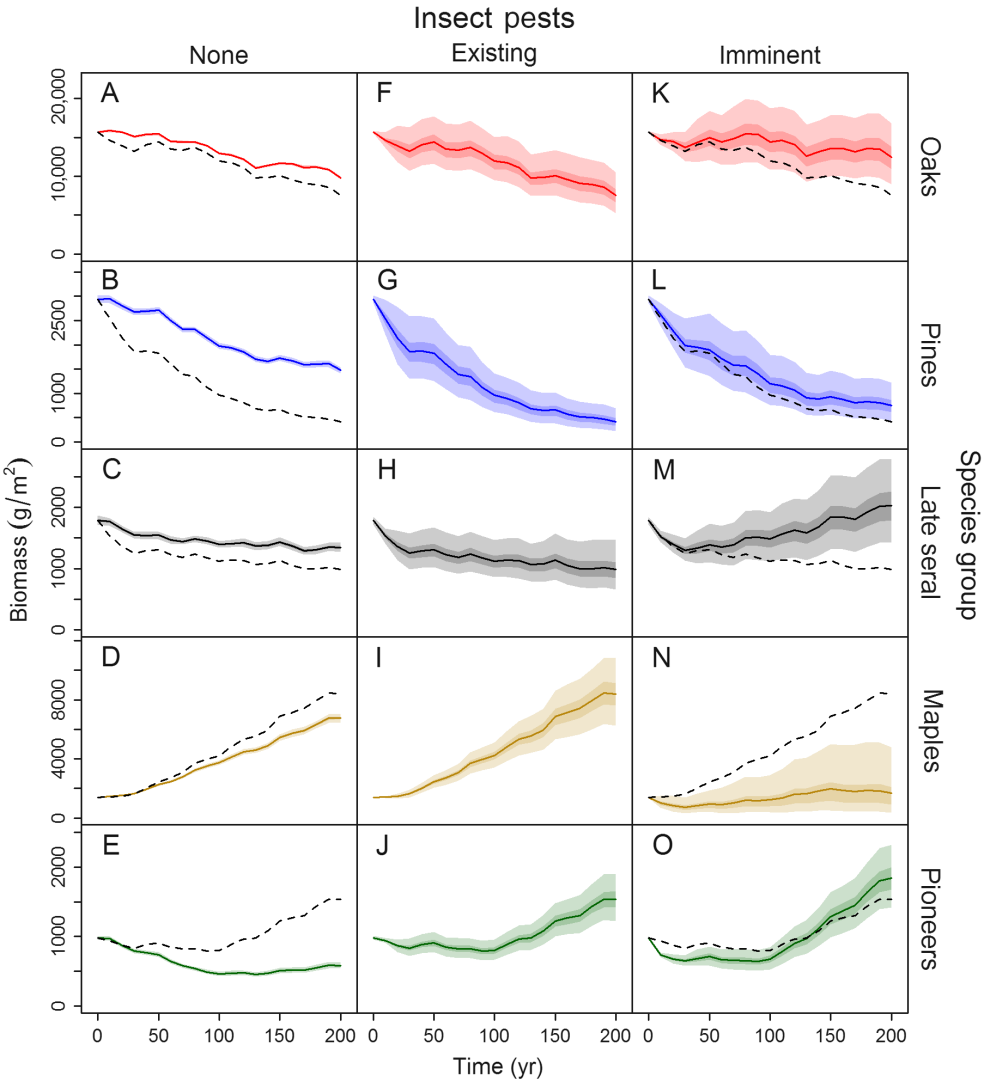


Fig. 5. Effect of pest outbreak treatments on the average live biomass (wood and roots) of species groups under the business as usual (no chestnut restoration) scenario. Solid lines show mean trends over time, and shaded areas show 95% and 50% prediction intervals. The center panels show a reference condition, and the dashed line shows the trend for the reference condition to enhance comparisons within each restoration treatment. Note the different scales for each group. Species membership are shown in Table 1.

