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Prescribed fire management impacts on forest succession trajectories in future southern Appalachian forests

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ABSTRACT

Prescribed fire use has increased throughout the Southeastern U.S. and Southern Appalachian Mountains as an effective tool for landscape-scale fuels reduction and ecosystem restoration, yet may become more difficult in extreme weather conditions. The objective of this study is to assess long-term (100 year) forest response to divergent scenarios of climate and prescribed burning initiatives. We modeled 48, 6.25 ha sites distributed throughout western North Carolina that were selected by combining historical geospatial prescribed fire data and input from regional fire managers. For eight functional groups of tree species, we simulated 21 scenarios combining seven different prescribed fire intervals and three climate scenarios. We found that climate, burn interval, and initial forest community composition affect total biomass and functional group composition, with the least biomass occurring under hotter drier conditions and the greatest number of fires. Changes in functional group composition were most influenced by the initial forest community, then number of fires, then climate. Forest demographics were also sensitive to prescribed fire; young cohorts (<30 years) increased only when sites were burned every 10 years or more frequently, while intermediate age cohorts (30–60 years) increased only when burned every 5 years, regardless of climate and initial forest community. Our simulations and scenario design help to discern the effect of varying climatic and weather conditions, fire management, and existing forest composition on future forests. This work can be used to support fire and natural resource management planning by exploring a range of uncertainty associated with different fire and climate conditions.

1. Introduction

In the wake of land management policies enacted in the early 1900′s, wildland fire was removed from and actively suppressed in most terrestrial ecosystems in the United States for over a century (Hessburg et al., 2019; Nowacki and Abrams, 2008). Critical landscape patterns and processes that rely on frequent fire, such as forest and habitat heterogeneity (Saladyga et al., 2022), nutrient cycling (Knoepp et al., 2009), floral and faunal diversity (Holzmueller et al., 2009), and shade-intolerant plant species regeneration have been degraded or supplanted due to lack of fire (Nowacki and Abrams, 2008). To address these deficiencies, prescribed fire implementation has increased in recent decades (Hiers et al., 2020; Kolden, 2019). Prescribed fire is a widely used land management practice with critical ties to ecosystem health and cultural values (Riley et al., 2018) and is critical for reducing wildland hazardous fuels and reducing wildfire risk, promoting more resilient ecosystems, and restoring fire-adapted ecosystem function (Agee and Skinner, 2005; Kolden, 2019). We focus here on forecasting the effects of long-term prescribed fire use on forest composition in the Southern Appalachian region of the United States.

The Southern Appalachian Mountains are characterized by diverse, fire-adapted, temperate forests (Erlandson et al., 2021; Tripp et al., 2019). Trees and other species in these upland hardwood forests evolved with frequent (every 3 to 25 years), low to moderate intensity fires that were ignited by lightning and Indigenous peoples, who managed forests for multiple uses (e.g., hunting and foraging) and general land stewardship (Abrams et al., 2021; Aldrich et al., 2010; He and Lamont, 2018; Waldrop et al., 2007). Prior to fire exclusion in the late 19th and 20th centuries, more frequent, low-to-moderate intensity fires maintained less dense, more diverse, and more open forested ecosystems (Harrod

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et al., 2000). There is uncertainty about historical fire return intervals, ignition sources, and how fire return intervals may have varied throughout the region; however, there is general consensus that more fire occurred in most of the Southern Blue Ridge before the early 1900′s (Brose et al., 2001; Van Lear and Waldrop, 1989).

The onset and duration of fire suppression in the 20th century shifted forest structure and composition to more shade-tolerant and fire-intolerant mesophytic species (Abrams and Nowacki, 2015; Flatley et al., 2013, 2015). Mesophication is directly linked to the decline in oak regeneration and recruitment into the overstory, loss of fire adapted rare plant communities, and reduced biodiversity and forest heterogeneity (Brose et al., 2001, 2013). The accumulation of mesophytic forest litter limits shade-intolerant regeneration and understory biodiversity because the litter characteristics and moist microclimate inhibit the ignition and spread of lower intensity fires (Alexander et al., 2021; Dickinson et al., 2016; Kreye et al., 2013). Furthermore, during long periods of fire suppression, the formation of the organic soil layer (duff) is more pronounced near xeric species than mesic ones, which can cause more canopy decline via delayed mortality when fires consume this organic soil layer and potentially damage mature tree fine roots, typically under more severe drought conditions (Robbins et al., 2022; Carpenter et al., 2020). This positive feedback between forest composition and reduced fire negatively impacts wildlife habitat and regeneration of shade intolerant species (e.g., Quercus spp.) and raises long-term concerns for forest water use and drought resilience, particularly with increased climate variability (Caldwell et al., 2016; Hwang et al., 2020; McQuillan et al., 2024; Roman et al., 2015).

Following nearly a century of fire exclusion, prescribed fire use has increased substantially in the Southern Appalachians in recent decades, as it is one of the most practical tools to promote fire adapted vegetation, and ultimately, more climate resilient future forests. Fire adapted ecosystems and climate resilience are directly linked. Fire adapted forests burn more frequently at safer, lower intensities and promote climate resilience by reducing hazardous fuel loads to increase public safety), promoting fire-adapted oak and pine regeneration, improving wildlife habitat, and increasing forest heterogeneity and plant diversity - all of which improve ecosystem health and resilience(Elliott and Vose, 2010; Harper et al., 2016; Lafon et al., 2017; Saladyga et al., 2022). Nevertheless, questions remain regarding how often prescribed fires are needed to reset forest composition closer to a more fire-adapted state and how forest and fire use dynamics respond under different projected climatic conditions (Waldrop, 2016). Numerous field studies have been conducted to understand forest response to single and repeat prescribed fires (Keyser et al., 2017; Waldrop, 2016), varying burn intensities (Saladyga et al., 2022; Schwartz et al., 2016; Vaughan et al., 2021), and seasonality (Keyser et al., 2019; Melcher et al., 2023; Vaughan et al., 2022). Prescribed fires have been shown to promote oak regeneration and decrease overall sapling density (Brose et al., 2013); however, data do not necessarily support species composition shifts of more mature trees in response to low-intensity fires (Elliott and Vose, 2005, 2010) as these shifts are difficult to monitor and detect over 'shorter' time periods (years to a few decades).

In the Southern Appalachian region, general circulation climate projection models suggest multiple degrees of warming over the next century and increased precipitation variability. If these changes occur and cause extreme weather, prescribed burn planning and implementation become more difficult. This includes potential shifting of available prescribed burn days out of historical or known 'burn windows' or changing the total number of available days to burn (Kupfer et al., 2020; Mitchell et al., 2014). The need to manage landscapes for change amidst short- and long-term uncertainties can benefit from exploring tradeoffs and projected long-term outcomes of forest response and resilience under different management actions and climate scenarios (Scheller, 2020). Uncertainties about how temperature and precipitation regimes may change could affect forest succession patterns, raising questions about how the frequency and timing of prescribed burns may need to adjust to meet forest management goals (Hiers et al., 2020). Exploring multiple scenarios of fire management and climate or extreme weather patterns can support adaptive management by helping to inform and develop new management objectives and identify metrics for success, particularly in novel scenarios where no historical data exist (Littell et al., 2011). Previous work has shown that restoring ecosystems toward historic fire regimes (more frequent low-intensity fires) could increase resilience to future wildfires and other disturbances (Kalies and Yocom Kent, 2016).

To generate management-relevant results, we used a process-based forest change and fire model, LANDIS-II (LANDdscape DISturbance and Succession), to simulate forest composition under 21 modeling scenarios with divergent prescribed fire and climate scenarios in the Southern Blue Ridge Mountains of western North Carolina (Scheller and Mladenoff, 2004; Scheller et al., 2007). To aid model parameterization and assure management-relevance, we leveraged local wildland fire managers' knowledge to guide our simulations. We modeled scenarios with regular prescribed fire intervals (e.g., fire every five years) and restoration and maintenance intervals (i.e., where shorter, regular fire intervals were applied in the first 15 years and then longer maintenance intervals were adopted thereafter) (Warwick, 2021). We investigated how different climate scenarios interact with different prescribed fire intervals to affect forest composition using species and functional group biomass as metrics. We identify the most important and interacting effects of current forest composition, climate uncertainty, and prescribed fire management regimes on future forest composition and synthesize our results into four key management takeaways.

2. Methods

We combined historical burn permit and occurrence data (2010–2022), input from regional fire managers, and forest change modeling under three different climate scenarios and seven 100-year prescribed fire plans. We used the resultant 21 model scenarios to evaluate how forest composition responded to different prescribed fire regimes under different projected climate variations.

