Robbins *et al. Fire Ecology* (2024) 20:2
https://doi.org/10.1186/s42408-023-00231-1

Fire Ecology

ORIGINAL RESEARCH

Open Access

Fire regimes of the Southern Appalachians may radically shift under climate change

Zachary J. Robbins[1*], E. Louise Loudermilk[2], Tina G. Mozelewski[3], Kate Jones[4] and Robert M. Scheller[1]

Abstract

Background Increased drought due to climate change will alter fire regimes in mesic forested landscapes where fuel moisture typically limits fire spread and where fuel loads are consistently high. These landscapes are often extensively modified by human land use change and management. We forecast the influence of varying climate scenarios on potential shifts in the wildfire regime across the mesic forests of the Southern Appalachians. This area has a long history of fire exclusion, land use change, and an expanding wildland urban interface. We considered interactions among climate, vegetation, and anthropogenic influences to forecast future fire regimes and changes to the forest structure. We used climate scenarios representing divergent drought patterns (overall drought trend and interannual variability) within a process-based fire model that captures the influence of climate, fuels, and fire ignition on wildfire patterns and suppression.

Results Compared to simulations using historical climate (1972–2018), future total burned area (2020–2100: 782,302.7 (716,655.0–847,950.3) ha) increased by 42.3% under high drought variability (1,134,888.4 (1,067,437.2–1,202,339.6) ha), 104.8% under a substantial increase in drought trend (1,602,085.7 (1,511,837.5–1,692,334.0) ha), and 484.7% when combined (4,573,925.0 (4,434,910.5–4,712,939.5) ha). Landscape patterns of fire exclusion and suppression drove the spatial variability of fire return intervals (FRI). Our projections indicate wide spatial variability in future fire regimes with some areas experiencing multiple fires per decade while others experience no fire. More frequent fires corresponded with increased oak prevalence and a reduction in the biomass of mesic hardwoods and maple; however, mesic hardwoods remained prevalent under all fire intervals because of their contemporary dominance.

Conclusions Our study illustrates how future drought–fire–management interactions and a history of fire exclusion could alter future fire regimes and tree species composition. We find that increasing trends in drought magnitude and variability may increase wildfire activity, particularly in areas with minimal fire suppression. In ecosystems where fuel moisture (and not load) is the standard limitation to fire spread, increased pulses of drought may provide the conditions for more fire activity, regardless of effects on fuel loading. We conclude the effects of climate and human management will determine the novel conditions for both fire regime and ecosystem structure.

Keywords Climate–fire interactions, Landscape modeling, Southern Appalachians, Mesic forests, Fire management

*Correspondence:
Zachary J. Robbins
zjrobbins@lanl.gov
Full list of author information is available at the end of the article

Resumen

Antecedentes El incremento de la sequía debido al Cambio Climático alterará los regímenes de fuego en paisajes de bosques mésicos, donde la humedad del combustible limita típicamente la propagación de los incendios y donde las cargas de combustible son usualmente altas. Estos paisajes son frecuentemente extensivamente modificados por cambios humanos en el uso y manejo de las tierras. Pronosticamos la influencia de varios escenarios climáticos sobre desviaciones potenciales en los regímenes de incendios a lo largo y ancho de los Apalaches del Sur. Esta región tiene una larga historia de exclusión del fuego, de cambios en el uso de la tierra, y una creciente expansión de las áreas de interfaz urbano-rural (WUIs en Inglés). Consideramos las interacciones entre el clima, vegetación, e influencias antropogénicas para pronosticar futuros regímenes de fuego y cambios en la estructura forestal. Usamos escenarios climáticos que representan patrones de sequía divergentes (tendencia total de sequía y variabilidad interanual) dentro de un modelo de fuego basado en procesos-base que capturan la influencia el clima, combustibles, e ignición de incendios sobre patrones de incendios y supresión del fuego.

Resultados Comparados con simulaciones que usan datos climáticos históricos (1972–2018), el área a quemarse en el futuro (2020–2100: 782.0302,7 [716.655,0–847.950,3]067.437,2] ha) se incrementan en un 42,3% bajo alta variabilidad de la sequía (1.134.888,4 [1.067.437,2–1.202.339,6] ha, y 484,7% cuando fueron combinadas (4.573.925,0 [4.434.910,5–4.712.939,5] ha). Los patrones de paisajes de exclusión del fuego y supresión fueron los que dirigieron la variabilidad espacial de los intervalos de retorno del fuego (FRI). Nuestras proyecciones indican una amplia variabilidad espacial en los futuros regímenes de fuegos con algunas áreas que experimentarán múltiples incendios por década mientras que otros no experimentarán ningún fuego. Los fuegos más frecuentes se corresponden con un incremento en la prevalencia de robles y una reducción en la biomasa de árboles de madera dura (hardwoods) y arces; sin embargo, los rodales mésicos de madera dura serán prevalentes bajo todos los intervalos de fuego debido a su dominancia contemporánea.

