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Forecasting effects of tree species reintroduction strategies on carbon stocks in a future without historical analog

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Abstract

American chestnut (*Castanea dentata*) was once an important component forests in the central Appalachians (USA), but it was functionally extirpated nearly a century ago. Attempts are underway to reintroduce blight-resistant chestnut to its former range, but it is uncertain how current forest composition, climate, and atmospheric changes and disturbance regimes will interact to determine future forest dynamics and ecosystem services. The combination of novel environmental conditions (e.g. climate change), a reintroduced tree species and new disturbance regimes (e.g. exotic insect pests, fire suppression) have no analog in the past that can be used to parameterize phenomenological models. We therefore used a mechanistic approach within the LANDIS-II forest landscape model that relies on physiological first principles to project forest dynamics as the outcome of competition of tree cohorts for light and water as a function of temperature, precipitation, CO_2 concentration, and life history traits. We conducted a factorial landscape simulation experiment to evaluate specific hypotheses about future forest dynamics in two study sites in the center of the former range of chestnut. Our results supported the hypotheses that climate change would favor chestnut because of its optimal temperature range and relative drought resistance, and that chestnut would be less competitive in the more mesic Appalachian Plateau province because competitors will be less stressed. The hypothesis that chestnut will increase carbon stocks was supported, although the increase was modest. Our results confirm that aggressive restoration is needed regardless of climate and soils, and that increased aggressiveness of chestnut restoration increased biomass accumulation. The hypothesis that chestnut restoration will increase both compositional and structural richness was not supported because chestnut displaced some species and age cohorts. Although chestnut restoration did not markedly enhance carbon stocks, our findings provide hope that this formerly important species can be successfully reintroduced and associated ecosystem services recovered.

KEYWORDS

American chestnut, *Castanea dentata*, central Appalachians, climate change, elevated CO_2, forest carbon stocks, forest succession, LANDIS-II, PnET-Succession

1 | INTRODUCTION

The world's forests provide a fundamental ecosystem service to humans through carbon sequestration and storage that help to mitigate anthropogenic carbon emissions (Pan et al., 2011), moderating the rate of climate change (IPCC, 2013). Forests play a major role in the global carbon budget because trees accumulate and store carbon over long life spans, functioning as large terrestrial carbon sinks (Dixon et al., 1994; Schimel, 1995). Changes in the global coverage of forestland, harvesting and regrowth are an important factor in determining carbon transfer between terrestrial ecosystems and the atmosphere (Houghton, 2005). Management that increases carbon stocks in forests, including those processes that affect tree community composition or tree growth and productivity, will have important implications for this carbon flux. As the climate warms or management practices change, there is concern that the influence of forest carbon stocks on the global carbon budget may be transitory, with forests becoming net emitters of CO_2 (Kurz et al., 2008; Lutz, Shugart, & White, 2013).

Anticipated climate and atmospheric changes have the potential to significantly modify the composition and dynamics of forested ecosystems by differentially impacting growth rates and competitive abilities of tree species and modifying disturbance regimes (Scheller & Mladenoff, 2008). Forest tree species composition has been shown to alter forest carbon stocks (Bunker et al., 2005; Gamfeldt et al., 2013; Hu, Su, Li, Li, & Ke, 2015; Kirby & Potvin, 2007) because tree species differ in rates of photosynthesis, biomass production, life span, and wood decay. Therefore, management activities that favor species with fast growth or slow decay have the potential to increase forest carbon stocks, but relatively little data exist to support this idea. Also, new tree species are being added to most ecosystems around the world by natural or human-assisted migration (Chapin, Danell, Elmqvist, Folke, & Fresco, 2007; Kirby & Potvin, 2007; Schuster et al., 2008) and by restoration of formerly abundant species (Gustafson, De Bruijn, et al., 2017), while other species or genera are at risk of extirpation by exotic insects or pathogens (Flower & Gonzalez-Meler, 2015; Liebhold, Macdonald, Bergdahl, & Mastro, 1995). These phenomena interact at local and landscape scales in complex ways to produce altered species assemblages and modified temporal ecosystem dynamics that have no contemporary analog, making long-term ecosystem services such as carbon storage difficult to predict.

American chestnut (*Castanea dentata*) was an abundant species (Ellison et al., 2005) in many eastern US forests prior to its functional extinction by an invasive fungal pathogen, the chestnut blight (*Cryphonectria parasitica*). Blight-resistant American chestnut progeny have been produced using backcross hybridization (4% Chinese chestnut, e.g. Diskin, Steinera, & Hebard, 2006) and transgenic techniques (inserting wheat genes, e.g. Zhang et al., 2013). Efforts led by The American Chestnut Foundation and others are seeking to re-introduce this hybrid chestnut throughout its former range to restore its ecological and commercial values. The goal of reintroducing American chestnut to its former range (e.g. Clark et al., 2014) necessitates a prediction of the likely ecological outcomes of introducing a novel (yet formerly occurring) species into an established ecosystem. This requires assessment of (a) how the success of alternative chestnut restoration strategies may be impacted by disturbances and a changing climate and (b) how successful restoration of chestnut might impact carbon stocks. Because American chestnut is fast-growing, long-lived, and has high wood density that is resistant to decay (De Bruijn et al., 2014; Ellison et al., 2005; Youngs, 2000), its re-establishment could significantly enhance carbon stocks within its re-established range.

Gustafson, De Bruijn, et al. (2017) used a mechanistic landscape model based on first principles to investigate the impacts on carbon stocks of chestnut reintroduction within the Ridge and Valley physiographic province of Western Maryland (USA) under historical climate and contemporary disturbance regimes, including both current and impending insect pests, and forest management practices of multiple owners. They found that while restored chestnut successfully competed for growing space under an aggressive restoration strategy (i.e. planting chestnut after certain harvesting activities landscape-wide), it only moderately enhanced carbon stocks of forests in that system. However, it is unclear whether the competitive interactions of chestnut with the comparatively xeric communities in the Ridge and Valley province can be generalized to forests in more mesic physiographic regions within the former American chestnut range, or whether those interactions will be further modified by interactions with native and nonnative insect pests. Moreover, temperatures by 2099 for the northeastern US are projected to be 2–5.3 degrees (C) higher and precipitation 5%–14% higher (Hayhoe et al., 2007). Differences in the competitive ability of chestnut relative to established conspecifics across gradients of climate and soils will be further modified by interactions with native and nonnative insect pests that are currently the major natural disturbances structuring this ecosystem. Consequently, forest land managers seeking to enhance ecosystem services such as carbon storage, biodiversity, and ecosystem resilience to novel disturbances must wrestle with the uncertainty of alternative future ecosystems without a contemporary analog (Chapin et al., 2007). A modeling approach robust to novel environmental conditions, species assemblages, and disturbance (and management) regimes should help mitigate such uncertainty (Gustafson, 2013).

To this end, we applied the mechanistic PnET-Succession forest growth simulation extension linked to process-based disturbance extensions within the LANDIS-II forest landscape model to simulate the efficacy and ecosystem consequences of American chestnut restoration within its former range (Dalgleish, Nelson, Scrivani, & Jacobs, 2016). We designed a factorial simulation experiment to bracket a plausible range of chestnut restoration scenarios (Passive, Thin and underplant, Clearcut and plant), physiographic moisture regimes (xeric and warmer: Ridge and Valley, mesic and cooler: Appalachian Plateau), and climate scenarios (current, extreme change) potentially affecting competitive interactions between American chestnut and existing species. Each simulation included a common background of forest harvesting and disturbance by existing and imminent insect pests. We explicitly investigated the impact of the Asian Longhorned Beetle (ALB) (*Anoplophora glabripennis*) because it has the potential to curtail current successional trends towards maple (*Acer* spp.) within central Appalachian hardwood systems (Gustafson, De Bruijn, et al., 2017), but there is considerable uncertainty as to how successful ALB control efforts will be. Our study was driven by three fundamental questions: (1) How do variations in climatic regimes (including CO_2 enrichment) in space and time affect efforts to restore American chestnut? (2) How does the reintroduction of American chestnut affect ecosystem structure and function—specifically the ability to accumulate biomass for carbon storage, and forest structural and compositional diversity relevant to long-term system resilience? (3) Does the potential impact of a destructive invasive insect (ALB) have the potential to counteract oak (*Quercus* spp.) to maple transitions within the region (Abrams, 1998), and what would be the carbon stocks implications of such a shift?

Previous studies suggest that our simulated chestnut restoration scenarios will produce a gradient in restoration efficacy (i.e. chestnut dominance), ranging from negligible (passive restoration) to codominance (clearcut and plant) within a century (Gustafson, De Bruijn, et al., 2017). Across this gradient, and framed by question 1, we hypothesized that (a) climate change will favor reintroduced chestnut because it is relatively drought and shade tolerant, and has an optimum temperature for photosynthesis that is greater than or equal to that of more than half of its competitors, which should provide advantages under warmer and drier climates (Gustafson, Miranda, Bruijn, Sturtevant, & Kubiske, 2017); and (b) chestnut will be less competitive in the more mesic Appalachian Plateau province because its competitors will be less stressed. In the context of question 2, we also hypothesized that (c) the reintroduction of a fast-growing, long-lived, decay-resistant species (American chestnut) will enhance carbon stocks by increasing living and dead biomass accumulation, and that (d) chestnut restoration will increase both compositional and structural diversity as long as it remains codominant rather than (nearly) monospecific. Finally, in response to question 3, we predicted that (e) chestnut restoration will have the strongest effect on biomass accumulation under scenarios that include ALB (that target maples), because chestnut could offset the faster decay rates of maple litter and wood (Cornwell et al., 2008; Russell et al., 2014).