2.1. Study area

We modeled forest change across the Southern Blue Ridge Mountains of western North Carolina (Fig. 1). This landscape contains high elevation mountains ($\sim$ 2000 m) and exposed ridges, as well as moist, protected coves at lower elevation. Due to elevation gradients and topographic complexity, mean temperatures and mean precipitation vary across the landscape within a relatively temperate year-round climate. Mean July temperatures range from 19–25 °C and mean December temperatures range from 0–5 °C. Mean annual precipitation varies significantly throughout the region with some areas averaging $\sim$100 cm/year, while other localized areas average twice that amount (200–250 cm/year; PRISM Climate Group, 2024). The topographic variability and temperate climate of the Southern Blue Ridge landscape yields high forest biodiversity (Erlandson et al., 2021). Upland hardwood forests dominate western North Carolina and are mostly comprised of oak, maple, pine, and hickory species. Other common co-occurring species include tulip-poplar (*Liriodendron tulipifera* L.) and American beech (*Fagus grandifolia*).

2.2. Historic prescribed fire data and fire manager engagement

We used prescribed fire history and burn permit data (2010–2022) to map the locations of past prescribed burns and to identify areas in western North Carolina that are likely to experience continued prescribed fire use in the future. Fire history data consisted of geospatial prescribed fire boundaries provided by federal and state agencies and geospatial burn permit location data from the Southeast Prescribed Burn Geodatabase (Tall Timbers Research Station, 2022); these data were

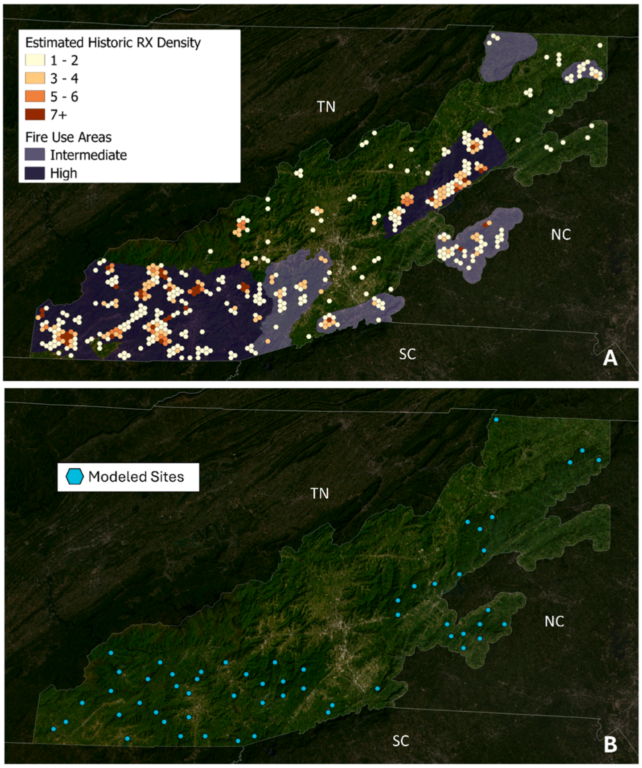

Fig. 1. Hexagonally aggregated geospatial prescribed burn permit and burn boundary data within high and intermediate fire use areas delineated by regional fire managers. Hexagons are displayed within western North Carolina and bounded by the eastern edge of the EPA Level III Southern Blue Ridge Ecoregion (A). Model sites ($n = 48$) selected from hexagons in (A) using stratified, semi-random sampling (B).

combined and known duplicates were removed to develop a single map that estimated historic prescribed (Rx) fire density (Fig. 1A). Over the course of two iterative online workshops, regional fire managers from The Nature Conservancy, The North Carolina Wildlife Resources Commission, and the Appalachian Consortium of Fire Managers and Scientists used this Rx density map to further delineate parts of the landscape thought to be high or intermediate fire use areas. Fire managers also provided generalized Rx parameters (Table 1). The fire use area boundaries and Rx parameters informed where and under what conditions prescribed fires were ignited in the simulations.

2.3. Forest change and prescribed fire modeling (LANDIS-II)

We simulated prescribed fire use and forest change using LANDIS-II, a spatially and temporally dynamic landscape change model (Scheller et al., 2007). LANDIS-II uses grid cells that interact with one another to simulate landscape processes and subsequent vegetation change in space and through time. Cells were simulated at a 250-m by 250-m (~15.5 acres) resolution, and the model was run at an annual timestep for 100

Table 1
LANDIS-II social and climate-driven fire extension (SCF) model parameters used to bound conditions when prescribed fires could occur during model simulations.

Parameter	Min	Max	Range
Temperature	−1 °C	26.5 °C	*NA*
Windspeed	*NA*	32 kph.	*NA*
Relative Humidity	20 %	60 %	*NA*
Fire Weather Index (FWI)	5	22	*NA*
Seasonality	*NA*	*NA*	334 - 65 Day of Year

years to capture forest succession, regeneration, dispersal, and mortality for 50 tree species. Species were parameterized according to their life history attributes (e.g., probability of establishment, longevity, age of maturity, shade tolerance, dispersal, etc.); species parameters are defined in Robbins et al. (2024) and are required inputs for LANDIS-II. Species cohorts (age class) were assigned to each cell, and cells can contain *Multiple species* across multiple age cohorts.

We initialized the model with near current forest conditions and assigned tree species age cohorts to each cell using US Forest Service Forest Inventory and Analysis (FIA) data (Gray et al., 2012). Each cell within the study area was assigned site characteristics (e.g., aspect, elevation, and soil composition) following Robbins et al. (2022, 2024).

We used the SCF (Social-Climate-Fire; Scheller et al., 2019), NECN (Net Ecosystem Carbon Nitrogen Exchange; Scheller et al., 2011), and Output Biomass (Scheller and Mladenoff, 2004) extensions to simulate prescribed fire occurrences and subsequent changes in aboveground living biomass. SCF simulates prescribed fire occurrences based on model parameters for average Rx fire size, seasonality, expected number of annual Rx fires, constraints on Fire Weather Index, and wind speed, and a probabilistic map indicating eligible locations (Scheller et al., 2019). LANDIS-II tracks cohorts, collections of similar aged trees of the same species, instead of individual trees. Stochastic post-fire cohort mortality is simulated using species fire-resistance curves which were parameterized using a database of field observations of bark thickness, DBH, and mortality from the Southern Appalachians (Cansler et al., 2020). Because LANDIS-II tracks age-based cohorts, tree sizes are not modeled, so an empirical model was fit for each species to relate bark thickness to age. Cohort level mortality is then probabilistically assigned by combining the effects of bark thickness and site level mortality, which is a function of effective wind speed, soil clay percentage, evapotranspiration, and climatic water deficit. When a cohort dies, Leaf Area Index (LAI) decreases and the cohort's carbon and nitrogen are then accounted for as dead biomass in NECN. Robbins et al. (2022) provides additional SCF model parameterization and calibration. To isolate the effects of prescribed fire, wildfires and other modeled disturbances (e.g., biological disturbances, wind throw, harvest) were excluded.

NECN tracks ecosystem exchanges of carbon and nitrogen between living biomass, dead biomass, and soil pools following the CENTURY model (Parton, 1996). NECN models cohort establishment and growth based on temperature and competition for available water, nitrogen, and light. Cohort regeneration depends on temperature and availability of water and light, while growth depends on species' parameterized response to Minimum Growing Degree Days, Maximum Growing Degree Days, Minimum January Temperature, Maximum Allowable Drought, Leaf Longevity, and estimates of Maximum Biomass. Species' growth, carbon, nitrogen, and lignin parameters were gathered from existing LANDIS-II models, the TRY - Categorical Traits Dataset (Kattge et al., 2012), FIA data, or other regional sources (Davis et al., 2009). Robbins et al. (2022) provides additional information on parameterization and calibration. The Output Biomass extension summarizes data from NECN's total aboveground living biomass for every desired species and age class at any user-specified timestep.

