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Delayed fire mortality has long-term ecological effects across the Southern Appalachian landscape

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Abstract

Fire is a critical ecological process to the forests of the Southern Appalachians. Where fire was excluded from forest types that historically burned frequently, unanticipated changes can occur when fire is reintroduced. For example, the development of new fuel characteristics can change the patterns of fire mortality and associated ecological responses. To test the fire effects of delayed fire mortality (mortality initiated by fire that occurs subsequent to the fire year) in the Southern Appalachians, USA, we developed a fire-effects model using both field studies and remote sensing. We then simulated these effects at a landscape scale to estimate broader ecological effects. Fire-effects models that accounted for delayed mortality increased landscape biomass removed annually (~23%) and increased the number of sites with high light conditions (leaf area index < 4) when compared to simulations that only account for immediate mortality. While delayed mortality occurred across species and age classes, it was especially prevalent among older trees (>100 years old) and fire-resistant species (*Quercus* spp.). Overall, regeneration (trees <20 years old) changed very little, even with the inclusion of delayed mortality. This evidence suggests that, even when accounting for delayed mortality, individual fires are unlikely to shift the landscape composition toward the conditions of forests prior to fire exclusion and may even increase mesophication long term due to the loss of overstory dominant xeric trees.

KEYWORDS
delayed fire mortality, fire ecology, fire modeling, landscape simulation mesophication, Southern Appalachians

INTRODUCTION

Fire fundamentally shapes biomes worldwide and alters vegetation on an evolutionary time scale (Bond et al., 2005; McLauchlan et al., 2020). In response to fire, plants have evolved by adapting their survival and reproduction to best thrive under these conditions (Keeley et al., 2011). Biodiversity is promoted by fire at the landscape scale as various stages of disturbance and recovery allow for the persistence of species that may be shade or drought intolerant (He & Lamont, 2018). Fire's impact on ecosystem function and community composition can be greater in warmer humid forests where other common limiting agents such as temperature and moisture requirements are readily met (Bond et al., 2005). In more humid biomes, fire frequency and intensity are not limited to fuel production due to high levels of primary productivity. Instead, fire is often limited by fuel moisture, ignitions, and weather, resulting in a mixed-intensity fire regime (Lafon et al., 2017). Understanding how these fire dynamics shape the vegetative landscape requires us to understand climate, vegetation, and fire interactions (Whitlock et al., 2010).

Delayed fire mortality is a major source of uncertainty about the ecological effects of low- or mixed-intensity fire regimes in forests. While low-intensity surface fires may initially kill only a few trees, burned sites may show significant mortality in the years following, sometimes concentrated within large diameter trees that initially survived the fire (Barlow et al., 2003). Many fire mortality models estimate immediate mortality using flame length and bole or crown damage (Rothermel, 1983; Van Wagner, 1974) but make little inference about the effects of delayed mortality (Hood et al., 2018). While a fine-scale mechanistic understanding of delayed mortality is advancing (Bär et al., 2019; Hood et al., 2018; O'Brien et al., 2010), gaps exist in predicting delayed mortality and the underlying phenomena (O'Brien et al., 2018).

Capturing delayed mortality is crucial to understanding the ecological structure and function of the Southern Appalachian Forests of the southeastern United States. This area historically experienced a mixed severity fire regime where infrequent high-intensity fires removed the overstory and encouraged regeneration, while frequent low-intensity fires maintained open stands by removing understory competition (Aldrich et al., 2010; Flatley et al., 2013; Lafon et al., 2017). In the 20th century, active fire suppression by managers was implemented to protect forests from the damage of wildfires (driven by industrial logging) and has limited fire size and eliminated a majority of fire (Flatley et al., 2015; Fowler & Konopik, 2007). Fire spread has further been hindered by human development fragmenting vegetation on the landscape and decreasing the capability for fire to spread (due to discontinuity of fuels and ease of suppression; Duncan & Schmalzer, 2004; Terando et al., 2014; Driscoll et al., 2021). Fire suppression and exclusion have led to a decline in oak and pine recruitment and a rise in mesophytic hardwoods (Nowacki & Abrams, 2008). These shifts can become self-reinforcing as species convert the amount of fuel, the flammability of litter composition, and canopy structure, ultimately altering the undercanopy wind speeds and solar radiation (He & Lamont, 2018; Kreye et al., 2013). Interrupting the fire regime has resulted in the buildup of a novel fuel, duff, which when burned can increase mortality by damaging fine and coarse roots (Varner et al., 2016) and result in canopy decline (Carpenter et al., 2021). Larger overstory trees, which are often initially resistant to fire injury, may be particularly susceptible to delayed mortality, due to decreased vigor and greater root injury (Carpenter et al., 2021; Hood et al., 2007; O'Brien et al., 2010). Loss of overstory trees to delayed mortality can result in large changes in the live biomass of the stand, resulting in far more open conditions (Harrod et al., 2000).