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted our study in western Maryland (USA) because it is in the approximate center of the former chestnut range, and because sites representative of two large physiographic provinces (Ridge and Valley and Appalachian Plateau) that together comprise 54% of the former range of American chestnut are in close proximity (Figure 1). The study sites were centered on the Green Ridge and Savage River State Forests, and included adjacent public and private lands in Maryland, Pennsylvania and West Virginia. Prior to European settlement, lightning and Native American ignitions maintained a low-to-moderate intensity surface fire regime in this region (LANDFIRE, 2103). 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 forests between 1880 and 1912. Fire suppression greatly reduced the incidence of fire beginning around 1930, resulting in increased red maple (*Acer rubrum*) and black birch (*Betula lenta*) recruitment (Shumway, Abrams, & Ruffner, 2001). Any remaining mature chestnut trees were killed between 1914 and 1950 by the chestnut blight.

The Savage River State Forest (SRSF) is located on the Appalachian Plateau (AP), and receives the highest annual precipitation in Maryland (114–140 cm/year; Brown & Brown, 1984). Elevation within the AP ranges from 375–900 m, with topography ranging from steep and dissected ravines to undulating terrain on broad ridgetops underlain by sandstone and shale (Stone & Mathews, 1977). The AP 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 subcanopy. The Green Ridge State Forest (GRSF) is located approximately 35 km east of SRSF in the Ridge and Valley (RV) physiographic province. Elevation ranges from 140–600 m, and unlike the Appalachian Plateau, this area receives the lowest annual rainfall in Maryland (76–88 cm/year; Brown & Brown, 1984). 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 & Matthews, 1974). The shallow and well-drained soils of RV are more xeric, with forests dominated by upland oaks, with pine (*Pinus* spp.) common on the driest slopes (Hicks & Mudrick, 1994).

2.2 | Model overview

We implemented the simulation experiment using LANDIS-II, which uses extensions (plug-ins) to mechanistically simulate forest growth and disturbance (e.g. insect outbreaks and timber harvesting) at landscape spatial and temporal scales (Scheller et al., 2007). The model tracks species cohorts rather than individual trees, representing space as a grid of cells (30 m resolution here). Each ecological process is formalized in an independent extension that modifies cohort biomass. The interactions among climate, growth, succession and disturbance are not specified a priori, but are emergent properties of the cumulative effects of the independently simulated processes.

To simulate growth processes (establishment, growth, competition, senescence), we used the PnET-Succession extension of LANDIS-II (De Bruijin et al., 2014) because its mechanistic use of physiological first principles is well suited to model novel situations such as climate change and the introduction of new species (Gustafson, 2013). Growth is modeled as a competition of tree species cohorts for available light and water, and cohorts can die any time their respiration requirements exceed photosynthetic input long

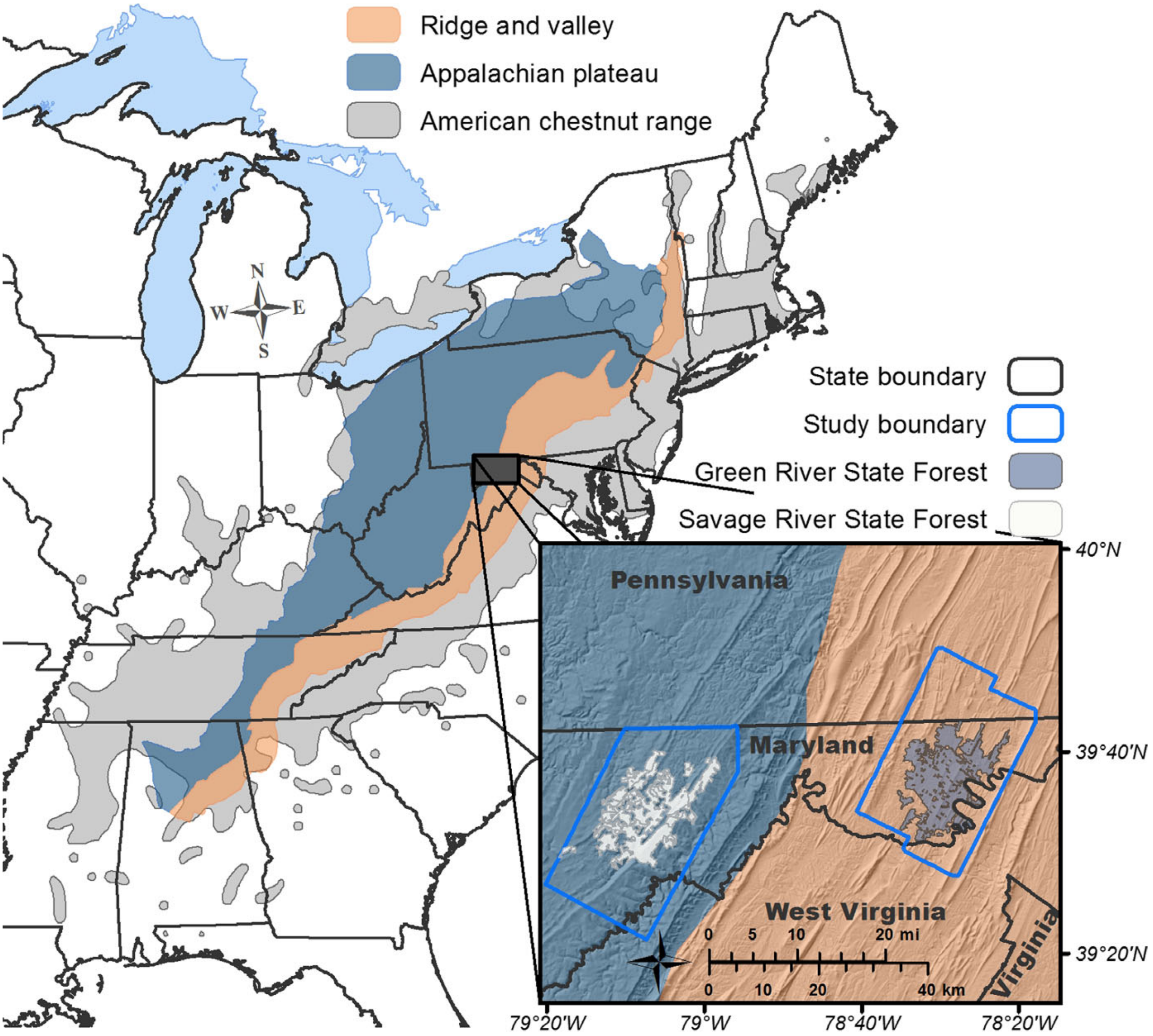

FIGURE 1 Location of the study areas in relation to the former range of chestnut and the extent of the physiographic provinces (Fenneman & Johnson, 1946)

enough to deplete their carbon reserves. Soil water availability is determined by precipitation, loss to evaporation and runoff, soil porosity, and consumption by species 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. As soil water availability decreases, photosynthesis also decreases. Temperature also affects vapor pressure deficit, respiration and evapotranspiration rates. Thus, in PnET-Succession, growth rates vary monthly by species and cohort as a function of precipitation and temperature (including extreme events), directly affecting competition and ultimately successional outcomes. Net photosynthates are allocated to four pools: foliage, wood, roots and nonstructural carbon reserves. Biomass is moved to woody and litter dead pools through turnover or mortality (including by disturbances), which decay according to species-specific decomposition rates (see Gustafson, De Bruijn, et al., 2017 and De Bruijn et al. (2014) for details). Carbon stocks in mineral soil are not tracked, but soil carbon tends to be the most stable of the carbon pools (Jackson et al, 2017). A more detailed description of the model can be found in De Bruijin et al. (2014).

2.3 | Experimental design

We conducted a factorial simulation experiment with five main factors. The Physiographic Province factor had two levels representing contrasts in both regional climate and initial forest communities:

Ridge and Valley province (lower precipitation and elevation currently dominated by oak and pine forests) and Appalachian Plateau (higher precipitation and elevation currently dominated by mixed mesophytic forests). The Climate Change factor had two levels encompassing extremes of climate scenarios: no climate change and a high emissions "climate change" scenario (RCP 8.5). The Chestnut Restoration factor had three increasingly aggressive levels of restoration applied across the landscape: passive chestnut dispersal (Passive), thin and underplant chestnut (Thin), and clearcut and plant chestnut (Clearcut). The ALB factor contrasted scenarios where the ALB was introduced and spread throughout each study area, versus scenarios where ALB invasion was successfully prevented (see Parameterization section).