(Appendix S2: Fig. S2). Pines and late seral species (Appendix S2: Figs. S3, S4) were also largely unaffected. In contrast, maples and pioneers were affected by interactions between chestnut restoration and pests. Maple biomass in the No pests and Existing pests scenarios increased less rapidly under Aggressive restoration than Passive or no restoration (Appendix S2: Fig. S5), while late rebound in biomass of pioneer species was less dramatic under Aggressive restoration, particularly under the Existing and Imminent treatments (Appendix S2: Fig. S6). Overall, chestnut restoration had a somewhat larger effect on compositional diversity than pest outbreaks did, although the Aggressive restoration treatment produced the lowest average species diversity (Fig. 6A), but the highest age-class diversity (Fig. 6B). An increased number of pests reduced both species diversity (Fig. 6A) and age-class diversity (Fig. 6B) across restoration scenarios.

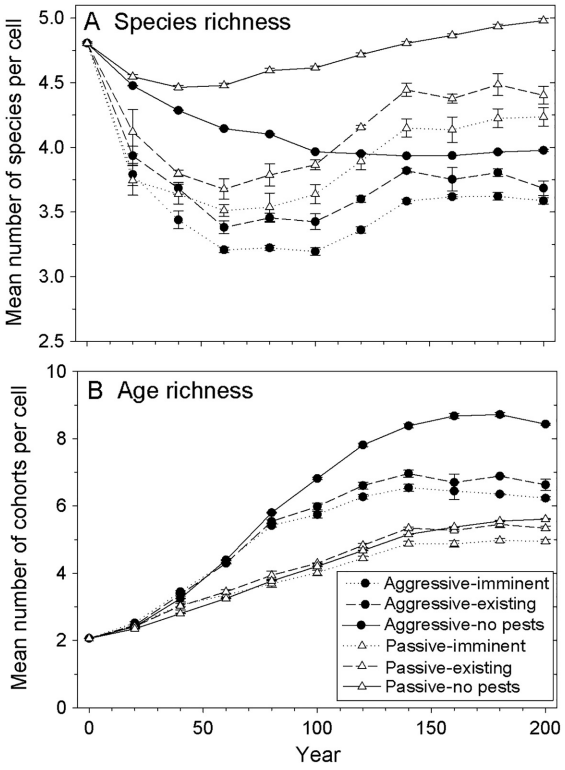


Fig. 6. Indices of diversity (richness) by chestnut restoration treatment combination. Business as usual (no chestnut restoration) is very similar to Passive and is not shown for clarity. Error bars show one standard deviation.

Carbon dynamics

Under the reference BAU-Existing pests scenario, average total biomass remained relatively constant through time, varying according to episodic pest outbreaks (Fig. 7, Appendix S2: Fig. S7). The average value increased slightly over time, but this trend was negligible relative to model uncertainty. Neither chestnut restoration nor pest outbreak treatments had a substantial effect on total biomass. The total biomass (live wood and roots, dead wood and litter) was greatest with No pests and similar between the Existing and Imminent pests treatments (Fig. 7). However, the Aggressive restoration treatment resulted in slightly higher average total biomass regardless of pest treatment. In the reference scenario (BAU-Existing), the accumulation of biomass of woody debris equilibrated at approximately 3.2 kg/m^2 (Fig. 8). The pest outbreaks treatments had a non-trivial effect on woody debris biomass relative to the uncertainty, and the effect of the Aggressive restoration treatment was even greater (Appendix S2: Figs. S7, S8, S9). After 100 yr, the differences in dead biomass between the Aggressive scenarios and the reference scenario were relatively constant, indicating that Aggressive chestnut restoration increased the steady-state stock of downed wood, as would be expected given its low decay rate.

Discussion

The ability of forested landscapes to sequester and store carbon is contingent on the proportion of the landscape that is allocated to forest vs. other land uses (Drummond and Loveland 2010), and secondarily on the developmental stages of the forest stands in that landscape (Xu et al. 2016). Our simulation study addressed a potential third source of variation in carbon dynamics, differences caused by tree community composition and corresponding variations in growth tissue decay rates, as well as species- or genus-specific susceptibility to both native and invasive insect pests. Although differences in carbon storage have previously been noted between coarse forest types (e.g., hardwood vs. coniferous forests in the United States; Birdsey et al. 1993), we specifically examined the potential consequences of management actions aimed at restoring a single species (American chestnut) that was extirpated by an epidemic disease, and did so in the context of both existing and imminent insect pests.