2.3.1. Climate

We used three climate projections: hotter and wetter (HW), hotter and drier (HD), and a historical random (HIST). HW and HD, are the highest emission projections (RCP8.5) and are downscaled to 4 km by 4 km from the Coupled Model Intercomparison Project (CMIP) 5 using Multivariate Adaptive Constructed Analogs (MACA) data (Abatzoglou and Brown, 2012). The 4 km by 4 km pixels are then spatially intersected and averaged within the 10 climate regions (defined by clustering historic 30-year temperature and precipitation normals; Robbins et al., 2024) of the LANDIS-II landscape. This spatial differentiation allows for different weather to be simulated daily in each of the 10 climate regions. The MRI CGCM3 RCP 8.5 projection represents the HW projection, and the HadGEM2 ES365 RCP 8.5 represents the HD projection. The HW and

HD projections were selected to bound the range of climate conditions that may shift forest composition under extreme future emissions and divergent precipitation regimes. The HW projection is one of the wetter global climate projections for the Southern Appalachian region over the next 100 years and projects a 3 °C increase in mean temperature and a mean increase of 60 mm/year in precipitation by 2100; the HD projection simulates extreme and prolonged droughts with a mean warming of 7 °C and a mean decrease in precipitation of −177 mm/year by the end of the century and has been used to evaluate forest change scenarios in the study region (Robbins et al., 2024). The HIST scenario uses data sampled from random years of GRIDMET weather data between 1979 and 2016 (Abatzoglou, 2013).

2.4. Scenario design and analysis

2.4.1. Site selection & simulations

To test the effects of different Rx frequencies and different climate projections on forest composition, we evaluated 48 sites under 21 future fire scenarios (Table 2). The 48 sites were selected from within high and intermediate fire use areas where prescribed fires have previously occurred or were permitted (Fig. 1A,B). The precision of the geospatial fire history data varied, so we aggregated all information to coarser hexagons for the final historical Rx density map. To select modeled sites based on historical prescribed fire use, we identified groups of four or more contiguous hexagons where historical Rx data occurred. From these contiguous groups of hexes, a random hex was selected (if the group contained >10 hexes, two random hexes were selected). Within each site hexagon, a contiguous group of 3 × 3 (9 total) 250×250 m cells were selected to delineate an average sized burn site (~55 ha) based on fire manager input (Table 1). Therefore, selected hexagons and modeled cells contained representative, not exact, sites of previous prescribed fires.

In addition to a scenario with no prescribed fire, we modeled six Rx management plans for each site belonging to two categories: *regular burn intervals* and *restoration + maintenance burn intervals* (Table 2). The regular interval Rx frequencies provide a comparison for the restoration and maintenance intervals which are a common management approach (Warwick, 2021). Each of these *management* scenarios was run under three climate projections for a total of 21 *future fire scenarios* (with 3 replicates each for 63 total simulations). LANDIS-II generally does not require a large number of replicates due to components of the model that tend to converge to a mean value when measured over many sites and long time periods (e.g., Loudermilk et al., 2014; Inglis and Vukomanovic, 2020). We ran each model scenario for 100 years and prescribed fire seasonality was held constant in all scenarios with burns only occurring in the dormant season (early December to early March) at low intensities. This reflects the most active season for prescribed fire in this region, and when held constant, allows for more straightforward comparisons across modeling scenarios (Van Lear and Waldrop, 1989).

2.4.2. Measuring changes in forest composition

Across these 63 simulations, we tracked aboveground living biomass for 29 species at 20-year intervals (years 0, 20, 40, 60, 80, 100). Within a single cell, biomass in year 0 is identical across all simulations. We summarized forest composition combining aboveground living biomass into two main groups—xeric species and mesic species—as defined by eight functional groups (adapted from Flatley et al., 2015; Robbins et al., 2024). Five functional groups (white oak, xeric red oak, xeric hardwood, yellow pine, and white pine) were defined as xeric, while three functional groups (maple, mesic hardwood, and hemlock) were defined as mesic. We assigned the 29 most abundant species (of 50 total) to these eight functional groups (Table 3).

We included species in the analysis if they were previously assigned a functional group by Robbins et al. (2024) *or* if the importance score ranked in the top 25 of 50 parameterized species based on basal area and count derived from Forest Inventory Analysis (FIA) data. For example, we added tulip-poplar, the third most important species, to the mesic hardwood functional group, and we removed shagbark hickory from the mesic hardwood functional group because it was ranked 46th in landscape importance. In total, we added nine species to the classifications used by Robbins et al. (2024), guided by the functional groupings of Flatley et al. (2015), and removed four species.

We aggregated forest composition data from the model replicates in three ways. First, within each of the six timesteps (years 0, 20, 40, 60, 80, 100), we averaged biomass within the eight functional groups across *all* cells for all scenarios and replicates. Second, to better understand the effect of initial forest composition on response to fire and climate, we assigned each cell to one of three categories, xeric-dominated, mesic-dominated, or mixed, based on the initial (time zero) percent composition of xeric and mesic functional group biomass. We identified cells as xeric-dominated if the five xeric functional groups contributed >66.7 % of total cell biomass; we identified cells as mesic-dominated if the three mesic functional groups contributed >66.7 % of total cell biomass; we identified cells as mixed if neither the xeric nor mesic functional groups comprised 66.7 % of total biomass. We classified 150 cells as xeric, 73 cells as mesic, and 173 cells as mixed. From here on, these are referred to as initial forest community classes or classes. Third, to understand the composition of young and intermediate aged trees that would comprise the future forest canopy, we separated biomass into two age groups: trees less than or equal to 30 years of age and trees between 30 and 60 years of age. Biomass within these age groups was output for the two or three most abundant species (defined by initial biomass) within each functional group: two maple species - *Acer rubra* (red maple) and *Acer saccharum* (sugar maple); three mesic hardwood species - *Carya alba* (mockernut hickory), *Carya glabra* (pignut hickory) and *Liriodendron tulipifera* (tulip poplar); two species within the white oak functional group - *Quercus alba* (white oak) and *Quercus prinus* (chestnut oak). We selected age 30 as a cutoff for younger biomass for all functional groups as it is an average age (near) sexual maturity for upland hardwood forest

Table 2

Categories of Rx fire management plans (A) separated by burn intervals with abbreviations (B), fire frequency (C), and the total number of fires within all LANDIS-II model runs (D) across 100 years. The description (E) of each management plan explains why it was selected for simulation.

A. Management Plan Category	B. Scenario Abbreviation	C. Fire Frequency	D. D. Total Number of Fires	E. Description of Management Plan Over 100 Years
No Fire	Unburned	NA	0	No fires occur. This scenario acts as a ‘control’.
Regular	3R	3-yr	32	Highest fire frequency to provide an upper bound for prescribed fire use.
	5R	5-yr	20	High fire frequency to simulate an actively managed site.
	10R	10-yr	10	Moderate fire frequency closer to an “average” amount of fire for most managed sites.
	20R	20-yr	5	Lowest fire frequency used to provide a lower bound for prescribed fire use on a managed site.
Restoration & Maintenance	3R10M	3-yr x 4, followed by 10-yr interval	12	12 years of frequent fire followed by a shorter maintenance interval.
	3R20M	3-yr x 4, followed by 20-yr interval	8	12 years of frequent fire followed by a long maintenance interval.

Table 3
Functional groups (adapted from Robbins et al., 2024 and Flatley et al., 2015) are separated into xerophytic and mesophytic species groups and individual species are classified into one of eight functional groups. *Indicates a species not included in Flatley et al. (2015).

Xerophytic						Mesophytic		
Yellow Pines	White Oaks	Xeric Red Oaks	Xeric Hardwoods	White Pine	Maples	Mesic Hardwoods		Hemlock
Pinus echinata	*Quercus alba*	*Quercus coccinea*	*Nyssa sylvatica*	*Pinus strobus*	*Acer rubrum*	*Betula lenta*	*Lirio- dendron tulipifera*	*Tsuga canaden-sis*
Pinus pungens	*Quercus montana (prinus)*	*Quercus stellata*	*Oxydendrum arboreum*		*Acer saccharum*	*Betula alleghen-sis*	*Magnolia macroph-ylla*	
Pinus rigida		*Quercus velutina*	*Robinia pseudoacacia*			*Carya alba*	*Quercus falcata*	
*Pinus taeda**			*Sassafras albidum*			*Carya glabra*	*Quercus rubra*	
*Pinus virginia**						*Fagus Grandi-folia*		
						Fraxinus Ameri-cana		

species (Jensen and Anderson, 2005).

2.4.3. Evaluating effects of climate, fire, and forest composition on biomass change

To quantify the relative contributions of climate, fire, and initial forest community class on increased or decreased site-level mesophication, we used the three climate levels, seven fire levels, and three initial forest community class levels as categorical 'treatments' and included a continuous covariate, site biomass at time 0. We averaged results across three replicates yielding 7583 observations across 396 sites and used *change in mesic biomass percent composition* (from time 0 - 100) as the response variable for three-way ANCOVA and PERMANOVA (Anderson, 2017) tests with interactions. We conducted Tukey Honest Significance Difference tests to understand significant interactions between factor levels.