Model simulations allows us to assess the effect of delayed mortality under multiple interacting factors of topography, soils, climate, and vegetation heterogeneity that may lead to varied levels of delayed mortality (Jeronimo et al., 2020). We aimed to investigate the influence of delayed mortality on ecological structure and function of forests in the Southern Appalachians. To do this, we parameterized two statistical models: the first from data on mortality within the first year following a fire (immediate mortality) and the second from data on the cumulative mortality for 3 years postfire (immediate + delayed mortality). These models were trained using remote sensing and field data to simulate relative rates of mortality. Models were then run within a forested landscape model; these models operate on finer scales than dynamic global vegetation models (DGVMs) and are designed to capture spatial interactions and to operate at a management-relevant scale (Gustafson et al., 2016). This was used to simulate the fire frequency and severity regime of forests of the Southern Appalachians in north Georgia, USA. We analyzed this model to investigate the additional effects delayed mortality has on live biomass, light conditions, and regenerating species.

METHODS

Our focal landscape was outlined using Omernik's (1995) definition of the Blue Ridge ecosystem of the Southern Appalachians within the states of Georgia, North Carolina, South Carolina, and Tennessee, USA (Figure 1). This area consisted primarily of upland hardwood forests (Appendix S1: Table S1). The elevation in this area ranged from ~300 m to nearly 1600 m. The area is quite humid through the summer and receives on average ~600 mm of precipitation annually. Precipitation happens consistently throughout the year, though late summer droughts occasionally occur.

To estimate the relative effects of immediate and delayed mortality on ecosystem structure, separate models were built from two sets of fire measurement data. The first built from data measured a single season and the second from measurements 3 years following a fire (Table 1, Figure 1). Both models were designed for

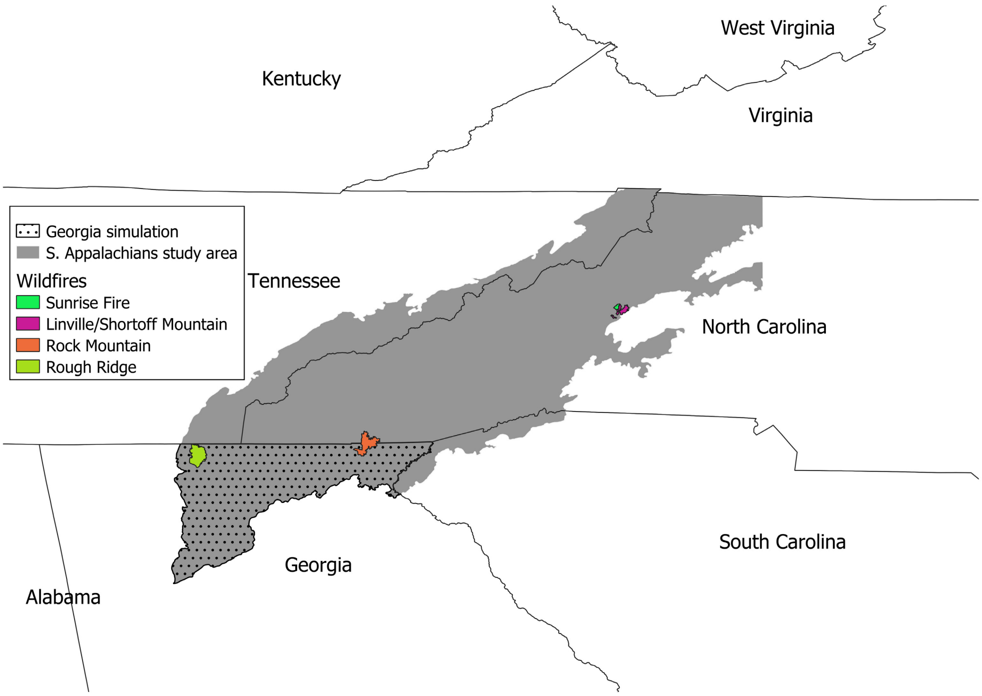

FIGURE 1 The Southern Appalachian study area, the Georgia portion used for simulations, and the location of the fires used in this study.

TABLE 1 Fire events, year of occurrence and measurement, and classification within model framework.

Fire (event name)	Location	Year	Measured	Mortality class
Sunrise	North Carolina (USA)	2008	2009	Immediate
Rough Ridge	Georgia (USA)	2016	2017	Immediate
Rock Mountain	Georgia/North Carolina (USA)	2016	2017	Immediate
Linville Complex (Pinnacle + Shortoff Fires)	North Carolina (USA)	2007	2010	Delayed
Rough Ridge	Georgia (USA)	2016	2019	Delayed
Rock Mountain	Georgia/North Carolina (USA)	2016	2019	Delayed

implementation in a forested landscape model simulation (Figure 2). We estimated cohort (defined as a single age class for a single species) mortality by linking these field measurements to remotely sensed estimates of severity. Mortality from the field sites was calculated as overstory tree death, not including the potential to resprout. Thus, trees that were observed as dead and then showed basal resprouting were considered in this mortality. To estimate severity at the landscape scale, we calculated the relative difference in normalized burn ratio (RdNBR) images for the five fires (Table 1) included in this study. The RdNBR measures the relative difference in multispectral vegetation indices as a way to approximate the burn severity of a fire (Appendix S1: Equation S2; Miller & Thode, 2007). This includes composite images for 1 and 3 years follow the fire to the tree mortality data measured from five fires in the region (Table 1).