Contextual dynamics

Restoration of a forest tree species does not take place in a vacuum, but in the context of established competitors and their relative resilience to the dominant disturbances. The study area represents a dry region of the broader central Appalachian hardwoods, which has higher tree species diversity relative to many temperate systems (Flower and Gonzalez-Meler 2015), but is also currently dominated by a single genus (*Quercus*). As observed across the region, our simulations suggest a general decline in oak (Hanberry and Nowacki 2016), and increasing dominance by maples, primarily red maple (Abrams 1998). Decreasing oak trends are due to the cumulative effects of lack of fire, increasing understory shading (Nowacki and Abrams 2008), and an aging oak population established

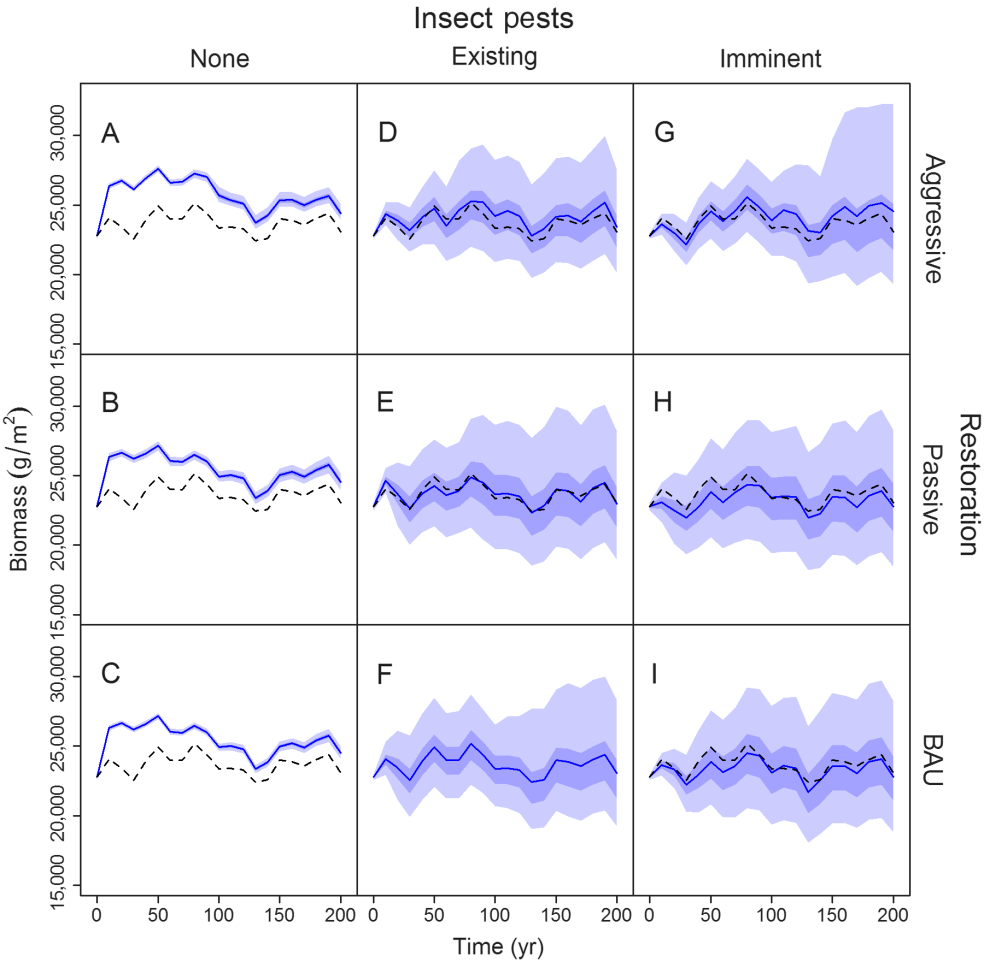


Fig. 7. Total average biomass (live wood and roots, dead wood, and litter of all species) by chestnut restoration and insect pest treatment. Solid lines show mean trends over time, and shaded areas show 95% and 50% prediction intervals. The dashed line shows the trend for the business as usual (BAU)-Existing Insects scenario to enhance comparisons.