We used nonparametric multivariate analysis of variance, or PERMANOVA, to corroborate our ANCOVA findings. For each treatment group (e.g., modeled scenario), we had almost 400 observations that yielded close to normally distributed residuals (Appendix A15), but the variances across our treatment groups were not truly homogeneous, necessitating a comparison of ANCOVA and PERMANOVA results. We conducted the PERMANOVA tests using the 'adonis2' function with a Euclidean distance matrix within the Vegan Community Ecology Package (v2.6–10) (Oksanen et al., 2025) in the R statistical language (v4.2.1; R Core Team, 2022). PERMANOVA uses permutations ($n = 999$) and pseudo-F statistics to estimate p-values; it leverages between-observation distances to partition distance matrices among multiple sources of variation and fits linear models using distance matrices. This approach is recommended when multivariate normality and homogeneous variance cannot be assured because it attempts to differentiate statistical differences between different locations of a group means versus differing amounts of dispersion around group means (Anderson and Legendre, 1999).

3. Results

3.1. End of 100-year simulation total biomass - all scenarios

We assessed the percentage change in mean total biomass from time 0 to time 100 for all sites for each of the 21 modeled scenarios. Biomass increased the most in the unburned scenario (HD: 16.2 %, HIST: 18.1 %, HW: 29.4 %), while biomass decreased the most in the 3R scenario (HD: −91.0 %, HIST: −82.6 %, HW: −66.8 %) (Fig. 2). HD (hotter, drier) climate consistently yielded the lowest mean biomass at year 100 for all Rx scenarios, except 5R, while HW (hotter, wetter) climate yielded the greatest mean biomass. For all climate projections, the largest increase in mean biomass between adjacent Rx scenarios occurred between the 3R and 5R, with 33 and 20 burns, respectively (Table A1). For HD and HIST climate, biomass only increased under the 20R and unburned scenario, five and no fires, respectively; for HW climate, biomass increased for all Rx scenarios except 5R and 3R (Fig. 2).

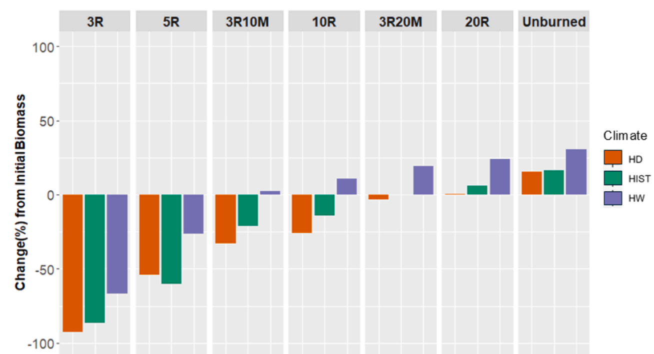

Fig. 2. Mean percent change from starting biomass (time 0) to end of 100-year biomass (time 100) colored by climate scenario (hotter, drier - HD; historical – HIST; hotter, wetter – HW). The number of fires in each Rx scenario increases from left to right, with no fire in unburned.

3.2. Time-varying mean total biomass and percent composition by functional group

We initialized 48 sites with ~12,000 g/m^2 mean cell biomass and with the following functional group composition, by percent composition (averaged across all sites): white oak (30.2 %), mesic hardwood (21.3 %), xeric red oak (13.5 %), maple (11.4 %), white pine (12.0 %), xeric hardwood (4.6 %), yellow pine (4.7 %), and hemlock (2.3 %) (Fig. 3).

Climate-induced differences in mean total biomass are most apparent in later years of the simulations. Under HD climate and no fire, mean total biomass decreased (~1000 g/m^2) between year 80 and year 100 (Fig. 3, top left), while HW and HIST biomass stabilized; for the 3R Rx (i.e. most fire) scenario, mean biomass under HD and HIST climate decreased in all years while mean biomass for HW climate stabilized between year 60 and year 100 (Fig. 3, top right). HD and HIST climate only increased between year 80 and year 100 under the 20R Rx scenario (Appendix A5). Generally, differences between HW climate and the other two climates became more pronounced in later years.

Variability in cell biomass declined from time 0 for all Rx and climate scenarios. The 5R Rx scenario was an exception, as biomass variability increased for all climate scenarios from year 20 to year 100 (Appendix A1). For all scenarios, end-of-100-year mean biomass for HW climate was greater than the upper quartile of mean biomass in the HD climate (Fig. 3, Appendix A1–5). Differences in mean biomass and interquartile

Fig. 3. Boxplots of total biomass per cell (top row) and percent composition for the eight functional groups (bottom row) at 20-year intervals for all climate projections (hotter, drier - HD; historical – HIST; hotter, wetter – HW) and for the burn scenarios with no fire (unburned, left) and the most fire 3R (right). Time 0 biomass is identical for all panels.

range (IQR) were greatest between the 5R Rx scenario (20 fires, more variability) and the unburned (no fires, less variability). For example, the average IQR for all climate projections within the 5R Rx scenario is 5445 g/m^2, while the average IQR within the control scenario is 1863 g/m^2, which is, on average, a 65.8 % reduction in the IQR between 20 fires and no fires (Fig. 3, Appendix A1). The most fire scenario (3R) maintained relatively equal IQRs across climate scenarios from early to mid-simulation, but the climate scenarios diverged between years 80 and 100 where the greatest difference in IQR across climates for any Rx scenario was observed in year 100 (HW: 3907.5 g/m^2 and HD: 1085.0 g/m^2) (Fig. 3).

Across all climate projections, the unburned scenario (Fig. 3, bottom left) experienced small but consistent increases in white oak, xeric red oak, maple, and hemlock through time, with consistent decreases in mesic hardwoods, xeric hardwood, and yellow pine. Without fire, xeric hardwoods and yellow pine decreased considerably by year 40 and were nearly eliminated by year 100 (Fig. 3, bottom left). Maples increased to ~20 % composition from their original composition (11.4 %) in the early to middle years of the simulations and then decreased to near initial percent composition, except under the HD climate, in which maples end of 100-year biomass increased by ~5 % composition to a total composition of 15 %. Mesic hardwoods decreased by about ~25 % to year 40 under all climate scenarios and then stabilized until year 100.

The 3R Rx scenario experienced the greatest decline in percent composition of maples, xeric red oaks, and white pines, respectively. Decreases in percent composition showed a small but clear response to climate scenarios and declines were most pronounced from year 80 to year 100 (Fig. 3, right). The white oak functional group increased through time and across all climate projections from 30.2 % initial composition to year 100 % composition of 39–47 %. With fire every three years, xeric hardwoods and yellow pine functional groups declined in the middle of the simulations but increased in percent composition toward the end of the century under all climate projections (Fig. 3, bottom right). With frequent fire, mesic hardwoods declined less than under the unburned scenario.

3.3. 100-year change in functional groups

We synthesize mean changes in percent functional group composition by comparing time zero mean biomass with mean biomass at time 100 across all functional groups, modeling scenarios, and initial forest community classes (Fig. 4). We chose to report change in percent composition, instead of percent change, so as not to inflate the importance of increases in functional groups with less biomass or decrease the importance of change in functional groups with more biomass. For example, a change in percent composition from 2 % to 3 % is equivalent to a change of 1 % not 50 %.

Percent total biomass composition varied with prescribed fire (3R, 5R, 3R10M, 10R, 3R20M, 20R, unburned), climate (hotter, drier; historical; hotter, wetter), and initial forest community class (xeric, mixed, mesic). Generally, xeric functional groups (top five rows of an individual grid) declined (1 - >15 %) or remained the same under all climate scenarios, except in mesic initial communities where xeric red oak and white pine biomass increased under all fire scenarios. The white oak functional group is an exception, as it behaved differently than all other xeric functional groups. White oaks increased the most (5 - >15 %) of all