To estimate RdNBR for projection in the landscape model, we tested multiple models (hence the site-level mortality models) to capture 1- and 3-year RdNBR. For the site-level mortality model, each unique combination of effective wind speed, and soil clay and soil sand content and proxies for productivity (evapotranspiration), and drought (climatic water deficit) were fit to a generalized linear model with a linear normal, log normal, and inverse Gamma structure and assessed by Akaike information criterion (AIC) for model specification and parameter selection (Akaike, 1973; see supplemental code at https://doi.org/10.5281/zenodo.6353798 for further information).

To parameterize immediate and immediate + delayed mortality model, training (a random draw of 80% of data) and validation (remaining 20%) sets were separated from each fire dataset (Table 1). We parameterized our statistical model of the probability of cohort-level mortality from the

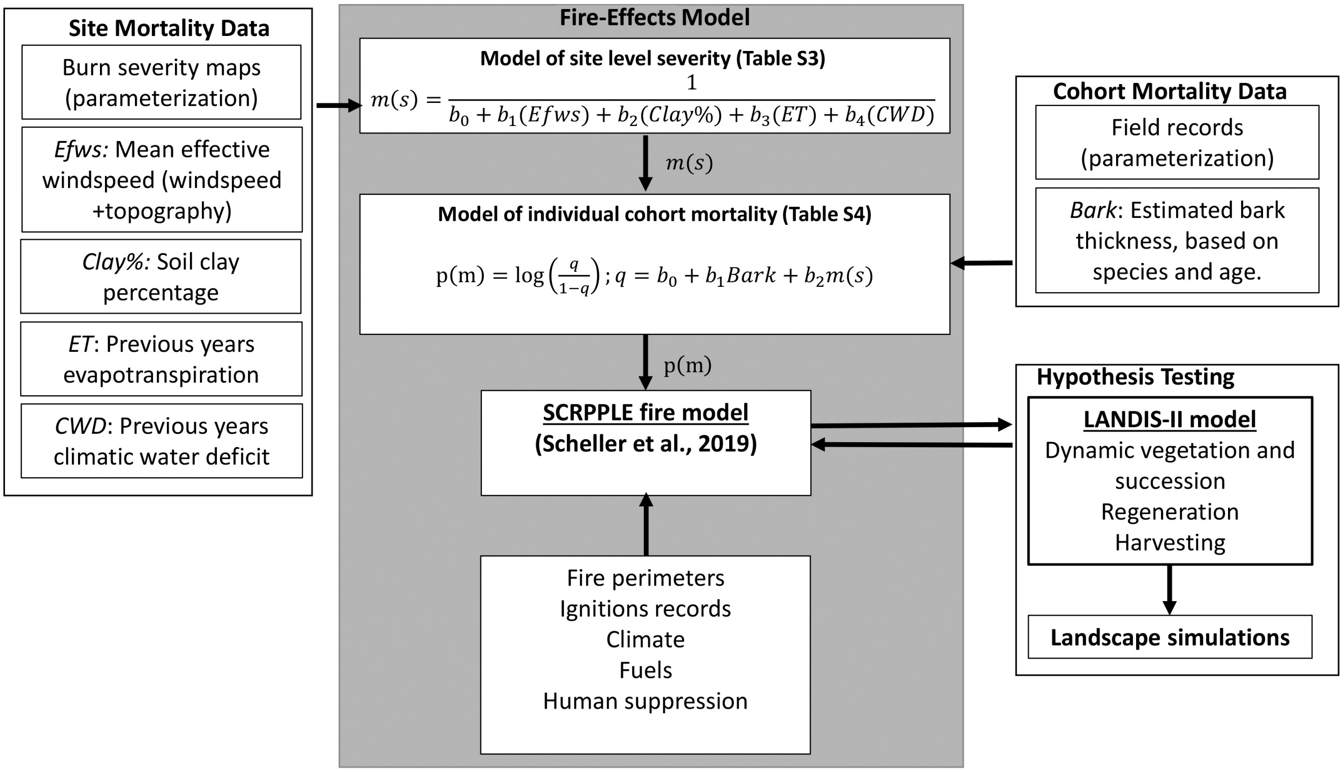

FIGURE 2 Workflow overview of the fire mortality simulations. This highlights the different data used in parameterizing the model. It additionally shows how the model interacts with the SCRPPLE and LANDIS-II models. Italics represent model variables.

site-level severity and the individual cohort's expected bark thickness based on their species and diameter at 1.37 m. Generalized linear models, with a binomial distribution and logit link, were fit to the training data to predict the probability of death given the bark thickness of the individual trees and the estimated site-level severity. We assessed the model by the area under the receiver operating characteristics (AUC), which provides a single number summary based on a classifiers performance based on the error rate and performance across categories (Brown & Davis, 2006). We additionally assessed both models by using a random binomial draw of each site condition to simulate the amount of landscape mortality that was suggested from each dataset, for each model fit.