All factor combinations included a background timber harvest regime representing the management plan of the state forest in each study area ("Business as Usual"; BAU), applied to both public and private land within each study area and the "existing and imminent insect pests" scenarios used by Gustafson, De Bruijn, et al., 2017—holding the extreme case of ALB as an experimental factor (see above). The Chestnut Restoration factor represented three plausible but contrasting chestnut restoration scenarios. The "Passive" chestnut restoration treatment represented a hypothetical short-term restoration effort, simulated by planting chestnut prior to simulations on single cells at 500 m intervals along a central north–south transect crossing each study area, depending on unaided (natural) dispersal of chestnut for landscape colonization. The other two chestnut restoration treatments converted stands to chestnut by specifying a harvest method (thin or clear cut), followed by planting of chestnut and preventing competitors from establishing for one year. Chestnut restoration modified BAU activities, holding total area harvested constant. The Climate Change treatment was implemented using weather time series for current climate and a harsh future climate scenario (RCP 8.5). Historical weather data (including PAR) for an area (~900 km^2) within the ecological Province surrounding each state forest was subset from the Daymet Daily surface weather 1 km grid for North America, 1980–2015 (Thornton et al., 2014). Because the historical record does not extend back far enough for "spin-up" of the biomass of existing cohorts, we used monthly averages prior to 1980, and actual records through 2014, repeating the observations of the period 1980–2014 through 2,216 to create a "No climate change" weather scenario into the future. For No climate change, CO$_2$ was set to 335 ppm prior to 1980, gradually increasing to 390 ppm by 2010, and held constant after that. For the climate change scenario, we used GCM projections centered on each study area for the period 2006–2,100, repeating the last 30 years of the projections through 2,216. We used the GFDL-CM3 climate projection for the period 2006–2,100, using the RCP 8.5 emissions scenario (run = r1i1p1). The climate change scenario produced an average temperature 4.5 and 4.6°C higher than the historical scenario for Green Ridge and Savage River, respectively, and 10% and 7% more precipitation. We used the RCP8.5 CO$_2$ concentrations of Meinshausen et al. (2011), with CO$_2$ concentration reaching 1902 ppm by 2,216. Because the GCM data we used did not include PAR, we repeatedly applied the historical PAR data from 1980 to 2014.

The other treatments were implemented using the Biomass Harvest disturbance extension (Gustafson, Shifley, Mladenoff, Nimerfro, & He, 2000). The Passive chestnut restoration treatment included the BAU harvest regime, but no further planting of chestnut was simulated. The Thin and plant treatments were implemented by the removal of 50% of the biomass of all cohorts older than 40 years and planting (establishing) a new cohort of chestnut. The Clearcut and plant treatments removed 100% of the biomass of all cohorts and planted a chestnut cohort. Stands eligible for active chestnut restoration were selected and cut using an "oldest first" selection rule that attempted to avoid stands dominated by oak. In the active chestnut restoration treatments, less than one quarter of the area normally targeted for harvest (BAU) on each study area (2.5% by area) was diverted to cutting and planting of chestnut each decade. Active restoration activities were discontinued after 100 years, and total area harvested was held constant across all treatments and time steps. Harvest input files are available in the Supplement. Fire was not simulated because fire suppression has made fire a rare and low-intensity occurrence in the region. Each factorial combination was simulated for 200 years and replicated six times.

2.4 | Model inputs and parameterization

Simulation initial conditions maps for RV were those used by Gustafson, De Bruijn, et al., 2017, derived from Foster and Townsend (2004). Initial conditions maps for AP were generated using methods similar to those used for RV to ensure comparability of results. Initial vegetation conditions (tree species-age cohorts) were derived from a combination of classified airborne hyperspectral imagery, digital state forest stand maps and forest inventory plot data. 1,768 plots of species composition data from FIA, the Maryland Continuous Forest Inventory and our past studies (Chastain & Townsend, 2007; Singh, Serbin, Kingdon, Townsend, & PA, 2015; Townsend et al., 2012) were intersected with NASA AVIRIS hyperspectral imagery collected on 14 July 2009 to map basal area for 18 species using partial least squares regression. ROC curves for presence and absence by species were used to identify a lower threshold of species relative abundance at any location, and map accuracy across species ranged from 2.1% to 13.9% relative basal area. We also prepared LANDIS landtype maps that represent relatively homogeneous spatial zones in terms of climate (temperature and precipitation), and soil conditions (soil texture, slope and aspect), and 58 landtypes were mapped by binning combinations of climate and soils from the SSURGO database (Soil Survey Staff, Natural Resources Conservation Service, & United States Department of Agriculture, 2013).

PnET-Succession requires tree species life history and physiological parameters, most of which are estimated empirically. We used the species parameters of Gustafson, De Bruijn, et al., 2017 for the RV (Supporting information Tables S1–S4), using similar methods to estimate and validate parameters for the two species found only on the AP study area (*B. lenta*, *F. grandifolia*). Parameter settings of all species were validated by comparing growth curves of species simulated in monoculture to published measures of growth through time (various sources). Similarly, we used the methods of Gustafson, De Bruijn, et al., 2017 to estimate landtype parameters for AP (Supporting information Appendix S2).

BAU timber harvests and the active chestnut restoration treatments were simulated using Biomass Harvest (Gustafson et al, 2000), which requires input maps of stand boundaries and management zones. Such maps were available for the state forests, but not for private land. To create generic stand maps of the land surrounding the state forests, we generated a regular grid of square, 9 ha stands across each study area and superimposed the stand maps of the state forests on them. 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 two state forests about 40% of the land is reserved from timber harvest. Forty percent of the arbitrary stands outside each state forest were randomly assigned to the "unmanaged" management area and the remainder to a "managed" management area. Forest management activity on the GRSF was simulated using the harvest prescriptions developed by Foster (2011) based on the GRSF management plan (MDNR-FS, 2011) that actively uses thinning, shelterwood cutting and prescribed burning to enhance oak regeneration (Supporting information Appendix S2). On sites not optimal for oak management, other prescriptions favor white pine (*Pinus strobus*), shade-intolerant species or other hardwoods, designed to enhance diversity. We similarly developed prescriptions for the SRSF based on the SRSF management plan (MDNR-FS, 2012). Harvest rates simulated by the model were calibrated to match harvest rates specified in the management plans of each state forest, and were applied on "managed" areas of both state and private lands.

Pest outbreaks were simulated using two different extensions, following the methods of Gustafson, De Bruijn, et al., 2017. Impacts from gypsy moth (*Lymantria dispar dispar*) and forest tent caterpillar (*Malacosoma disstria*), introduced and native insect defoliators, respectively, were simulated using the Biomass Insects extension (v2.0; Foster, 2011; Foster & 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 quasicyclic with variability in outbreak and nonoutbreak 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 (Foster, 2017). For the remaining exotic insects either recently introduced or imminent to the study area [emerald ash borer (*Agrilus planipennis*) and hemlock woolly adelgid (*Adelges tsugae*)], and also the ALB treatment, we used the simpler Biological Disturbance Agent (BDA) extension (v3.0, Sturtevant, Gustafson, Li, & He, 2004; Sturtevant, Gustafson, He, Scheller, & Miranda, 2017). 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. In the case of emerald ash borer and hemlock woolly adelgid, we simulated worst-case scenarios. Emerald ash borer killed all ash (*Fraxinus* spp.) trees within a decade regardless of age (Herms & McCullough, 2014), and although the ash could resprout, simulations killed the remaining ash a decade later, consistent with (Siegert, McCullough, Liebhold, & Telewski, 2014). Likewise, all age classes of eastern hemlock (*Tsuga canadensis*) are susceptible to hemlock woolly adelgid in our study areas (Vose, Wear, Mayfield, & Nelson, 2013), and the BDA killed all infected hemlock within a decade. ALB preferentially attacks red maple over sugar maple and American elm (*Ulmus americana*), and larger trees are most susceptible (Dodds & Orwig, 2011). Simulated ALB spread across each study area from two "inoculation sites" within 20 years (Sawyer, 2007), with cohorts of red maple older than 40 years, of sugar maple and elm older than 40 years, all of three species 10–39 years old killed with 100%, 50%, and 25% probability per decade, respectively, within affected regions. Cohorts less than 10 years old were never killed. More parameterization details for insect disturbance regimes can be found in Gustafson, De Bruijn, et al., 2017 and the Supporting information Appendix S2.

2.5 | Analysis

For the purposes of our study we selected the following response variables, which were monitored as landscape level averages across all forested cells: total biomass of six species groups (Table 1); total of the living and dead biomass pools combined; species and age–class richness (mean number of species or age classes on forested cells). The species groups were designed to inform our hypotheses that oak species are generally intermediate in shade tolerance and have relatively decay-resistant wood and litter, while maple species are shade tolerant and have greater rates of decay (Mattson, Swank, & Waide, 1987; Melillo, Aber, & Muratore, 1982); chestnut is a strong competitor, with shade tolerance approaching that of maples and has decay characteristics similar to oaks. Gymnosperm litter and wood generally decompose more slowly than that of angiosperms (Cornwell et al., 2008; Weedon et al., 2009), and given the impending loss of hemlock, the pine species group represents an important source of functional diversity within these central hardwood forests. The remaining species were grouped as either shade-intolerant "pioneer" species, or shade-tolerant "late seral" species, where the former should be responsive to growing space released by harvest and insect disturbance, and the latter should be more competitive with less disturbance. Graphs showing the effect of all factors through time for each response variable were produced to allow visualization of trends and their uncertainty in comparison to a reference condition (Historical climate-passive restoration) using an approach similar to statistical emulation (Oakley & O'Hagan, 2004). Specifically, a Bayesian statistical emulation model was fit to each of the species groups and the dead woody and litter biomass variables, yielding 2000 predicted time series for each response variable under each treatment scenario (details in Gustafson, De Bruijn, et al., 2017). When long model run times limit the number of replicates that can be simulated, statistical emulation better accounts for model uncertainty by estimating the distribution of results expected with many simulations using the results of a much smaller sample of simulations. Our inferences are based on direct comparisons of the predictive distributions among scenarios.