by timber exploitation, and we show that these trends can be exacerbated by the susceptibility of oak to periodic growth reduction and partial mortality of oaks by both native and nonnative defoliators (Appendix S2: Fig. S2). We found that pioneer hardwood species have enough dispersal capacity to maintain themselves within the mix of forest types at harvest rates under BAU, and their abundance was generally enhanced by insect disturbances (Appendix S2: Fig. S6). By contrast, "yellow" pines (*Pinus echinata, Pinus pungens, Pinus rigida, Pinus virginiana*), also considered pioneer species, decline to near extinction under all treatments reflecting their inability to persist under the simulated disturbance rates (Appendix S2: Fig. S4). However, simulated trends for the more shade-tolerant white pine (*P. strobus*) suggest it could maintain its current abundance if it were not for the "spill-over" (sensu White and Whitham 2000) of late-instar GM larvae from oaks to pine (Davidson et al. 1999) that may also restrict the ability of yellow pines to take advantage of space opened by defoliation disturbance (Appendix S2: Fig. S4). Species richness is somewhat reduced by aggressive chestnut restoration because it biases regeneration toward a single species (chestnut), while age richness is greatly increased by the introduction of a new, long-lived species to a large number of cells across the landscape (Fig. 6).

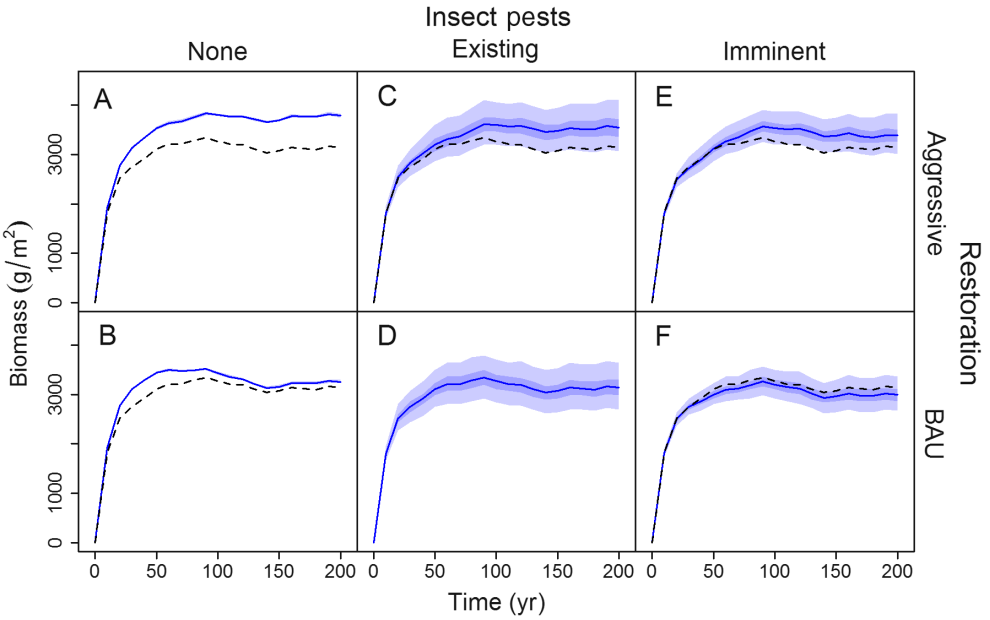


Fig. 8. Total average woody debris (coarse and fine) biomass by chestnut restoration and insect pest treatment. Solid lines show mean trends over time, and shaded areas show 95% and 50% prediction intervals. The dashed line shows the trend for the business as usual (BAU)-Existing Insects scenario to enhance comparisons. Only biomass accumulated from year 0 is included in plots.