To capture the ecological response to fire, we then incorporated both mortality model calculations (immediate and immediate + delayed) into the Social-Climate Related Pyrogenic Processes and their Landscape Effects (SCRPPLE) model of fire regimes (Scheller et al., 2019) for LANDIS-II v7.0 (Scheller et al., 2007), replacing the prior fire mortality equivalents. LANDIS-II represents the landscape as an interconnected grid, simulating vegetation, and disturbance processes within and between cells. Using the Net Ecosystem Carbon and Nitrogen (NECN v6.6) cohort growth extension incorporates the influence of temperature, available water, nitrogen, and light-based competitions to determine species growth and regeneration. The NECN tracks leaf area index (LAI) and above ground live biomass through landscape rasters for each yearly time step. The SCRPPLE model simulates the probability of fire ignition, spread, and the resulting mortality on a daily time step, based on climate, topography, and vegetation dynamics. Tree regeneration within the NECN model is simulated as a function of temperature as well as light and water availability. More information on the parameterization of LANDIS-II and the larger fire regime can be found in Appendix S1.

We ran two separate sets of landscape simulations using the immediate mortality and the immediate + delayed mortality model to simulate the Georgia portion of our study area. We ran five model replicates for 30 years using random climate drawn from 1992 to 2016 for each model. We simulated vegetation regeneration on an annual time step, growth on a monthly time step, and fire on a daily time step. These annual outputs of fire events and ecological properties were used to analyze the changes in LAI, and live biomass by age class between immediate and immediate + delayed mortality. Live biomass by age class was used to analyze mortality patterns as well as composition of young tree regeneration (trees <20 years old).

RESULTS

The final site-level severity model selected by AIC included effective wind speed, soil clay percentage, evapotranspiration, and climatic water deficit (Appendix S1: Table S2). This model is in the form of a Gamma distribution with an inverse link. Site-level mortality and bark thickness were significant with both the immediate + delayed and immediate cohort-level mortality models (Figure 3; Appendix S1: Table S3). The selected combined site-level severity and cohort-level immediate + delayed mortality model scored an AUC of 0.7411 when predicting the validation set. For the immediate mortality model, comparing the predictions of this dataset to a validation set had an AUC score of 0.6382.

Landscape simulations showed substantial increases in both the live biomass removed from the landscape per year and overall mortality rates with the inclusion of delayed mortality. Live biomass removed per time step increased 22.7% (95% CI: 6.1%–72.5%). This corresponded with a 63.5% (52.5–72.5%) increase in the stem mortality rate per fire event, with average mortality rates increasing from 23.7% (22.8%–24.8%) to 38.8% (37.8%–40.2%).

The LAI showed significant differences between the immediate mortality and immediate + delayed mortality models for both the postfire, 5- and 10-year period following a fire event (Figure 4). Postfire (3 years), high light conditions (LAI < 4) increased in the immediate + delayed mortality simulation from 24.3% of sites to 38.3% of sites, while immediate mortality increased from 21.3% of sites to 25.9% of sites. Overall neither simulation resulted in sustained high light condition plots (LAI < 4) over the 10-year period with the number of plots decreasing in the immediate + delayed mortality simulations from 24.3% to 10.1% of sites and immediate mortality decreasing from 21.3% to 5.1% of sites. The immediate mortality model had a much larger percentage (30.6% as compared to 19.8%) of sites in very low light conditions (LAI > 8) 10 years following the fire.

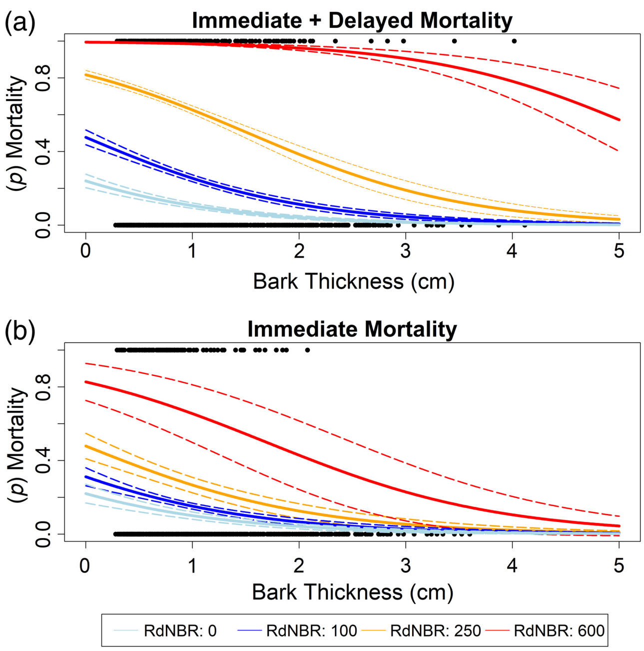

FIGURE 3 The probability of mortality at given values of site-level mortality for (a) the immediate + delayed mortality model and (b) the immediate mortality model. Dashed lines represent the SD of the predicted means. Black dots represent the status (alive/dead) of individual trees following a fire at the time census in the field studies.

We compared each species live biomass density after fire induced mortality implemented using the immediate and immediate + delayed mortality models. By live biomass, immediate mortality rate by species ranged between ~8% (*Pinus taeda*) and ~23% (*Oxydendrum arboreum*) and immediate + delayed mortality rate ranged from ~10% (*P. taeda*) to around ~40% (*Pinus virginiana*) (Figure 5). The high mortality rate in both models was the 0–25 age class even under though considerably more live biomass mortality occurred in the 25–50 and 50–75 age classes. Notably, in the 100+ age class, the major oaks *Quercus montana* and *Quercus alba* saw their mortality rates increase by ~500% with the inclusion of delayed mortality; however, this mortality rate was still less than 15% of original biomass in both cases and may be due in part to the limited live biomass in this age class. *Pinus strobus* also saw a large increase in the 100+ age class going from near 1% mortality rate to ~15% mortality rate.