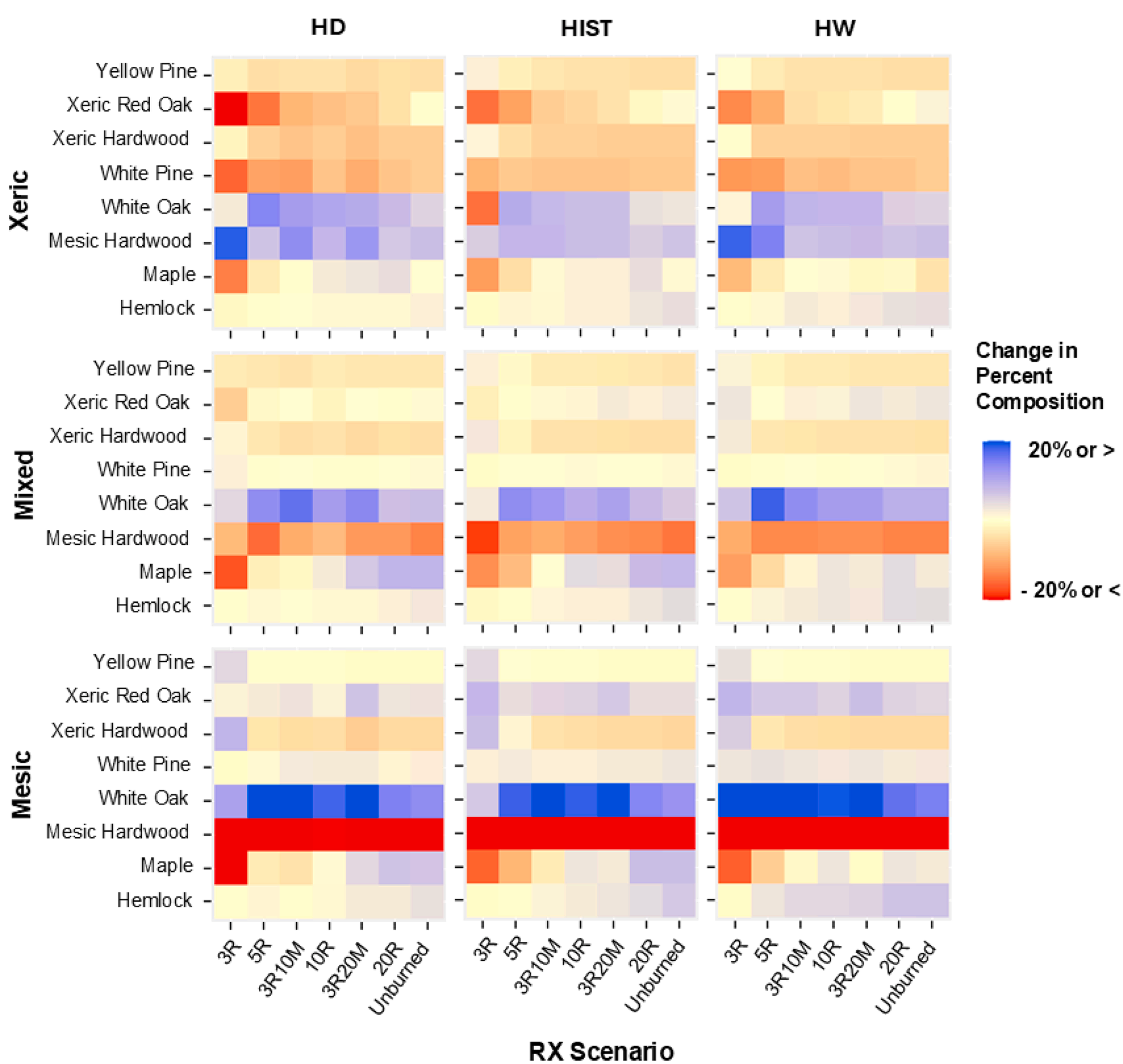

Fig. 4. Nine heatmaps (blue = increase, red = decrease) showing average change in total biomass percent composition between year 0 and year 100 for the eight functional groups (y-axis, individual grid) across the seven Rx scenarios (x-axis, individual grid) within the same climate projection (columns) and initial forest community class (rows). Xeric functional groups comprise the top five rows of each individual grid and mesic functional groups the bottom three rows.

eight functional groups under all climate projections, but biomass increases were generally smaller in scenarios with fewer fires, except in mesic communities where little to no response to the amount of fire was detected and biomass increased considerably (12 - >15 %). Notably, the only increases in biomass for xeric hardwoods and yellow pine occurred when burned every three years. Changes in xeric functional groups' biomass, both increases and decreases, varied more across the three initial forest community classes than across the three climate scenarios.

The three mesic functional groups (bottom three rows of an individual grid) responded dissimilarly to prescribed fire, climate, and initial forest community class. Maple and hemlock biomass clearly responded to the number of prescribed fires within the functional group individual row, while changes in mesic hardwood biomass were largely driven by the initial forest community class, as shown by increase or decreases driven by the xeric, mixed, and mesic heatmap rows. Mesic hardwoods increased (4 - >15 %) under all climate and fire scenarios in xeric communities and decreased (3 - >15 %) under all climate and fire scenarios in mixed and mesic communities. Unique from any other functional group, maples showed a 'negative-to-positive' pattern of change from the most to no fire scenarios, respectively. Maples only decreased under HW climate in xeric communities. Hemlock biomass mostly increased gradually for all communities and climates in response to decreasing amounts of fire. The greatest increases (~7 %) occurred under HIST and HW climates in scenarios with minimal to no fire, and the least change and muted response to the amount of prescribed fire occurred under HD climate in xeric communities.

Of the three independent factors and covariate - climate, fire, initial forest community class, and starting biomass, respectively - the factorial ANCOVA indicated that initial forest community had the largest effect on change in percent composition of mesic biomass, followed by starting biomass, fire, and climate (Table 4). All main effects were significant (P, 0.000), and there were significant (P, 0.000 – 0.05) but smaller interactions among all factors; the three-way interaction between climate, fire, and initial forest community had the smallest effect. The interactions including class and fire had larger effects than those with climate (Table 4); in turn, change in percent of mesic biomass composition was most stratified by initial forest community class, followed by fire and finally climate (Fig. 5).

The Tukey Honest Significant Difference (Tukey HSD) test showed the factor level relationships likely responsible for the significance in interactions by evaluating pairwise comparisons of all levels within each factor. For initial communities, all pairwise comparisons were significantly different when evaluating change in percent mesic biomass composition (Table A3). For climate, HW-HD (P, 0.001) and HD-HIST (P, 0.05) were each significantly different, while differences in HW-HIST were not significant (Table A2). For prescribed fire, comparisons involving the scenarios with the most fire (3R, 5R) were all significantly different. Comparisons of the unburned simulations to both the 20R and 3R20M simulations were not significantly different, while pairwise comparisons of low to moderate fire simulations (20R, 3R20M, 3R10M, and 10R) yielded mixed results of both significant and not significant differences (Table A4). Notably, 20R was significantly different from both the 3R10M and 3R10M, while 10R was not significantly different from either scenario modeling restoration and maintenance burn intervals.

Table 4
Summary of three-way ANCOVA using a single continuous covariate (Total_BM_Start; year 0 total biomass) to assess the effect of three factors - climate projections (Climate), prescribed fire (Rx), and initial forest community class (Class) - on percent change in mesic biomass. Significance indicated as: 0 (***), 0.01 (**), 0.05 (*), >0.1 (not significant).

Term	DF	Sum Sq.	Mean Sq.	Statistic	p-value	
Total_BM_Start	1	9.8681	9.8681	262.6939	0.0000	***
Climate	2	0.9649	0.4825	12.8436	0.0000	***
Rx	6	13.0562	2.1760	57.9272	0.0000	***
Class	2	108.2293	51.1147	1440.5586	0.0000	***
Climate : Rx	12	1.3650	0.1137	3.0280	0.0003	***
Climate : Class	4	0.3223	0.0806	2.1449	0.0726	.
Rx : Class	12	2.4262	0.2022	5.3821	0.0000	***
Climate : Rx : Class	24	1.5842	0.0660	1.7572	0.0125	*
Residuals	8252	309.9868	0.0376			

Both the ANCOVA and PerMANOVA identified initial forest community class as the most important and highly significant factor impacting change in percent mesic biomass (Tables 4, A2). Prescribed fire was second most important followed by climate – all factors and interactions were significant (Table 4). Because significant interactions occurred and often suggest that relationships between factor levels (i.e., climate: HW, HD, HIST) are not stationary, we conducted a Tukey HSD test to explore differences between factor levels. Factor importance and interactions, along with their significance results, were consistent between ANCOVA and PerMANOVA (Tables 4, A5). Both tests identified significant differences between the three initial forest community classes (Tables A3, A7). However, ANCOVA and PerMANOVA disagreed in their identification of significant pairwise factor level comparisons for climate and prescribed fire scenarios. For climate, PerMANOVA results were inverse of that for ANCOVA. HW-HIST was the only significantly different comparison (Tables A2, A6). For fire, the only insignificant comparisons identified by PerMANOVA were Unburned-20R and 3R20M-10R (Tables A4, A8).

3.4. *Forest demography response to Rx & climate scenarios*

The biomass responses of young trees (<30 years) to climate and Rx scenarios differed from that of intermediate age trees (30–60 years) for all species we investigated based on (1) general shape of the biomass curve through time, (2) timing of biomass local minima and maxima, and (3) end of 100-year biomass (Fig. 6). These three parameters varied most by functional group and species, but initial forest community class and climate increased biomass variability within a given burn scenario.