3 | RESULTS

3.1 | Efficacy of chestnut restoration

As expected, passive restoration (i.e. natural seeding and spread) of American chestnut was slow regardless of physiographic province or climate scenario (Figure 2). Note that chestnut spread was slightly slower under climate change than with historical climate, but where it was present, biomass was higher under climate change. This response suggests the establishment environment defined by light availability and/or soil moisture was diminished under a warmer climate, restricting chestnut's natural rate of spread, but where chestnut could successfully establish, its growth was enhanced.

Chestnut biomass established via the passive restoration treatment was negligible (<1% of total biomass by year 200), whereas the two active chestnut restoration treatments were successful at re-establishing chestnut codominance across all physiographic province and climate scenarios (Figure 3). The Clearcut treatment consistently produced more (18%–83% higher) chestnut biomass than the Thin treatment. Chestnut biomass response for both restoration treatments was greater within the drier Ridge and Valley province, and higher under extreme climate change. Notably, the increased biomass generated by planting in the first 100 years appeared to easily sustain its momentum after planting concluded in both provinces under the climate change scenarios. Given that passive dispersal only very slowly added new cohorts, especially under warmer climate (Figure 2), most of the increase after year 100 was the result of robust biomass growth as chestnut cohorts matured under climate change.

TABLE 1 Assignment of species to species groups

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

3.2 | Effects of chestnut restoration and climate change

Of all treatment factors, the climate factor had the most profound effect on total biomass across the landscape, with the RCP8.5 emissions scenario approximately doubling biomass compared to historical climate in both provinces (Figure 4). Total biomass within the historical climate scenarios equilibrated after year 80 in the AP province and appeared to be in equilibrium throughout the entire simulation in the RV province, whereas total biomass within the future climate scenarios continued to increase across all treatment combinations. Physiographic province (primarily reflecting differences in precipitation and soils) had the next most important effect on total biomass, with the AP province accumulating more biomass relative to the RV province under most combinations of climate and chestnut restoration, although under Clearcut chestnut restoration, total biomass on the RV approached that of the AP by the end of the simulation. Nonetheless, chestnut restoration method had the least effect of the treatment factors. The Clearcut treatment always produced the most total biomass and the Passive method always produced the least, although the differences were subtle.

Under historical climate, oak biomass declined to less than half its initial biomass in the RV, and rose and fell to approximately the same biomass between the start and end of the simulation (year 200) in the AP (Figure 5). By contrast, oaks generally retained landscape dominance within the RV across climate change scenarios, driven primarily by white oak (*Q. alba*), which is the most abundant species and is less susceptible to forest tent caterpillar than the other oaks, and has the highest optimum temperature for photosynthesis (26°C) of all the oaks, enabling a positive growth response to warmer climate. White oak is also long lived (400 years), so there was less senescence during the 200 year simulations compared to the AP province, where the shorter lived northern red oak (*Q. rubra*) (250 years longevity) dominated. In the AP province, none of the oak species except scarlet oak (*Q. coccinea*) increased in biomass under historical climate, and red oak was surpassed as the dominant species by year 150. Maples (principally red maple) steadily increased in the RV province (Figure 6) to overtake white oak as the dominant species by the end of the simulation, while maples (initially sugar maple followed by a steady increase in red maple) more rapidly surpassed oaks on the AP. There were subtle but consistent differences in both maple and oak biomass between the Clearcut and the Thin chestnut restoration treatments, corresponding with the greater chestnut restoration efficacy within the Clearcut treatment. Notably, chestnut biomass within the Clearcut treatment surpassed that of all

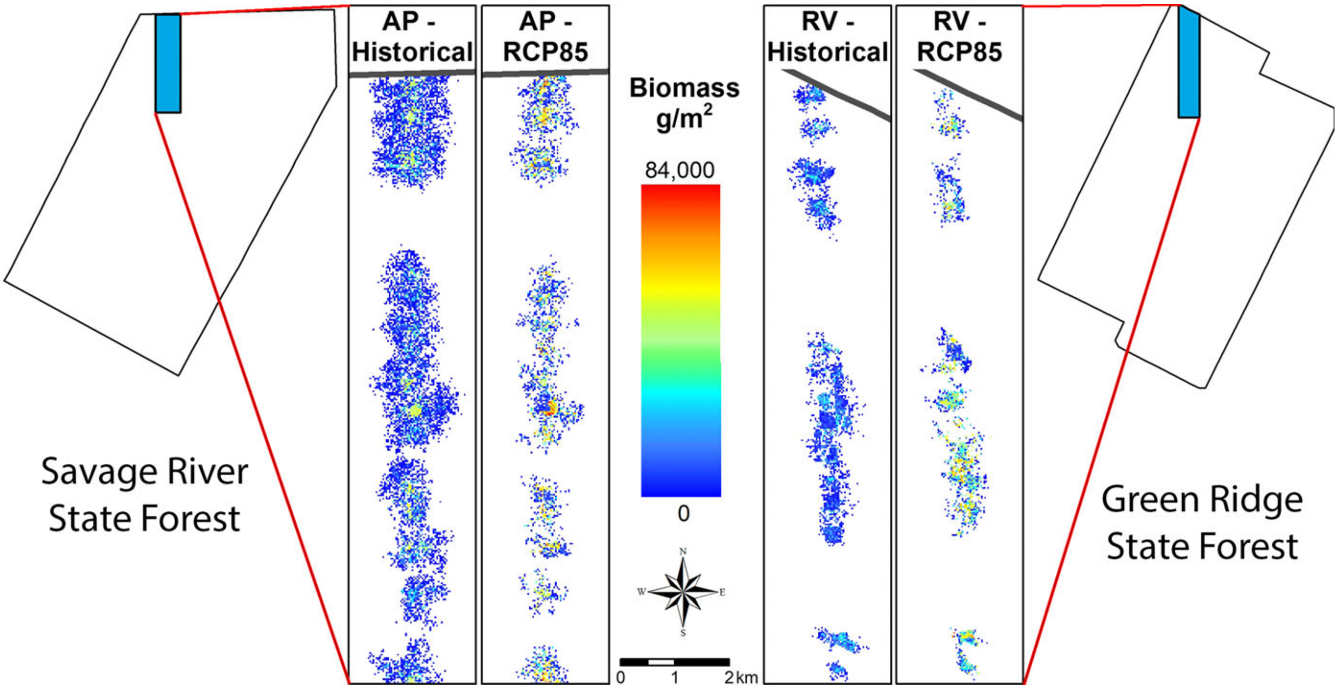

FIGURE 2 Maps of chestnut biomass at year 200 for each study area and climate combination under the Passive restoration method (planting chestnut on a transect of single sites at 500 m intervals), showing the slow amount of spread over two centuries. Only the northern portion of each transect is shown

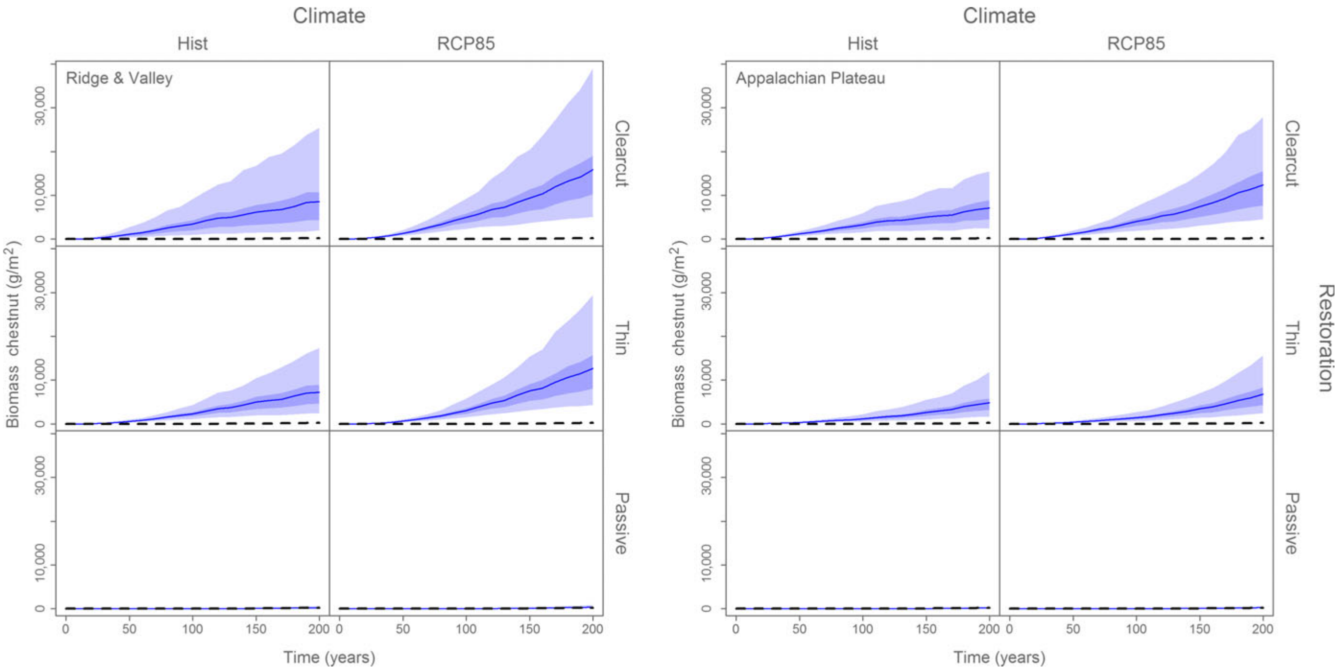

FIGURE 3 Average live biomass (wood and roots) of chestnut by province and climate and chestnut restoration treatment. Solid lines show mean trends over time and shaded areas show 95% and 50% prediction intervals. The dashed line shows the trend for the Historical Climate-Passive Restoration scenario to enhance comparisons within each restoration treatment [Colour figure can be viewed at wileyonlinelibrary.com]

oaks combined by the end of historical climate simulations within the RV, and approached the combined oak biomass on the AP by the same point in time (Figures 3 and 5). Most species accumulated much more biomass under climate change compared to historical climate, and they generally accumulated somewhat more biomass on the AP province compared to the RV province.