We note that our results show a more modest increase in total biomass in the next 50 yr (Fig. 7) than appears to be underway in the region (Lichstein et al. 2009) and might be expected from a forest with the age structure of GRSF. We cannot be certain of the precise interacting causes of this result, but the transition of the forest from primarily oak and pine to maples and other hardwood species has also been reported elsewhere in the region (Abrams 1998, Hanberry and Nowacki 2016) and likely contributed to observed trends (Fig. 5). Although the average age of sites in the study area at the start of simulations is about 70 yr, there are many sites with cohorts old enough for senescence and succession to develop in early time steps. The area harvested under all restoration scenarios is 5.4% of the study area per decade, which removes biomass that requires decades to recover. There is considerable uncertainty and variability surrounding harvest rates, and we used a fixed rate on the high side to produce our Aggressive restoration scenario. It is also possible that the assumed decline of photosynthesis in old cohorts (Bond 2000) is exacerbated by increased physiological stress induced by the relatively xeric nature of this landscape, even for oak and pine (Pedersen 1998).

Realized impacts by invasive pests depend on the susceptibility of their respective hosts, and the relative dominance of those hosts within the ecosystem. In the case of HWA and EAB, the hosts are very susceptible, but are minor components of the study landscape. Impacts consequently are projected to be limited in extent, although localized impacts (e.g., flood plains, stream corridors, "cove" forest stands.; Ellison et al. 2005) may still be important. By contrast, ALB effectively restricted a genus (*Acer*) to the subcanopy that was otherwise projected to become codominant with oaks (Appendix S2: Fig. S5). The timing of the arrival of ALB was apparently important. Despite abrupt impacts to naïve hosts, total forest biomass was virtually unchanged by ALB because maples had not yet achieved codominance and non-susceptible competitors were able to fill the released growing space. By contrast, GM and FTC defoliation impacts were diffuse and far less severe, but because they impacted the dominant genus (*Quercus*) they had a measurable influence on

total forest biomass relative to the no insect treatment (Appendix S2: Fig. S7). Our results for chestnut reintroduction scenarios are therefore best understood within the broader context of the dominant dynamics of the study landscape.

Chestnut restoration and carbon dynamics

Although chestnut is fast-growing, fairly shade-tolerant, and decomposes slowly, our results do not support the hypothesis that it may substantially increase carbon storage in eastern U.S. forests. Our Aggressive restoration treatment was designed to approximate a best-case restoration scenario, and while it may have restored chestnut to something near its former dominance in 100 yr, the carbon implications were modest. Both pest outbreaks and chestnut restoration had some effect on forest composition, but neither factor had a substantial effect on the overall biomass associated with trees in our study system. Even under a worst-case scenario for pest outbreaks and a best-case scenario for chestnut, live biomass was barely affected. However, our simulations did show that Aggressive chestnut restoration can lead to a positive shift in the predicted biomass distribution of woody debris stocks, most likely due to the fact that chestnut wood decays at an unusually slow rate (De Bruijn et al. 2014*a*). To the extent that dead wood is relatively resistant to disturbance (other than fire), locking carbon into slow-decaying woody tissues may have a positive effect on the length of carbon storage, even if it does not affect the total mass of stored carbon.

There are other important reasons to restore chestnut. While the existing ecosystem appears resilient to current and imminent forest health threats, tree species diversity should remain an important regional goal to enhance long-term system resilience to global changes affecting forests (Reyer et al. 2015). In addition, harvesting of chestnut will produce valuable, decay-resistant timber (Youngs 2000) that will allow for storage of carbon in the form of wood products. Chestnut restoration provides potential additional benefits, such as a more consistent and quality food source for wildlife compared to common associates (Dalgleish and Swihart 2012) and altered ecosystem function through its influence on productivity, decomposition, and nutrient cycling (Ellison et al. 2005).

Interactions between chestnut restoration, pest outbreaks, and timber harvest

Our Aggressive restoration treatment was designed to approximate a best-case scenario in which agencies and societal stakeholders fully commit to restoration without sacrificing other desired species such as oak. Under these circumstances, chestnut became a significant and stable component of the forest within a century. These results are encouraging; however, our simulations did not include potential mortality or pathology due to blight. Of the blight-resistant cultivars currently under development, the backcross hybrids are expected to remain susceptible to the disease but suffer reduced morbidity (Jacobs et al. 2013, Steiner et al. 2017), while transgenic cultivars may experience substantial societal resistance to widespread planting. Lower-than-expected levels of blight resistance in cultivars used for restoration (e.g., due to pathogen mutagenicity) may lead to declines in restored populations that were not observed in our model.