For all species, young trees comprised a small fraction of initial biomass, which increased as young cohorts aged and grew. Young trees were more likely to gain biomass up to one, or two, mid-simulation peaks and then decline relatively symmetrically toward the end of the simulation, with the exceptions of young trees under the 3R and 5R scenarios which varied more in response to more fires (Fig. 6C, Appendix A11). The maximum mean young biomass occurred under the 3R20M prescribed fire scenario and was just under 600 g/m^2 in year 40 (white oak, xeric -Fig. 6B). Intermediate-age tree biomass declined from its initial biomass in all scenarios for all species on all sites; though, under all but the most-fire scenarios, intermediate biomass experienced a local maximum around year 60.

For a given species and age class, less inter-climate variability in mean biomass occurred in the unburned than in the 3R20M and 3R scenarios (Fig. 6). Mesic and mixed sites yielded slightly greater biomass for both young and intermediate-aged maple species and mesic hardwood species, while xeric sites yielded the greatest biomass for white oak species. Red maple, tulip poplar, white oak, and chestnut oak contributed most to young and intermediate-aged biomass, with the greatest biomass occurring under scenarios with moderate amounts of fire (3R10M, 10R, 3R20M). For sugar maples and hickories, young and intermediate cohorts generally required moderate to frequent amounts of fire to gain any biomass throughout the 100-year simulation, but young sugar maples declined under the most frequent fire scenarios (3R & 5R) (Fig. 6, Appendix A11–14).

4. Discussion

Natural resource managers are challenged with managing forests under climate uncertainty (Hwang et al., 2020; McQuillan et al., 2024), and there is consensus that increasing prescribed fire use is a key

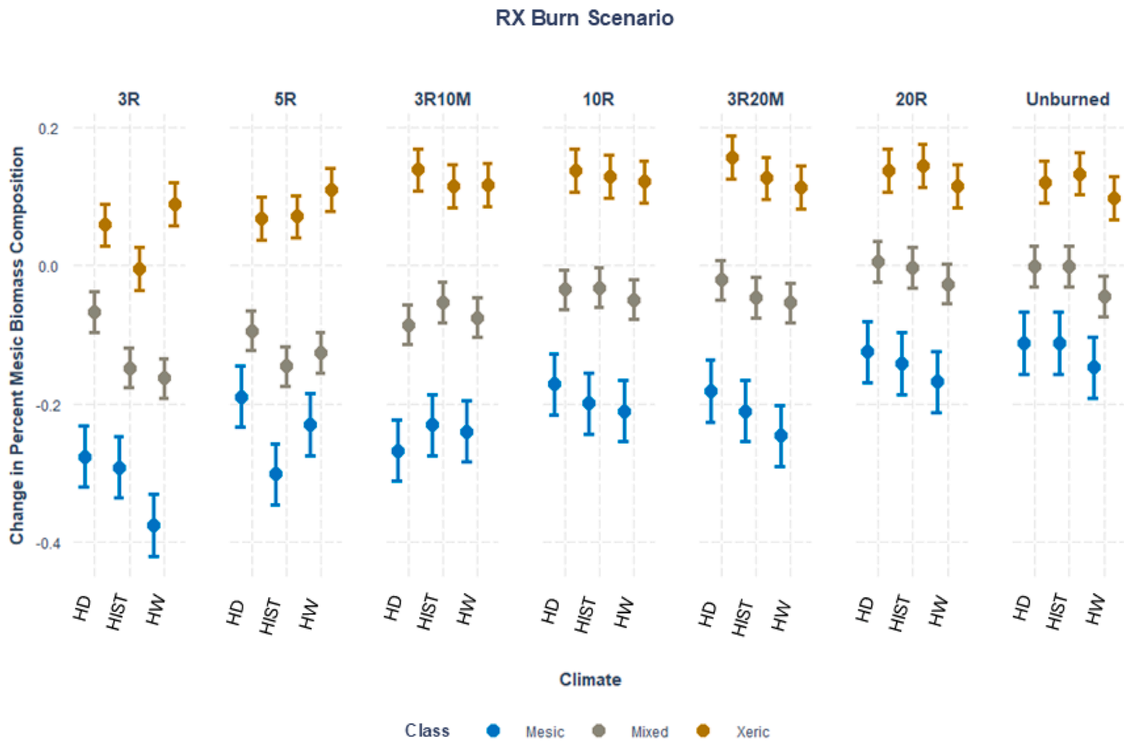

Fig. 5. Three-way ANCOVA interactions for seven prescribed fire scenarios, three climate scenarios, and three initial forest community classes.

component of promoting more diverse, wildfire-resilient, and healthy future forests (Elliott and Vose, 2010; Harper et al., 2016; Lafon et al., 2017; Saladyga et al., 2022). But, restoration and maintenance of forest communities is made challenging by the interacting effects of current forest composition, climate uncertainty, and prescribed fire management regimes. Here, we identify four specific findings relevant to fire managers from this work: (1) burning more than every 10 years is required to reduce biomass, while burning more than every five years is required to promote pine and xeric hardwoods, (2) hotter, drier climate may present unique fire management considerations particularly with frequent fire use (<10 years), (3) future forest composition is most dependent on the current forest community, followed by prescribed fire, and then climate and, (4) it is necessary to understand co-occurring changes and treatment effects on total, intermediate, and young biomass to develop future climate-adaptive forest management strategies.

In this study, the current forest community was the single most important determinant of future forest composition, outweighing prescribed fire use and climate as the second and third most impactful, respectively (Table 4, Fig. 5). Therefore, managing future forests may depend most on current stand composition and prescribed fire regime and less on future climate variability. Attempting to restore pre-fire suppression forest communities under moderate prescribed fire use will take longer than the career of any natural resource manager. While it is possible to achieve more dramatic changes in biomass and substantially reduce mesic species with frequent burns (3–5 years) (Fig. 4), higher burn frequencies are difficult to achieve over large spatial extents with existing barriers to prescribed fire and will ultimately present tradeoffs between reducing biomass, carbon storage, and forest regeneration (Smithwick et al., 2024; Martin et al., 2015; McDowell et al., 2021). Though, future climate does directly impact total biomass, under all prescribed fire scenarios, and underscores the need for long-term monitoring of forest response to inform adaptive fire management (Figs. 2, 3). The trend of forest mesophication has taken hold in less than a century, but fire-adapted forests evolved over millennia and will take time to shift toward more open, less mesophytic forests that are characteristic of pre-fire suppression conditions.

Comparing aboveground forest biomass trajectories under different climates for the same prescribed fire management scenario provides a metric for climate's influence on increasing or decreasing the amount of biomass on the landscape. We found end-of-100-year biomass increased most from starting biomass under hotter, wetter (HW) climate, with less pronounced differences between hotter, drier (HD) and historical (HIST) climate (Fig. 2, Table A2). This is consistent with other work that has estimated HW climates will increase Aboveground Net Primary Production (ANPP) and biomass for this region and globally (Mickler et al., 2002: Mekonnen and Riley, 2023). Of note, the HD climate has twice the amount of end of 100-year warming as HW. Variability in 100-year biomass was greatest under the 5R scenario for all climates, while the unburned scenario displayed the least variable mean and IQR for 100-year biomass (Appendix A1–5). No clear differences in biomass trends emerged between restoration and maintenance interval scenarios when compared to scenarios with comparable regular burn intervals.

Higher biomass on xeric sites was driven by increases in dominant white oak and mesic hardwood functional group biomass for all climates, while lower biomass on mixed sites was driven by losses within the yellow pine, xeric hardwood, and mesic hardwood functional groups (Arthur et al., 2015; Brose et al., 2013). Increased percent composition of the white oak functional group suggests continued dominance, but losses of other xeric functional groups on xeric and mixed sites is consistent with the patterns of shifting species composition caused by mesophication (Flatley et al., 2015). Increases in the mesic hardwood functional group, specifically tulip poplar, may drive xeric functional group losses across a variety of Rx scenarios (Fig. 6). Complementary to our findings of increased white oak biomass in all scenarios, other works suggest that future conditions may favor oak functional groups, even under passive management, but active fire management will help to promote healthier, oak-dominated forest (Vose and Elliott, 2016; Robbins et al., 2024).