Pines were comparatively less responsive to the main experimental treatments than other taxa (Figure 7). In the RV province there

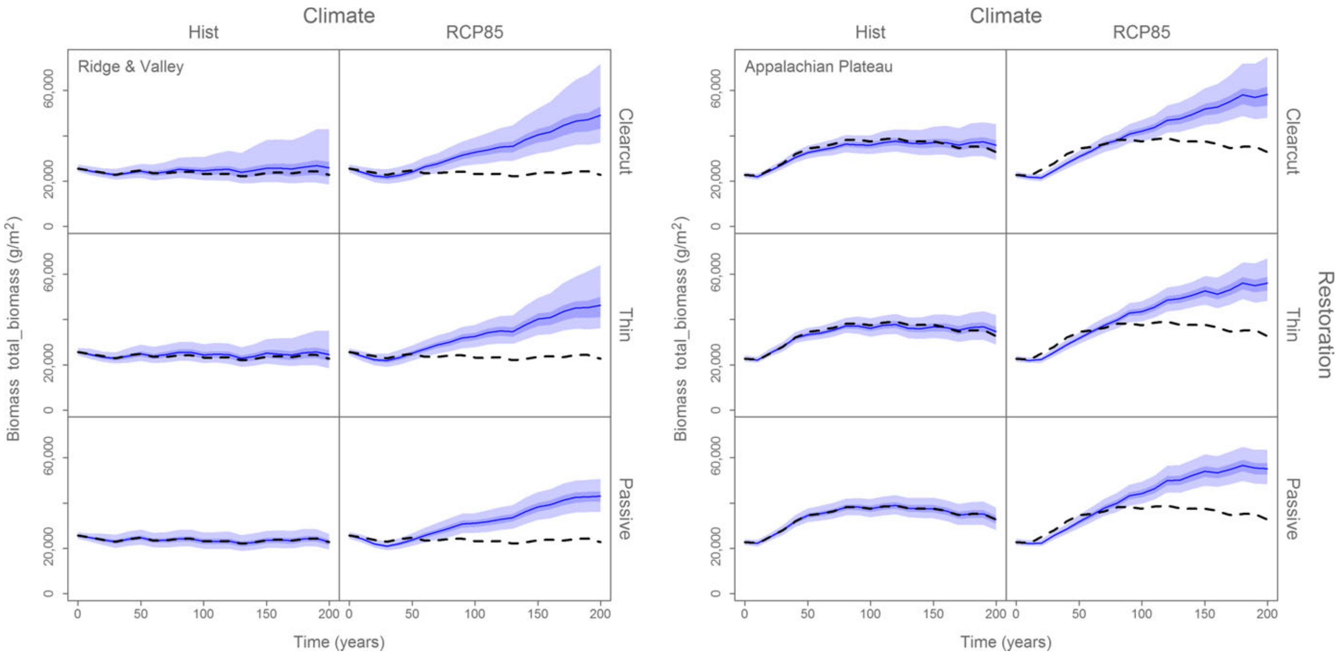

FIGURE 4 Total average biomass (live wood and roots, dead wood, and litter of all species) by province and chestnut restoration and climate treatment. Solid lines show mean trends over time and shaded areas show 95% and 50% prediction intervals. The dashed line shows the trend for the Historical Climate-Passive Restoration scenario to enhance comparisons within each restoration treatment [Colour figure can be viewed at wileyonlinelibrary.com]

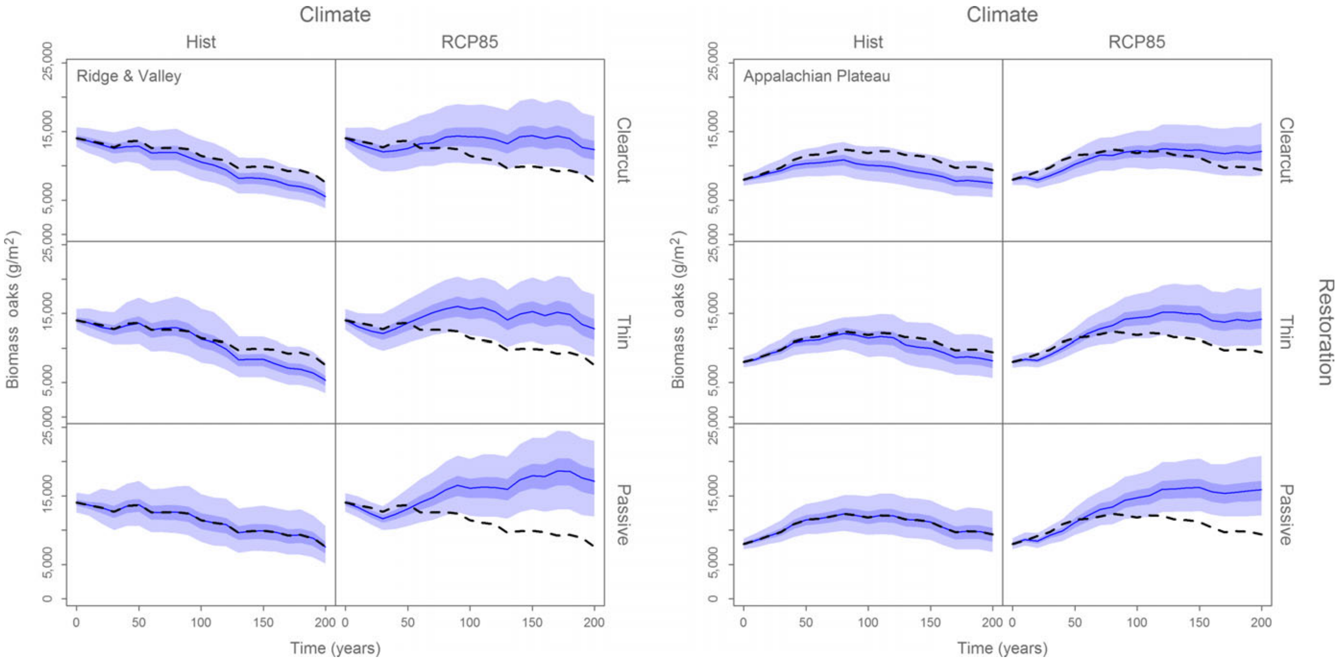

FIGURE 5 Average live biomass (wood and roots) of oaks by province and climate and chestnut restoration treatment. Solid lines show mean trends over time and shaded areas show 95% and 50% prediction intervals. The dashed line shows the trend for the Historical Climate-Passive Restoration scenario to enhance comparisons within each restoration treatment [Colour figure can be viewed at wileyonlinelibrary.com]

was a general decline by primarily shade-intolerant pine species because there were no silvicultural prescriptions designed specifically to retain them (with the exception of the less common Virginia pine, *P. virginiana*). Consequently, the hardwoods outcompeted shade-intolerant pines even on disturbed sites because of the ability of hardwoods to reproduce vegetatively. On the AP, the primary pine species was white pine, the abundance of which was better maintained through an active planting prescription. As in other species, there was a general increase in pine biomass under the future climate scenario, but chestnut restoration consistently depressed that