In addition to the continuing challenge of blight, the area targeted for reintroduction of chestnut covers nearly four million ha and largely overlaps the regions potentially affected by GM, HWA, and EAB. The susceptibility of American chestnut to common insect pests in eastern United States is unclear (Oliver and Mannion 2001, Rieske et al. 2003). Chestnut restoration may be impacted by GM and ambrosia beetles (*Xylosandrus crassiusulus* Mot. and *Xylosandrus saxeseni* Blandford). The oriental gall wasp (*Dryocosmus kuriphilus* Yasumatsu) also forms galls on actively growing chestnut shoots, which may lead to severe damage or mortality (Anagnostakis 2001). While insect pests may thus limit chestnut's influence on carbon cycling in contemporary and future forests, the ability of chestnut to spread and become re-established in forest stands may ultimately be determined by the susceptibility of its competitors to pests.

Our simulations allowed timber harvest to reduce chestnut biomass, but the colonization of the landscape by chestnut was largely unaffected by harvest because chestnut begins reproducing by 8–20 yr of age and cohorts younger than 80 yr were never removed from stands (Paillet and Rutter 1989). Chestnut biomass removed from the landscape reached as high as 10^6 Mg per decade, so its removal was not inconsequential. As with

the harvesting of any species, harvest of mature cohorts of chestnut reduced standing biomass, but the growth rates of regenerating cohorts (including chestnut) were higher than the older cohorts they replaced. Although we could have assessed the sequestration potential of never harvesting chestnut, we assumed that the economics of forest management are most likely to preclude leaving mature chestnut unharvested even in a future when sequestration as an ecosystem service may have increasing economic value. Other studies have evaluated the optimal harvesting strategy to maximize carbon sequestration (Englin and Callaway 1995, van Kooten et al. 1995, Gutrich and Howarth 2007), concluding that managing for larger carbon stocks lengthens rotation ages compared to managing to maximize timber revenues. Rotation ages increase further as the value of carbon mitigation increases, though there are likely benefits to periodic partial harvesting following mid-rotation (Gutrich and Howarth 2007); such findings would also apply to chestnut.

Biological and model uncertainties

Given American chestnut's century-long absence from contemporary forest canopies, its ecology is subject to considerable uncertainty. To address this biological uncertainty, our modeling approach relied heavily on first principles of tree physiology and biophysics. The life history and physiological traits of individual chestnut trees have been intensively studied as of late (reviewed by Jacobs et al. 2013), and our mechanistic approach allowed us to estimate most model parameters for American chestnut although with less confidence as for other species. In general, mechanistic approaches also provide the most robust way to model systems under novel conditions (such as restoration of a long-extirpated species) that fall outside the domain in which empirical or phenomenological models were developed (Rastetter et al. 2003, Gustafson 2013). Consequently, we have a relatively high level of confidence that our simulations are accurate within the context of the modeled scenarios and represent the best achievable visualization of potential chestnut growth and competitiveness in the modeled system. That said, our results should not be interpreted as a forecast because the model necessarily neglected many factors that could potentially affect both chestnut restoration and forest carbon dynamics. In addition, our assumption that the future disturbance regime will be similar to our best representations of recent disturbance regimes, such as insect outbreaks, may over- or underestimate potential patterns of species mortality that could release growing space for chestnut restoration. In particular, mortality patterns of species and age classes resulting from highly novel ALB are based on very limited data (Dodds and Orwig 2011), and susceptibility of American chestnut to this insect is simply not known. Insects were the major drivers of large biomass changes in our results, which means that uncertainty in future insect disturbance regimes produces great uncertainty in projections of future carbon storage. There are other introduced insect species known to feed on chestnut species (e.g., Case et al. 2016), but it is not clear how impacts that today can only be quantified locally will scale up to landscapes once chestnut is restored to its historic abundance. Finally, we acknowledge that *P. cinnamomi* represents a major impediment to chestnut restoration that may require additional breeding to overcome (Steiner et al. 2017).