White oak, tulip poplar, and red maple young and intermediate biomass curves experienced the most climate variability under scenarios with the most fire (3R, 5R, 10R), which supports the need to further

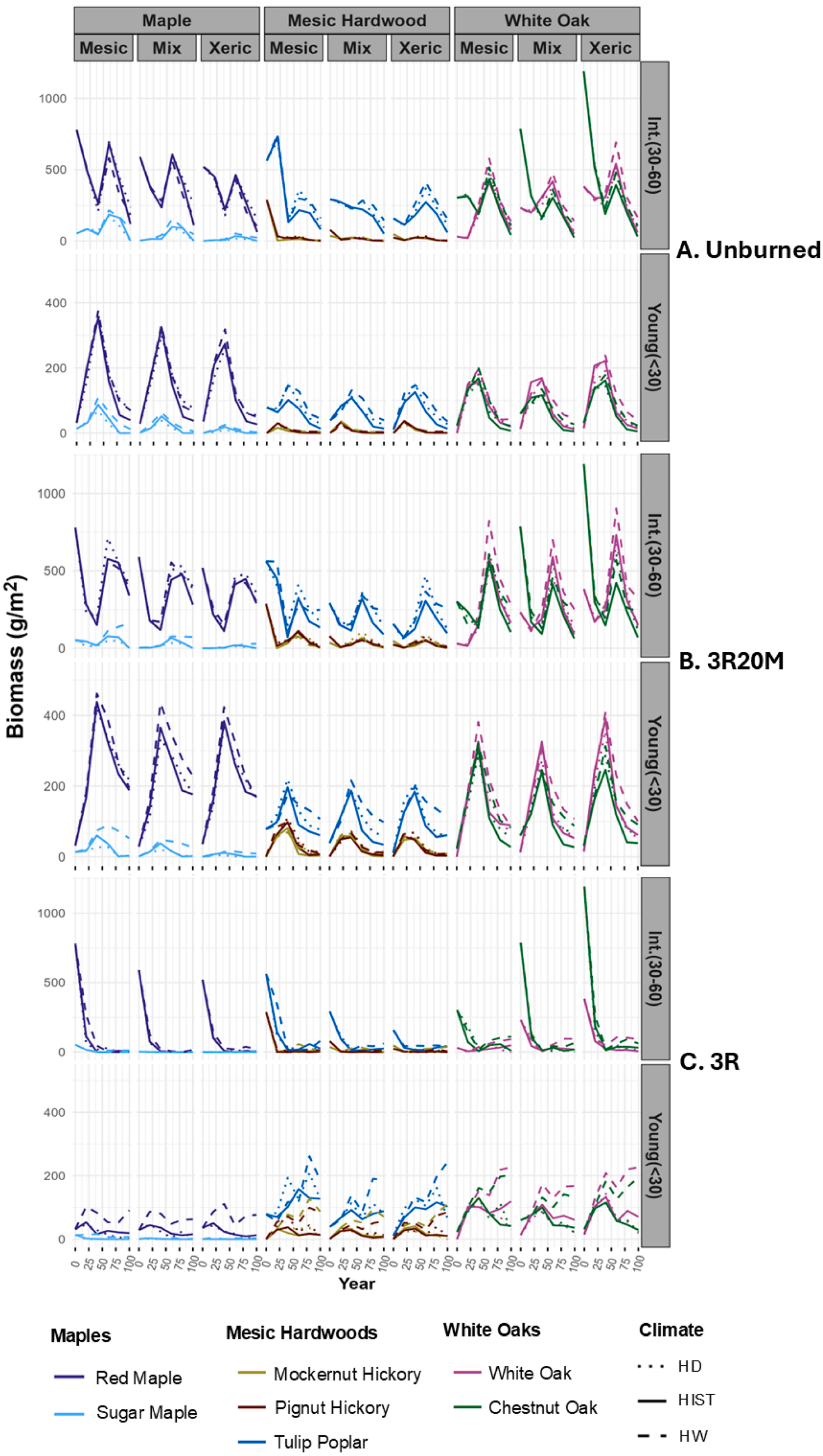

Fig. 6. Individual plots represent the Unburned (A) 3R20M (B) and 3R (C) Rx scenarios. For individual frames within plots, lines show mean biomass for each species across all timesteps (0, 20, 40, 60, 80, 100) with line type indicating climate. Individual frames are defined by one of three functional groups with the greatest biomass (Maples, Mesic Hardwoods, White Oak) and one of three initial forest community classes (mesic, mix, xeric) and by intermediate biomass 30–60 years of age (top row) or young biomass < 30 years of age (bottom row). Each species' time 0 biomass is the same across all frames.

monitor species response to future climate. No observed data span the length of our simulations or capture the same number of fires, but plot-level monitoring data have found after repeated fire (three or four prescribed fires) species' responses are increasingly variable and may depend more on site characteristics (Jenkins et al., 2011; Schwartz et al., 2016). Adaptive management priorities and objectives should be designed with these site-level differences in mind. Our findings suggest that continued mesophication, stabilization, or reversion to pre-fire suppression xeric-dominated composition depends most on the existing forest community. Specifically, mixed and mesic sites will require increased fire use to reduce maples while mesic hardwoods (hickories, tulip poplars, ashes, red oaks, birches) may decline under most fire scenarios. The 5R and 10R fire scenarios yielded increases in young mesic biomass over the 100 years, which is consistent with other work that has shown small stems of red maples and other species resprouting with frequent fire particularly on more mesic sites, while white oaks tended to respond positively to more frequent fire on mixed and xeric sites (Arthur et al., 2015; Keyser et al., 2017). Of note, sharp declines in intermediate Chestnut Oak biomass observed in earlier years (0–40) are due to the composition of initial communities parameterized from FIA data. Most sites with Chestnut Oaks were initialized with Chestnut Oaks between 30–60 years of age, so these trees 'age out' of intermediate biomass within the first 40 years of the simulation. Declines in biomass are most pronounced on Mixed and Xeric sites, as Mixed and Xeric sites contain more than double and triple, respectively, the mean initial Chestnut Oak biomass of Mesic sites (275 g/m^2) (Fig. 6). In turn, white oak functional group composition is projected to increase *most* on mesic and then mixed sites (Fig. 4). These compositional increases in white oak biomass did not correspond with increases in young or intermediate biomass for any fire scenario, which may indicate that increased white oak composition is due only to biomass gained by existing large trees not regeneration (Fig. 6, Appendix A10–14).

The mesic hardwood group stabilized and gradually increased in percent composition with fire every five years, which may be due to the mixed composition of more and less fire adapted species within the mesic hardwood functional group. The established functional groups are not monoliths - the mesic hardwood functional group includes a collection of species with different levels of fire adaptation (e.g., *Quercus rubra* vs. *Liriodendron tulipifera*) and some species that are not at all fire adapted (e.g., *Betula allegheniensis*) (Warwick, 2021). By aggregating into functional groups, we have averaged fire and climate responses that may be dissimilar enough to merit reevaluating the traits of individual species and exploring different groupings. Individual response to fire and anticipated responses to climate depend on co-occurring species and site characteristics (Schwartz et al., 2016; Vose and Elliott, 2016; Waldrop et al., 2007), so a more in depth analysis of individual species and sites may yield additional variation in pyrotolerance and climate, beyond that characterized in Figs. 3–6.

Further separating the data by age *and* species showed that relatively few species drive biomass change within functional groups, and generally, within the same functional groups, species responses were similar regarding the shape and magnitude of biomass change through time (Fig. 6). It is important to note that species' growth and biomass accumulation is not directly related to the occurrence of fire but rather the decrease in competition for water and light following a fire. Competition for light is generally the limiting factor on regeneration and growth in this ecoregion, and prescribed fire directly reduces this competition by probabilistically (based on age, fire tolerance, and site conditions) removing cohorts in the under-, mid-, and overstory. Few species being responsible for biomass change is consistent with other field-based studies that have shown existing dominant species strongly influence future forest composition (Arthur et al., 1998), even with the introduction of prescribed fire and alternate climates (Table 4, Fig. 5). Though, these dominant species (red maple, tulip poplar, white oak, and chestnut oak) behaved differently across climate and Rx scenarios and within different communities (xeric, mixed, and mesic), which further emphasizes the need for tailored species- or site-specific management objectives.

4.1. Implications for managing forests with fire under variable climate conditions

Burning more than every 10 years was most likely to stabilize biomass or decrease it from initial levels, regardless of climate scenario (Fig. 2). Without fire, increased biomass can be attributed, in part, to infilling and densification of the forest under- and midstory (Nowacki and Abrams, 2008). But given broad forest management objectives to reduce fuels to limit wildfire risk and reduce forest density to promote forest resilience (drought, disease, etc.), fire every 10 years or more is necessary to meet these objectives. Our results support previous work that found fire intervals shorter than 10 years may reduce maple biomass and possibly shift forest composition in favor of more xeric species (Boerner et al., 2008; Keyser et al., 2019). Our results suggest that burning every five years or more has mixed effects on different sites. Burning more than every 10 years was required to decrease maple composition, while only the 3R Rx scenario increased composition of white pine, yellow pine, and xeric hardwoods (Fig. 3). We also found that more fires lead to the most variability in total biomass and species' response to different climates (Figs. 3, 6, Appendix A1–2), further highlighting the need for adaptive management as we move into a future with more fire use.