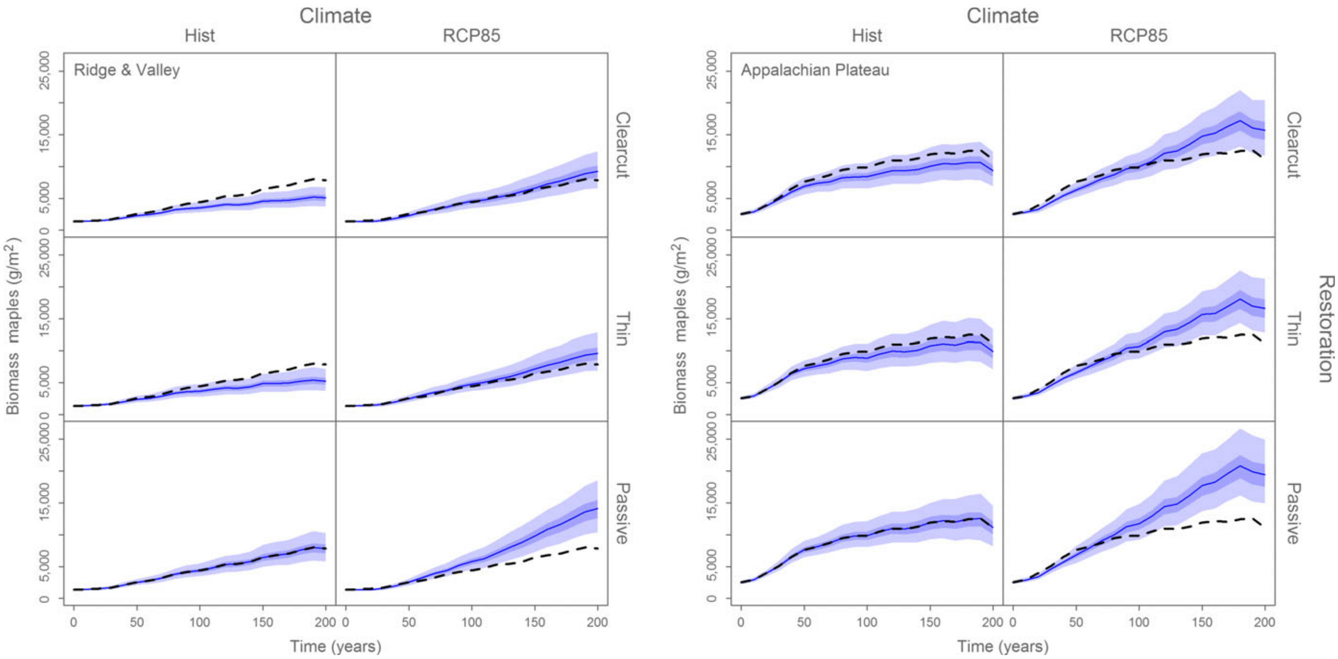

FIGURE 6 Average live biomass (wood and roots) of maples by province and climate and chestnut restoration treatment. Solid lines show mean trends over time and shaded areas show 95% and 50% prediction intervals. The dashed line shows the trend for the Historical Climate-Passive Restoration scenario to enhance comparisons within each restoration treatment [Colour figure can be viewed at wileyonlinelibrary.com]

increase in both provinces. Closer inspection of individual species (data not shown) reveals that the moderately shade-tolerant white pine was responsible for all increases in pine biomass under warming climate, while the remaining pine species (*P. echinata*, *P. pungens*, *P. rigida*, and *P. virginiana*)—all dependent on disturbance and only present on the RV—consistently declined under the climate warming treatment.

Similar to pines, treatment effects on pioneer and late seral species were more subtle than those observed for oaks and maples, with one exception (i.e. late seral species on the AP under climate change). Pioneer species showed initial declines due to loss of ash to emerald ash borer, and late seral species similarly declined early due to loss of hemlock to hemlock woolly adelgid; in each case the short-term decline was more noticeable on the AP where each of the respective host species were more common (Supporting information Figures S1 and S2). Pioneer species in the RV exhibited a slight increasing trend that was enhanced by climate change and depressed by chestnut restoration. Biomass of this group on the AP suggested an initial increase, perhaps due to space released by ash and hemlock, followed by decline across all scenarios, with an otherwise consistent response to climate change and chestnut restoration as observed for the RV. Late seral species remained stable within the RV, but were more sensitive to treatment effects on the AP, indicating relative stability under historical climate but a strong increasing trend under the climate change scenario that, similar to pioneer species, was tempered by chestnut restoration.

Patterns of tree species richness indicated consistent responses to treatment effects across the physiographic provinces (Figure 8). Species richness initially dropped within the first decade due at least in part to the loss of ash and hemlock. Species richness then stabilized in the historical climate scenario, but continued to decline in the climate change scenario. Within that general pattern, more aggressive chestnut restoration consistently reduced species richness. Age–class diversity, by contrast, indicated strong interactions among treatments that were nonetheless consistent in temporal patterns between the RV and AP. The strongest factor was chestnut restoration method that strongly increased age–class diversity under the Thin and Clearcut treatments. Climate change decreased age diversity across all restoration treatments and provinces, but its negative effect on the age–class diversity in the Clearcut treatment was particularly strong.

3.3 | Effects of Asian long-horned beetle

As expected, ALB impacted maples severely, to the extent that maple biomass stabilized at lower levels (70%–80% and 80%–90% reduction at years 100 and 200, respectively, relative to scenarios without ALB) as essentially an understory species, rather than gaining dominance (compare Table 2 with Figure 6). This decline of a major competing genus enabled consistent increases in the other species groups (Table 2). Oak decline, and to a lesser extent pine decline, were clearly mitigated by ALB activity. Proportionally, pioneer species responded more strongly to ALB activity on the AP than on the RV, particularly under climate change, while late seral species most strongly increased on the RV under climate change. The doubling of late seral species biomass across all treatments on the AP was most significant in terms of relative dominance, due to robust compensation by species such as basswood and beech.

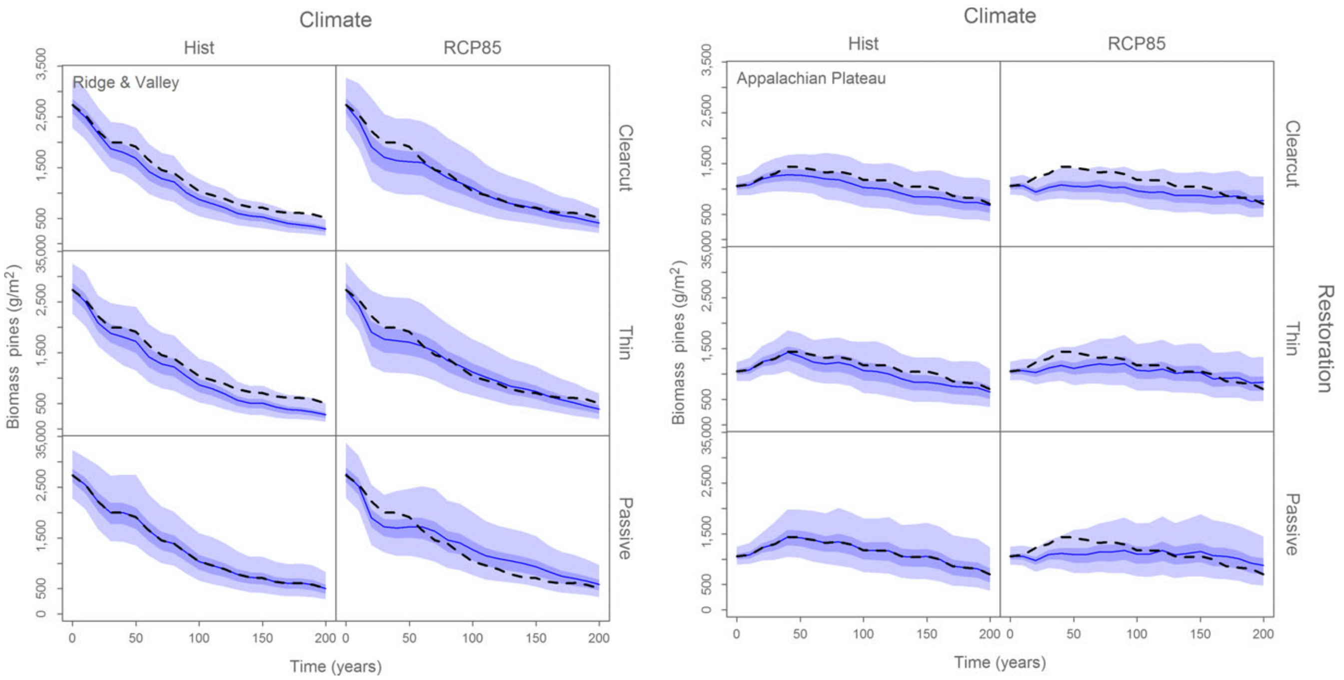

FIGURE 7 Average live biomass (wood and roots) of pines by province and climate and chestnut restoration treatment. Solid lines show mean trends over time and shaded areas show 95% and 50% prediction intervals. The dashed line shows the trend for the Historical Climate-Passive Restoration scenario to enhance comparisons within each restoration treatment [Colour figure can be viewed at wileyonlinelibrary.com]

Patterns of chestnut biomass were the most complex in their response to ALB activity across the treatments; its earlier growth was negatively affected by ALB activity at year 100—especially for the Thin treatment—but chestnut biomass was consistently greater by year 200—robustly so on the AP (relative to scenarios without ALB).

Despite the compositional responses to the diminishment of maples by ALB, whole system responses were weak. Total biomass slightly increased (range = −1.3 to +9.3%), with the most robust increases occurring on the AP under the aggressive chestnut restoration scenarios (Table 2). Patterns of species richness were very similar to those observed without ALB (Figure 8). However, structural diversity (age classes) was far more strongly affected; unlike the simulations without ALB, chestnut restoration treatments slightly reduced age–class richness, suggesting that much of the structural diversity resulted from the interaction between increasing maple dominance and chestnut restoration. Age–class richness was further reduced by climate change (Figure 8).