Comparison of the composition of young trees (<20 years old) in burned and unburned sites under the immediate + delayed mortality model showed several significant differences as measured by Wilcoxon nonparametric test (Figure 6). However, the overall effect size was small. The relative species composition of young trees (as a relative proportion of live biomass) changed very little in the years immediately after fire and in the 10 years following. Species thought to benefit from fire (*Q. montana*, *Q alba*, *Q. coccinea*, *Q. montana*, *P. strobus*, and *P. taeda*) do not seem to make meaningful gains (on average) as a proportion of the relative live biomass following fire. Mesic species like *Acer rubra* and *Liriodendron tulipifera* seem to have benefited from the return of fire (Figure 6).

DISCUSSION

Our study suggests that measures of fire severity that only account for mortality immediately postfire (up to 1 year) may significantly underrepresent the actual mortality and

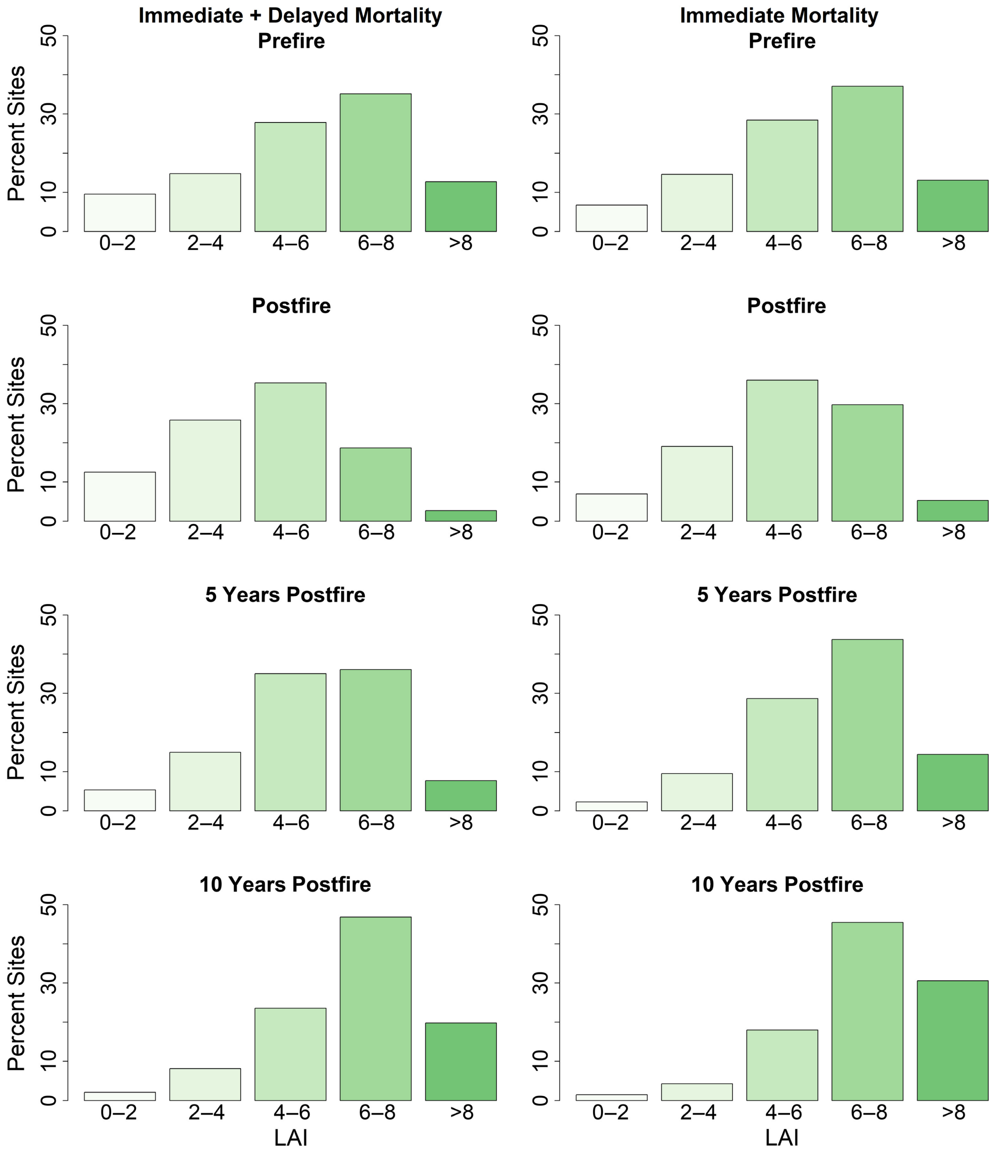

FIGURE 4 The percent of sites across the simulated landscape that experienced fire in each of five light area index (LAI) classifications (0–1, 2–3, 4–5, 6–8, 8+) for the period prior to fire, immediately following mortality, 5 years postfire, and 10 years postfire for the delayed and immediate mortality models.

thus the long-term ecological impact of fire. When simulated across a wide range of climate, vegetation, and soil conditions in the upland forests of the Southern Appalachians, the inclusion of delayed mortality resulted in a ~24% to ~40% increase in the number of stems killed in fire events each year. While neither simulation sustained high light conditions (<4 LAI) 10 years following a fire, immediate + delayed mortality resulted in a longer period of high light conditions, which should allow for a greater regeneration by early-successional plants on the landscape.