Climate effects on total biomass and functional group percent composition were amplified over longer timescales (mid to late simulation) and these differences were most apparent within young biomass (<30 years) (Fig. 6). While we found a loss of total maple biomass on all sites under 5R, red maple young biomass doubled or more under hotter, wetter and historical climates (Fig. 6). Field-based studies confirm that mid- and understory red maples and other hardwoods will increase in stem density, largely due to resprouting following multiple fires (Blankenship et al., 2023; Harrod et al., 2000). This slower but consistent 'release' of young species biomass across all sites and climates—-most pronounced under the 5R, 3R10M, and 10R Rx scenarios—supports the need for maintaining a regular fire interval that creates open canopy, reduces competition for maturing trees, and promotes continued regeneration throughout the century (Fig. 6) (Brose et al., 2013; Vose and Elliott, 2016). Our models suggest fire as much as every three years is necessary to substantially reduce composition of maple biomass, but in turn, substantially decreases total site biomass, and ultimately, recruitment into the mid- and overstory (Fig. 3). Adding an additional age class of 0–5 years or 0–10 years would better highlight these changes in younger biomass due to stem regeneration, resprouting, and recruitment.

Young and intermediate biomass response is the longer-term indicator of forest composition in the absence of other major disturbances, which we have excluded here. Without fire, modeled young and intermediate age trees declined substantially in the last 50 years. This decline may be attributable to biomass 'aging out' of the age classes we designated and indicating a steady progression of maturing trees, as well as densification or mesophication of forests limiting overall regeneration. However, in the case of the 3R Rx scenario, the precipitous drop and suppression of the intermediate biomass curve indicates that few young trees are being recruited, and the upward trends in most species' young biomass may be due largely to increased resprouting following fire.

The pronounced decreases in total biomass modeled under the 3R scenarios are a combination of fire reducing existing mid-story cohorts and preventing regeneration and recruitment from seedlings to saplings, as well as non-fire related mature tree mortality occurring throughout the 100-year simulation. Field studies have observed losses in overstory and mid-story trees and minimal regeneration with fire every three years (Peterson and Reich, 2001; Waldrop, 2016; Knapp et al., 2022; Melcher et al., 2023). Previous work in northern oak savannahs observed a mean annual decrease in tree density of 2–8 % when burned every 2 to 4 years for a decade and a mean annual decrease of 1–7 % for basal area (Peterson and Reich, 2001). Additionally, a field study in the southern Appalachians observed decreases in overstory basal area and stem density following three prescribed fires in one decade; overstory basal area decreased $1m^2$/ha, while overstory density decreased by more than one-third from 632 to 401 stems/ha (Waldrop, 2016). Other field studies focused on regeneration, recruitment, and altered canopy cover in temperate broadleaf forests indicate that fire free intervals may be necessary to promote regeneration and recruitment (Knapp et al., 2022) and early growing season burns can reduce canopy closure (Melcher et al., 2023).

Our modeled results suggest frequent fire may considerably alter forest structure. This generally parallels the field-based observations described above, particularly considering these studies rarely reference more than a decade of forest response to frequent fire. Modeling thirty-three fires in 100 years yields a more frequent and persistent fire regime than even the most fire-adapted species in this region would have evolved under and does not represent a likely fire management scenario. The probabilistic mechanism controlling cohort mortality within the SCF extension could overestimate loss of biomass relative to empirical conditions, as it may struggle to mimic the realistic patchiness of fire effects across a site. We suspect SCF may artificially inflate post-fire mortality, specifically for low severity fires as modeled here, for two main reasons 1) as more fires are simulated, even the most fire-adapted cohorts are more likely to experience random mortality due to the repeated exposure to fire and 2) entire cohorts are removed from the system, not randomly selected individual trees.

While this overestimate of young cohort mortality skews results toward large declines in biomass that may be magnified through time, we believe the fire management implications remain the same: frequent fire (<10 years) is needed to reduce mesophication and restore fire-adapted vegetation. Site and climate-specific adaptive management strategies must be revised as forest response to multiple treatments, disturbances, and climate pressures are learned. Specifically, additional long-term monitoring data at sites with repeated fires are needed to document changes in young biomass composition and shifts in overstory dominance to adaptively manage under different climate conditions and across a variety of managed sites.

Woody shrubs were not included among the 50 species we parameterized for the LANDIS-II model. Species such as *Rhododendron* spp. (rhododendron) and *Kalmia latifolia* (mountain laurel) are of management interest because they are abundant in the mid- and understory on mesic (rhododendron) and xeric sites (mountain laurel) and have been associated with reduced tree seedling recruitment and survival, limited mature tree growth, and more difficult fire management (Dharmadi et al., 2022). Excluding these species means excluding positive ecosystem feedbacks, such as less flammable litter and less sunlight in the understory, that facilitate shifts in forest composition in the absence of fire (Nowacki and Abrams, 2008). Due to the minimal light and airflow that perpetuates damp conditions within these woody shrub stands and the generally less flammable fuel structure of more mesic species, fire managers may need to burn during the growing season and into drier summer and early fall conditions (typically outside of the management prescriptions in this region) to reduce woody shrubs and other mid-story mesophytic species (Alexander et al., 2021; Dickinson et al., 2016; Vaughan et al., 2022). Because we do not capture the effects of these species, we may overestimate the composition of modeled species, such as white oaks, and may minimize signs of widespread mesophication, even under the unburned scenario.

Current forest communities are inherently tied to prior management and disturbance, and so, the continued burning of previously managed sites is important to maintain fire-adapted communities and realize the full suite of benefits of prescribed fire use (Pile Knapp et al., 2024). For sites with little to no recent prescribed fire use, older, established trees represent a large proportion of biomass and are unlikely to be killed in low severity burns, preventing any near-term significant shifts in forest composition. However, promoting future fire-adapted forest communities will require frequent fire (3–10 years) to control young and mid-story composition while forest succession progresses (Fig. 5). Frequent fire alone precludes young biomass regeneration, and so, consistent with other work, additional treatments (thinning, herbicides, etc.) in the mid- and understory, along with fire-free intervals, are likely necessary to promote regeneration of preferred species and avoid suppressing all regeneration and overstory recruitment from too much fire (Knapp et al., 2022; Cuprewich and Saunders, 2024; Pile Knapp et al., 2024; Turner et al., 2025).

Given the exclusion of natural disturbances (wildfire, wind, pests) from these simulations, our findings offer an experiment-based approach to quantify the estimated contribution of prescribed fires alone to shift forest composition under climate change. Field studies are rarely conducted without confounding disturbances that may be difficult to control for or to isolate the effects of any given variable, so this simulation approach offers a scenario-based, quantifiable assessment to inform existing questions about how consistent burning at different frequencies could alter forest composition. The future of southern Appalachian wildland fire modeling and research should integrate long-term studies like we have presented here with long-term monitoring data. Scenario modeling of divergent prescribed fire and climate scenarios, in the absence of complementary field data, provides a foundation for developing adaptive management objectives that incorporate uncertainty. Executing climate-adaptive forest management requires responding to trends in observed data, but with only a few decades of consistent monitoring data, the path to restoring more diverse, open forests includes consistent, low-to-moderate intensity prescribed fires at numerous managed sites.

5. Conclusion

This study uses a forest change model to simulate prescribed fire management strategies under different climate scenarios to explore alternate outcomes in future forest composition. It is the first known forest and fire modeling effort to focus solely on the outcomes of a range of prescribed fire regimes in the Southern Appalachian Mountains. Without extensive field-based observations over long time periods, process-based and stochastic modeling scenarios can help to bound possible future outcomes of prescribed fire and understand the relative impacts of climate, fire, and existing forest communities on future change. The results underscore the need for adaptive management and continued quality monitoring data that persist over long time horizons because the interactions between forest species composition, prescribed fire use, and climate are non-linear. These findings may guide the development of climate-adaptive fire management plans to meet forest health and restoration objectives by providing a blueprint for possible forest responses to long-term fire management and potential climate variations.

CRediT authorship contribution statement

Kate Jones: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jelena Vukomanovic:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Zachary J. Robbins:** Writing – review & editing, Methodology, Data curation. **Robert M. Scheller:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Kate Jones reports financial support was provided by Joint Fire

Science Program. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2025.111323.

Data availability

Data will be made available on request.

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