4 | DISCUSSION

Our experiment systematically varied the treatment factors and held everything else constant. We visualized the deviation of modeled state variables from a baseline in response to the treatments, rather than conducting statistical tests of our hypotheses, as recommended for simulation experiments by White, Rassweiler, Samhouri, Stier, and White (2014). Our approach enables visual evaluation of whether simulation results were consistent with our hypotheses. We assessed if the former dominance of American chestnut can be restored simply by planting hybrid chestnut trees as opportunity arises. In a prior paper (Gustafson, De Bruijn, et al., 2017), we discovered that a fairly aggressive planting effort would be required to restore chestnut to its former prominence, but that study did not examine how variations in climatic and physiographic regimes in space and time might affect restoration efforts. The results presented here include the effects of climate change (including CO_2 enrichment), physiographic province and restoration method. These results confirm that aggressive landscape-scale restoration is always needed, regardless of climate and physiographic province. Further, climate and physiographic province affected the ability of chestnut to compete and displace extant species in important ways. The climate change scenario (RCP8.5) tended to enhance the growth of all species, but species with higher growth potential (including chestnut) tended to outcompete slower growing species (Figure 3). Thus, chestnut can be considered a winner under climate change. Interestingly, in the physiographic province with greater precipitation and more mesic soils (AP), chestnut did not experience as much advantage from climate change, presumably because water stress was generally less and other species were better able to compete with chestnut. Finally, the Clearcut and plant chestnut restoration method gave chestnut the greatest advantage because its high growth potential allowed it to quickly dominate sites where no older cohorts were present. However, the Thin and underplant chestnut restoration strategy appears to be a viable option. Under historical climate the Thin treatment established 90% and 75% of the chestnut biomass achieved using the Clearcut treatment for the RV and AP, respectively, although climate change reduced these percentages to 83% and 57%, respectively (Figure 3). Chestnut tends to compete

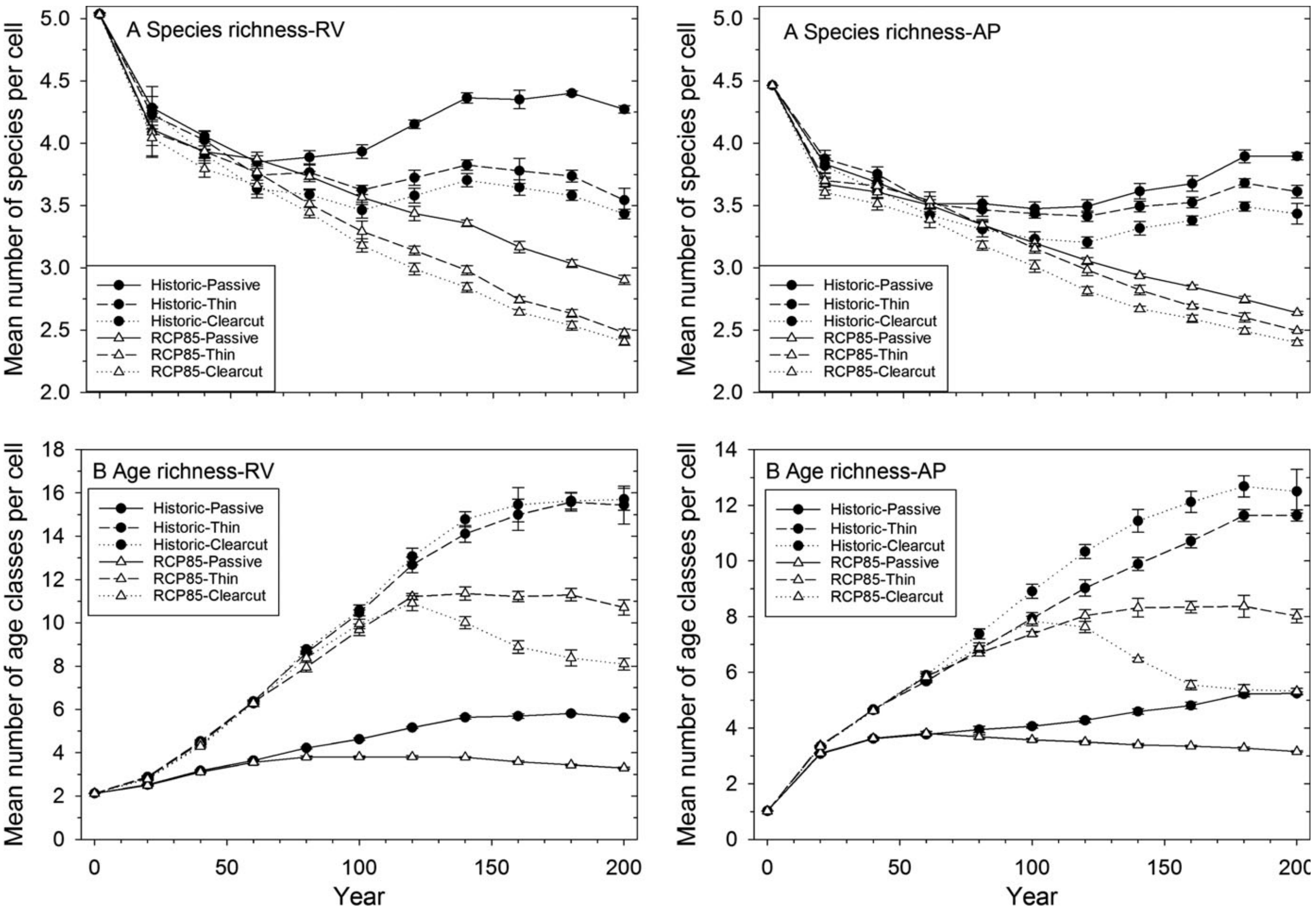

FIGURE 8 Change in species and age class richness by treatment combinations. Error bars show 1 standard deviation from the mean of six replicates

TABLE 2 Percent difference in the biomass of primary species groups and total biomass when ALB is added to the simulations

Climate	Restoration	Total biomass	Chestnut	Oaks	Maples	Pines	Pioneers	Late seral
a) Ridge and valley								
Historical	Passive	−1.3	30.0	**49.8**	**−80.8**	**83.3**	**74.5**	**74.5**
Historical	Thin	3.6	−1.3	**59.0**	**−72.9**	**102.5**	**69.9**	**69.9**
Historical	Clearcut	1.7	11.0	*32.5*	**−77.4**	*65.6*	**79.4**	**79.4**
RCP8.5	Passive	2.3	18.9	**52.6**	**−82.8**	**103.9**	**63.5**	**63.5**
RCP8.5	Thin	6.2	5.0	**53.2**	**−76.9**	**84.5**	**82.0**	**82.0**
RCP8.5	Clearcut	3.5	9.2	*37.7*	**−79.5**	49.1	**86.9**	**86.9**
b) Appalachian Plateau								
Historical	Passive	5.9	*61.1*	**48.9**	**−84.3**	**96.2**	**119.8**	**119.8**
Historical	Thin	*8.3*	*40.3*	**46.9**	**−87.3**	**118.3**	**98.7**	**98.7**
Historical	Clearcut	*9.3*	*43.4*	**46.1**	**−88.9**	*55.8*	**110.1**	**110.1**
RCP8.5	Passive	1.2	*71.6*	**49.1**	**−86.6**	*70.0*	**134.1**	**134.1**
RCP8.5	Thin	*7.0*	*41.1*	**43.2**	**−83.4**	**64.4**	**138.2**	**138.2**
RCP8.5	Clearcut	7.2	6.2	**61.5**	**−86.4**	**75.8**	**160.2**	**160.2**

Note. Italics indicate that the ALB mean was outside of the 50% confidence interval of the non-ALB simulations, and bold indicates it was outside of the 95% confidence interval.

favorably with other species because of its high growth potential (Jacobs, Selig, & Severeid, 2009; McEwan, Keiffer, & McCarthy, 2006) and relatively high shade and water stress tolerance (Joesting, McCarthy, & Brown, 2009; Wang, Bauerle, & Mudder, 2006).

The effects of climate change in our simulations were driven primarily by CO_2 enrichment up to 1,962 ppm. Greatly elevated temperatures (+6°C) tend to reduce productivity because of greatly increased respiration costs (Gustafson, Miranda, et al., 2017), but this can be more than offset by elevated CO_2, which directly increases productivity and indirectly increases water use efficiency (Curtis & Wang, 1998; Karnosky, 2003). The RCP8.5 emissions scenario that we used included a five-fold increase in CO_2 concentration by the middle of the second century of the simulations (Meinshausen et al, 2011). Our simulations projected up to a doubling of biomass accumulation under climate change (Figure 4), with the specific response related to the physiographic province and the traits of the species found on each study area. Total biomass response to climate was highest on the RV province, driven in part by a greater increase in chestnut biomass, compared to the AP province. The RV province is warmer and has less precipitation and more xeric soils, such that soil moisture is chronically lower there compared to the AP province. CO_2 enrichment proportionally enhances growth rates and water use efficiency of all species, which means that faster growing species gain an even greater competitive advantage as CO_2 increases. Although water use efficiency increases, water remains the primary factor limiting growth even under elevated CO_2 because of enhanced growth rates, so species with greater ability to extract water from the soil are more competitive. Thus, species with a competitive advantage have an even greater advantage under elevated CO_2.

Our research was partly driven by the question of how the restoration of American chestnut as an abundant species might affect ecosystem structure and function. In particular, we were interested in whether American chestnut restoration could enhance carbon stocks given potential losses of tree genera due to invasive pests. Several studies have suggested the importance of individual species for carbon stocks, and have demonstrated a higher rate of carbon uptake by faster growing tree species and a larger carbon stock in tree species with larger size, higher longevity, or denser wood (Balvanera, Kremen, & Martinez-Ramos, 2005; Brown, Schroeder, & Birdsey, 1997; Bunker et al., 2005; Caspersen & Pacala, 2001). Fewer studies have shown a clear relationship between species composition and biomass accumulation in forests (Kirby & Potvin, 2007). The literature consistently supports the idea that carbon stocks are best maintained by avoiding deforestation via land conversion, either by humans or disturbances (e.g. Houghton, 2005, Kashian, Romme, Tinker, Turner, & Ryan, 2006; Kashian, Romme, Tinker, Turner, & Ryan, 2013), because net carbon loss from forest ecosystems is negligible as long as the forest regenerates (Ryan et al., 2010). In our study, neither active restoration method produced perceivably higher total biomass than the passive method (Figure 4). These results are consistent with Gustafson, De Bruijn, et al., 2017 and support their conclusion that chestnut restoration on its own does not markedly enhance carbon stocks. Notably, our study also suggests that restoration of chestnut may *indirectly* enhance carbon stocks via its interaction with disturbance: chestnut restoration helped to mitigate the reduction of carbon stocks with increasing dominance of low wood density maple and concurrent oak decline.