However, while the immediate + delayed mortality model removed more biomass and increased stand-level light in our simulations (Figures 4 and 5), our results suggest that the current fire regime of the Southern Appalachians does not alter forest regeneration patterns at the landscape level (Figure 6). The primary reason is because conditions postfire often favor the reestablishment of more mesic species and often fail to create the conditions necessary for xeric regeneration. On average, fires only resulted in ~18.3% reduction in standing biomass in trees over 20 years old, which may not be sufficient for xeric regeneration, or these conditions may be short lived (Figures 4 and 5). The quick rebound in LAI is further facilitated by rapid resprouting. Six of the 10 most dominant species in this study can resprout following a fire (even if not resistant to fire), allowing them to persist into the next generation after these low-intensity surface fires.

Our results mirror other field-based studies that show that repeated fires are needed to shift the community to a more pine-oak dominated landscape and optimal

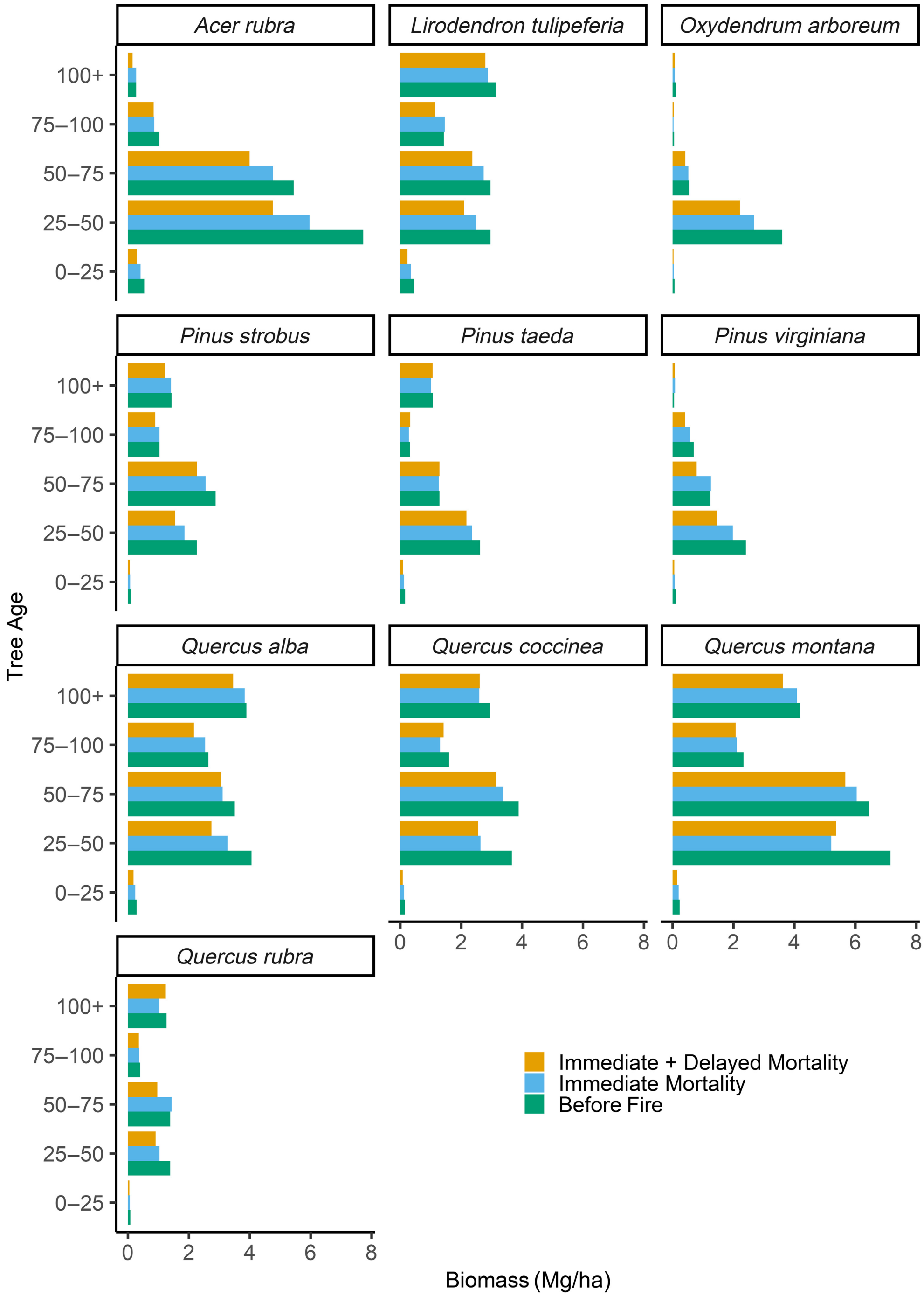

FIGURE 5 Average species composition in sites that experienced fire by age group prior to fire and simulated with immediate or immediate + delayed mortality.