Although mechanistic approaches allow us to simulate the behavior of ecological systems under novel circumstances, this flexibility is computationally expensive. As a result, it is often not feasible to run the large numbers of replicate simulations required to fully visualize model-derived uncertainty (i.e., variability in the outputs either due to uncertainty in input parameters or due to stochastic processes within the model itself). We used statistical emulation of stochastic variation to estimate posterior predictive distributions for the outputs. Statistical emulation has more typically been used to address parameter uncertainty in fully deterministic models (Oakley and O'Hagan 2004). We did not attempt this in our analysis because of the large number of parameters in LANDIS-II and the time required to complete each replicate. In principle, parameter uncertainty could be addressed in concert with stochastic variation by running a larger number of replicate simulations, each with a different parameter set selected either randomly from a joint distribution or according to a Latin hypercube design (Helton and Davis 2003). Our six replicates provided enough data to estimate heteroskedastic variation over time and treatments, but did not allow us to also estimate

reliable correlations among the response variables or to detect bifurcations, alternative stable states, or related phenomena that could theoretically arise in a complex dynamic system.

Other assumptions and caveats

Several assumptions and caveats should be kept in mind when interpreting our results. For instance, our results may be limited to the Ridge and Valley physiographic province of western Maryland or similar areas where soils are somewhat xeric and rainfall is limited. Furthermore, our study did not consider the effects of the global changes of climate and CO_2 fertilization. We have another study underway that addresses the effect of climate change on chestnut restoration in both the Ridge and Valley Province and the more mesic Appalachian Plateau, which together include more than half of the former range of American chestnut. Nevertheless, we believe that our study provides a robust initial look at the question of the sequestration potential of chestnut restoration at landscape scales without the confounding effects of multiple global changes and major site differences.

Management and policy implications

Our results suggest that, contrary to some assumptions, the process of recolonization by blight-resistant chestnut in existing forests may be a multi-generational process. More intensive silvicultural treatments, such as burning or aggressive harvesting, may be necessary to facilitate desirable rates of spread of blight-resistant chestnut following reintroduction. However, these treatments can be expensive and controversial, and may be impractical at large scales, especially on the public lands that represent a significant portion of the original native range of chestnut (Jacobs 2007). It is possible, however, that chestnut may spread and integrate into forests more quickly than suggested by our results. For example, Paillet and Rutter (1989) reported that 70 yr after the introduction of nine chestnut trees near West Salem, Wisconsin, chestnut had become an important canopy tree in adjacent oak–hickory woodlands and seedlings could be found >1 km from the founder trees. Chestnut seeds could occasionally be dispersed over several kilometers by blue jays (*Cyanocitta cristata*) (Johnson and Webb 1989), but the frequency with which such events might occur is unknown and is likely landscape-dependent, and therefore could not be modeled with any confidence. Similar constraints apply to oaks and some other species in the model. On the other hand, pollen records show that *Castanea* spp. spread substantially more slowly than did *Quercus* or *Fagus* spp. following the last glacial retreat (Johnson and Webb 1989), and Paillet and Rutter's (1989) results indicate that herbivory by white-tailed deer (*Odocoileus virginianus*) may pose a serious barrier to chestnut recruitment that was not accounted for in our simulations.

Conclusions

We draw four main conclusions from our study. (1) Chestnut cannot be restored in a short time frame and may require considerable effort and coordination at landscape scales. (2) It appears that chestnut restoration will not come at the expense of only a few species or genera, but modest declines will be experienced by most taxa. (3) Forests within the current system appear both growing space limited and diverse enough to be resilient to the principle disturbances at play, consistent with the predictions of Flower and Gonzalez-Meler (2015). (4) The enhanced growth rate and decay resistance of chestnut do not appear to markedly alter the carbon storage potential of eastern forests, although the uncertainty of future insect disturbance regimes makes this conclusion somewhat tentative. However, our results suggest that restoring chestnut to its former dominance is possible. Such restoration may have considerable value for wildlife, forest diversity and resilience, wood products and other ecosystem services, including carbon storage.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1773/full