If we assume that the resilience of forests is related to their composition and structural (age) richness (Stanturf, Palik, & Dumroese, 2014), our results suggest that climate change may reduce resilience (Figure 8), even while enhancing carbon stocks. This result was virtually identical on both physiographic provinces, and was likely driven by CO_2 enrichment that increased the intensity of competition. Enhanced resiliency that occurs via enhanced species richness can also mitigate the impact of new exotic pests (see Discussion of ALB below). Flower and Gonzalez-Meler (2015) predicted that if an ecosystem is sufficiently diverse, there will be enough species that are resistant to the pest to fill the gap left by species negatively impacted by the pest. If the resistant species has greater C storage potential than the species lost to the pest, C storage on the landscape could be increased because of the pest. Our results are consistent with that prediction.

Consistent with our expectations, species richness was impacted by chestnut restoration, with richness decreasing under the methods that enhanced chestnut dominance (Figure 8). An important tradeoff of aggressive restoration of a historical competitor means that some existing species will be partially displaced. Our results suggest that the Thin restoration treatment partially mitigates this effect, with the strongest mitigation effect observed on the AP. One might also argue that chestnut provides ecosystem services that some of the species that appear to be “losers” to chestnut (e.g. pioneers, pines) do not provide, such as more high-quality mast for wildlife, fine hardwood for the wood products industry and greater biomass and carbon accumulation (Jacobs et al., 2009; Jacobs, Dalgleish, & Nelson, 2013). On the other hand, with the imminent loss of hemlock in these systems, one can argue that conifer presence in these otherwise hardwood-dominated systems is a fundamental component of compositional diversity. Clearly there are tradeoffs with respect to the winners and losers in response to human-aided restoration activities that should be more closely examined.

The increasing dominance of maple is a regionally observed phenomenon throughout the Appalachians and elsewhere, and it is caused by increased survival of maples due to altered disturbance regimes, primarily fire suppression (Abrams, 1998; Nowacki & Abrams, 2008). The trend toward maple dominance was clearly observed in our results, and although chestnut was able to become an important component of these forests, it did not alter the historical trend toward maple dominance (Figure 6). When we simulated the invasive insect pest ALB, we found that chestnut achieved an additional advantage when competing maples were reduced by ALB. However, all other species groups also responded positively to the severe decline of this important competitor (Table 2), and chestnut increase was therefore moderated by other competitors. Some of those species, like chestnut, have more decay resistance than maple (e.g. oaks, beech), but others (e.g. basswood, black gum) do not (Mattson et al., 1987; Melillo et al., 1982), although there is some uncertainty about decay rates (Russell et al., 2014). Further, each species has its own unique life history characteristics (i.e. growth rate, longevity) that have consequences for biomass. The maples, especially red maple, are more resistant to the principle insect defoliators within this system, and the sustained presence of oaks in particular mean the forests in general remained susceptible to disturbance by gypsy moth and forest tent caterpillar. The cumulative effect on total biomass of community shifts associated with reduced maple was therefore quite modest (<10%), though most prevalent in the AP system, especially when combined with chestnut restoration (Table 2). The ALB scenario is a good example of an ecological surprise from a no-analog future that increases the uncertainty about future ecological structure and composition of forests. In this particular case, we found the forests of the study area to be resilient to a novel disturbance (ALB) in a way that supports predictions that species-rich systems such as the Central Appalachians are able to absorb the selective impacts of an invasive pest (Flower & Gonzalez-Meler, 2015).

Our modeling approach makes important assumptions that shape the interpretation of our results in terms of carbon storage. Our results quantify changes in carbon stocks with climate change and forest management rather than attempting to understand the net ecosystem carbon balance (NECB; Chapin et al., 2007). Our results should be interpreted as changes in biomass accumulation (carbon stocks) across multiple scenarios of climate change, disturbance and management rather than carbon storage, because several carbon pools and fluxes have not been accounted for in the model. For example, belowground processes in the model are estimated as a constant fraction of aboveground biomass, despite the possibility that aboveground–belowground biomass ratios may change with disturbance or management or if site factors are altered by climate change (Smyth, Kurz, Neilson, & Stinson, 2013). The model does not account for soil carbon because it is often assumed to be relatively stable (Jackson et al., 2017). However, it represents about 40% of the total carbon in forests of the U.S. and can be sensitive to harvest and management practices (soil compaction and reduced carbon input after harvest) and may be subject to losses if climate change increases soil decomposition rates (Ryan et al, 2010). We also assumed that restoration efforts will successfully minimize the risk of establishment failure by factors not modeled such as browsing, disease and competitor control. Despite these limitations, we focused on the component of the forest carbon budget most germane to American chestnut restoration.

As in any study of this type, there are also a number of biological and model uncertainties. (a) Maps of initial forest conditions were derived from a combination of stand maps (state forests), inventory plots and processed hyperspectral images. Such maps carry uncertainty, due to both mapping error (which ranged 2%–14% by species) and exclusion of uncommon species or species primarily in the understory that cannot be mapped accurately using remote sensing and inventory data. (b) The climate change projection that we used is not our best guess of the climate future of the region, but was chosen to send a clear climate signal to the experiment. (c) There is also some uncertainty associated with the PnET-Succession parameters we used. Although PnET parameters were designed to represent biological meaningful characteristics of species that can be empirically measured, these characteristics often vary with age, canopy position, site, and season; yet a single value must be input to the model. However, competitive interactions among species are not highly sensitive to any individual parameter. (d) Parameter values for backcross-hybrid chestnut were based on a synthesis of recent studies (Jacobs et al., 2013) rather than empirical data specific to these sites, and although less certain than parameters for some other species, they performed reasonably in a prior study (Gustafson, De Bruijn, et al., 2017). (e) Finally, there was uncertainty introduced because not all processes were included in our simulations, such as ozone pollution, novel diseases, other disturbances such as deer browsing and wind and ice damage, human development, and nutrient cycling. Some of these may have little impact on competitive outcomes because they affect all species about the same, but others may impact some species more than others. American chestnut is quite susceptible to the root disease caused by *Phytophthora cinnamomi* Rands. in the southern half of its former range, and this pathogen is expected to move northward (and upward) as conditions warm (Anagnostakis, 2012; Burgess et al, 2017). Although this disease has the potential to greatly impact restoration efforts throughout the former range of chestnut, we did not model it because of excessive uncertainty in its current and future distributions (Balci et al., 2007) and the susceptibility of hybrid chestnut to the disease (Steiner et al., 2017). Furthermore, many competitors of chestnut are also susceptible to *P. cinnamomi*, and we assumed that its effect on those species may be similar to its effect on chestnut. Management prescriptions may also help to reduce negative effects of *P. cinnamomi* on chestnut restoration (Rhoades, Brosi, Dattilo, & Vincelli, 2003). As some of the uncertainty about how climate change will affect *P. cinnamomi* distribution virulence is reduced, this factor could be integrated into future modeling studies. Until then, it should be recognized that uncertainty about the role of *P. cinnamomi* in the success or failure of restoration efforts is inherent in our results.

4.1 | Management and policy implications

Our results support the conclusions of Gustafson, De Bruijn, et al., 2017 that recolonization of blight-resistant chestnut in existing forests may be a multigenerational process. Our Clearcut and plant restoration treatment produced the most chestnut biomass, although simulated chestnut biomass was also quite high under the Thin and underplant treatment. This can be explained by the intermediate shade tolerance of chestnut (Joesting et al, 2009; Wang et al, 2006), which allows chestnut regeneration to effectively compete under partial canopy light conditions without aggressive pioneer species and herbaceous vegetation. Our results are also consistent with results from short-term field trials that demonstrated successful chestnut restoration under partial canopies (Brown, Bailey, Saunders, & Jacobs, 2014; Clark, McNab, Loftis, & Zarnoch, 2012; McCament & McCarthy, 2005; Rhoades, Loftis, Lewis, & Clark, 2009) created by midstory removal or thinning. Although the Clearcut restoration method produced the greatest biomass, it also produced the lowest richness (and likely resilience), so our results do not indicate which method should be preferred.

While chestnut restoration did not markedly enhance carbon stocks here and in Gustafson, De Bruijn, et al., 2017, results from these studies provide hope that this formerly abundant species can be successfully reintroduced, and its associated ecosystem services recovered (Jacobs et al., 2013). This outcome corresponds more closely with the primary goals of ecosystem restoration, increasing biodiversity, and improved wildlife habitat and forage for those conservationists and managers working toward chestnut restoration. Assuming a management regime of harvesting and planting, chestnut was easily able to sustain its momentum of biomass increase after the cessation of planting (after 100 years) under various province and climate change scenarios. Chestnut colonization and spread also do not appear to come at the expense of any particular species group, which should alleviate potential concerns of managers who are simultaneously working to maintain other species that are in decline (e.g. oaks).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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