recruitment environment (Blankenship & Arthur, 2006; Brose et al., 2006; Hutchinson et al., 2012). Single fires (both wild and prescribed) may foster regeneration of oaks, but also increase the density of mesic species through vigorous resprouting even in the case of top kill (Hagan et al., 2015; Keyser et al., 2017; Reilly et al., 2012). Frequent fire occurrence is likely to be necessary to confer advantage to fire adapted species. Fire regimes in the southern Appalachians historically maintained low densities, rather than frequently needing to reestablish them (Lafon et al., 2017). It is therefore logical that fire would have different effects when applied to this landscape and that merely restoring the fire regime may not be sufficient to reach the desired state. Multiple fires may do more to establish sapling-age oaks as compared to unburned stands, but this may also only lead to

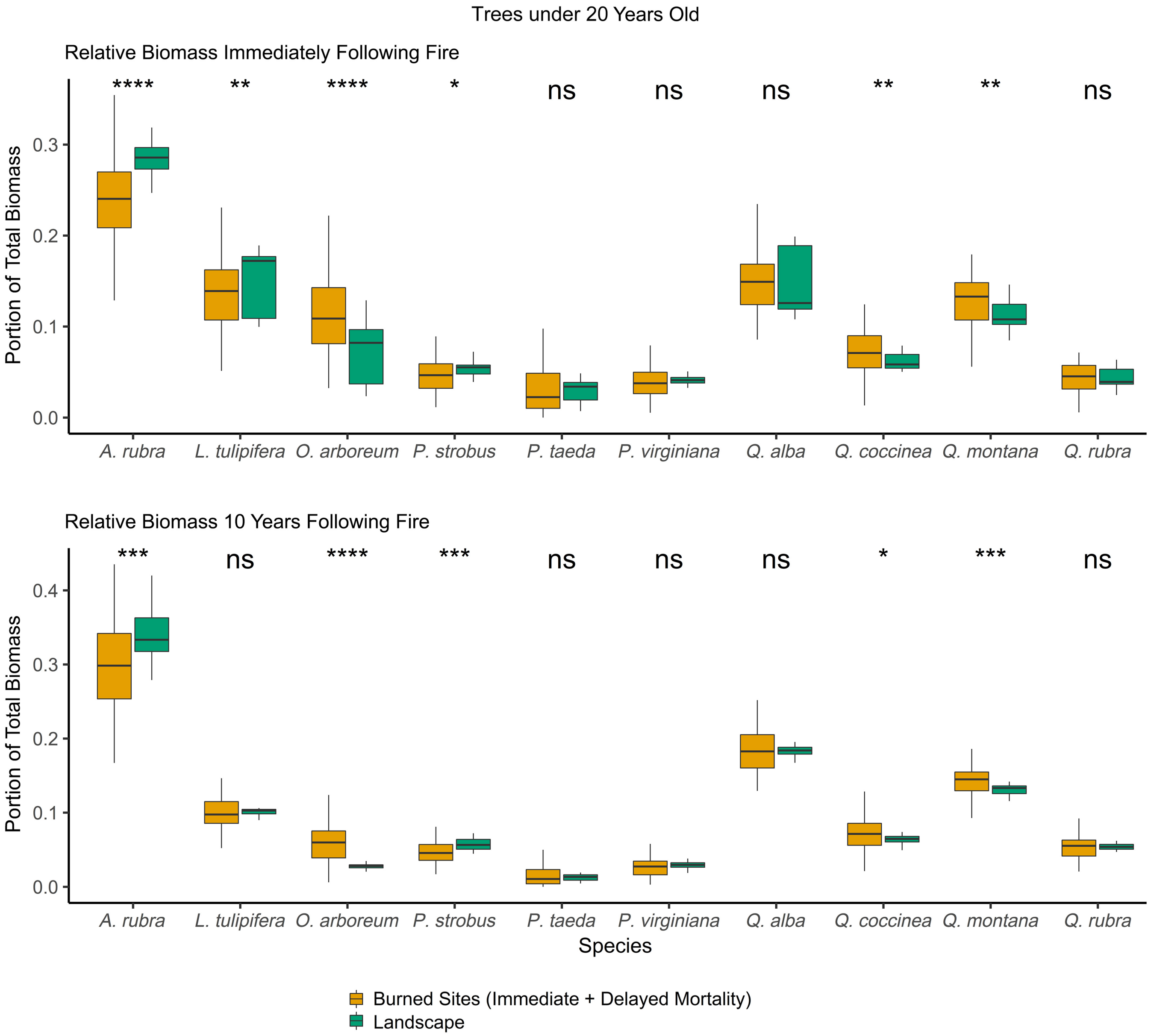

FIGURE 6 The relative landscape proportion biomass of tree cohorts younger than 20 years (portion of total <20-year-old biomass) of the 10 highest biomass species (Appendix S1) in sites burned in the immediate + delayed mortality model when compared to the landscape mean. Significance noted as "ns": $p > 0.05$; $*p \leq 0.05$; $**p \leq 0.01$; $***p \leq 0.01$; $****p \leq 0.0001$. Data points represent measured years across simulations. Species are *Acer rubra* (*A. rubra*), *Liriodendron tulipifera* (*L. tulipifera*), *Oxydendrum arboretum* (*O. arboretum*), *Pinus strobus* (*P. strobus*), *Pinus taeda* (*P. taeda*), *Pinus virginiana* (*P. virginiana*), *Quercus alba* (*Q. alba*), *Quercus coccinea* (*Q. coccinea*), *Quercus montana* (*Q. montana*), and *Quercus rubra* (*Q. rubra*).

modest changes in the tree community composition resulting in landscapes akin to prevegetation state in unless short fire-return intervals are continued (Keyser et al., 2017).

While the rate of recruitment is a crucial determinant of species composition, it must be weighted equally with the persistence of individuals (Bond & Midgley, 2001). The relationship between reproduction and the longevity of a species is a crucial aspect of their fire adaptation, as species that persist in the mature stage longer have a greater number of opportunities to successfully regenerate (Bond & Midgley, 2001; Brose et al., 2014). As modeled, delayed fire mortality increased the mortality of older fire-resistant trees (Figure 5). This suggests that fire exclusion across the last century has perhaps lowered the fire resistance of the ecosystem as a whole (as posited by Carpenter et al., 2021). The loss of older fire-adapted trees (*Q. alba* and *Q. montana*) during the reintroduction of fire may further accelerate the pattern of mesophication, resulting in a reversal of the anticipated historical fire effect, that fire would preserve or increase the presence of these species (Figure 5). Mechanical removal coupled with burning may increase the regeneration of oaks by opening the canopy further, but may also lead to additional loses of overstory oaks (Waldrop et al., 2016). However, our result suggests that a single disturbance is not sufficient to remove the older fire-adapted species on the landscape (mortality generally <20%) and that they could persist in the overstory following disturbance. Restoring historical fire regimes to these landscapes must balance both of these dimensions, retaining old individuals while fostering regeneration. Given the longevity of many of the oak species and the demographics of the landscape, we would expect them to maintain in the overstory for this century barring additional (nonfire) disturbances.

Tree stress following a fire exists on a continuum, so while field data could only report trees that experienced top kill, many of the other trees surveyed appeared to be approaching mortality (canopy decline; Carpenter et al., 2021). Additionally, many of the trees that resprouted may ultimately not grow into the mid or overstory and eventually perish. While the model attempts to account for this probabilistically, a mechanized understanding of the carbon reserved for resprouting would improve these dynamics. In the future, measuring vigor could be used to more mechanistically account for the decline that proceeds mortality. A longer-term study of the Rough Ridge and Rock Mountain fires could also illuminate the influence of long-term mortality.

Ecological models need to capture the immediate and long-term influence of fire on forest vegetation to quantify forest change accurately. In this study, incorporating remotely sensed burn severity data (such as those from RdNBR) and field studies of ecological change into a fire modeling framework provided a way to capture the spatial and temporal dynamics of the fire regime more fully (Morgan et al., 2014). We integrated both the heterogeneity of fire regimes and the relative influence of site conditions into ecosystem process modeling.

There are several key limitations of this study. Within the simulation, immediate + delayed mortality model was calculated and applied immediately; rather than over the course of the 3 years, this may lead to an overestimated advantage to shade-intolerant species that establish in the two intervening years and may overestimate the initial light conditions immediately following fire. In this study, we used productivity as the primary proxy for fuels in the calculation of severity, but future studies could separate out fuel quality and its contribution to simulated fire. Fuel accumulation may also be underestimated at sites where fire had long been excluded as well as fire exclusion's contribution to duff accumulation and smoldering fire. Using productivity as a proxy for fuels may underestimate fuel buildup in fire excluded stands. Also, the resistance of fire-adapted species to subsequent fires may be limited through development of a thicker organic horizon and increased fine root consumption during the fire (Carpenter et al., 2021). Therefore, subsequent fires may not be as severe, which would change the profile of mortality.

CONCLUSION

We synthesized models of immediate and delayed mortality resulting from fire for the mixed-intensity regime of Southern Appalachians, USA, using remote sensing, data products, and field data. Propagating these models within a landscape simulation illuminated that the inclusion of delayed mortality significantly shifted the ecological structure of the stand burned by wildfire beyond what was captured in the immediate mortality model. Crucially, it led to increased mortality in the older, larger cohorts. At the landscape scale, however, delayed fire mortality did not fundamentally shift regeneration patterns of species, owing to long intervals between fire and ephemeral windows of increased light conditions. Future changes in climate, fuel conditions, and fire weather patterns could alter this projection if fires become more prevalent on the landscape. This highlights the importance of incorporating delayed mortality into ecosystem process models for predicting future landscape fire effects and the need for further study into how wild and prescribed fire will shape the ecosystems of the Southern Appalachians.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Code and data (Robbins et al., 2022) are available from Zenodo: https://doi.org/10.5281/zenodo.6353798.

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SUPPORTING INFORMATION

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

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