Conclusiones Nuestro estudio ilustra cómo las interacciones entre fuego-manejo-sequía puede alterar los regímenes de fuego futuros y la composición de las especies de árboles. Encontramos que las tendencias incrementales en la magnitud de la sequía pueden incrementar la actividad de los incendios, particularmente en áreas con una mínima supresión del fuego. En los ecosistemas en los que la humedad de los combustibles (y no su carga) es la limitante principal para la propagación del fuego, el incremento en el pulso de las sequías puede proveer de condiciones para más actividad de incendios, sin tener en cuenta los efectos de la carga de combustibles. Concluimos que los efectos del clima y el manejo humano determinarán las nuevas condiciones tanto para los regímenes de incendios como para la estructura de los ecosistemas.

Background

Climate change will alter fire regimes through several mechanisms, which may fundamentally shift ecosystem structure and function (Turner 2010). Fire frequency and intensity are determined by fuel availability (live and dead biomass), weather and climate effects on fuel moisture, and ignition sources (Krawchuk and Moritz 2011). Warming temperatures will increase evaporative demand, drying fuels more rapidly, and will thus increase the flammability of fuels and expand the seasonality of available fuels (Flannigan et al. 2016; Ma et al. 2021). Extended drought periods may lengthen the wildfire season as fuels become drier and remain dry for longer periods of time (Abatzoglou and Williams 2016). Understanding how drought influences wildfire regimes is crucial to estimating climate change impacts and their ecological consequences (McLauchlan et al. 2020; Pausas and Keeley 2021). Drought's influence on moist forests may be especially pronounced, as significant increases in fire frequency within mesic forests have been observed globally (Abatzoglou et al. 2018). For example, in Sub-Saharan Africa, warming reduced the likelihood of fire in drier areas by limiting the available fuels due to lower vegetative productivity, yet more mesic regions increased in burned area as fuel aridity rose (Wei et al. 2020). Studies in central Australia have also found that moist forest systems will experience significantly more fire, owing to reduced fuel moisture, without an appreciable decline in fuel loads (King et al. 2013).

Understanding both the change in vegetation due to climate change and plant responses to the fire regime is crucial to estimate future fire regime changes. Following a shift in vegetation, fuel combustibility, drying rates, fuel bed thickness, and forest floor moisture will change, altering the fire regime (Kreye et al. 2013). A more frequent fire return interval may favor species that promote fire whereas less frequent fire may favor species that dampen fire's likelihood and are more susceptible to fire mortality, each creating a positive feedback cycle (Nowacki and Abrams 2015). This is confounded by evidence that more fire-adapted species can produce a thicker organic layer than more fire sensitive species, causing a positive feedback loop of potentially higher delayed mortality in fire-adapted species due to more fine-root death as the organic layer is consumed by fire (Carpenter et al. 2021; Robbins et al. 2022). State changes or extirpation may occur if fire regimes are drastically altered (Johnstone et al. 2016; Serra-Diaz et al. 2018; Nowacki and Abrams 2008; Lindenmayer et al. 2022).

A purely biophysical representation of fire regimes fails to capture changes due to human influences (Andela et al. 2017). The wildland urban interface (WUI) defines areas where wildland vegetation and human development intersect, illustrating where humans are directly impacted by and actively modifying fire regimes (Stewart et al. 2007). Housing development in the WUI and associated forest fragmentation can increase fire likelihood, particularly in areas where natural ignitions are sparse (Alencar et al. 2015). However, interactions between forest fragmentation and fire will vary as development can lead to increased access for fire suppression via additional roads, create new fuel breaks, and lead to increased suppression efforts near structures (Syphard et al. 2019; Driscoll et al. 2021). Fire suppression and exclusion (preventing ignitions or limiting fire spread due to infrastructure barriers) have led to global declines in area burned, particularly in more developed areas (Stewart et al. 2007; Yang et al. 2014).

In the USA, the Southern Appalachian region represents a transition zone between mesic and xeric forests, where changes in precipitation regimes are projected to increase fire risk due to prolonged droughts during the fire season (Mitchell et al. 2014). The 2016 fire season occurred during the most severe drought in the southeastern USA has experienced in the last 50 years (Williams et al. 2017). During the fall of 2016, wildfires occurred throughout the Southern Appalachians; these wildfires burned more than $^1/_3$ of the total combined area burned in the preceding 23 years (1992–2015) (James et al. 2020).

Land management and urban expansion have greatly influenced the fire regime and vegetation of the Southern Appalachian Mountains. Fire exclusion and suppression in the last century have shifted forest composition, particularly in xeric and sub-xeric forests (Flatley et al. 2013, 2015). Historically, the landscape experienced fires frequently (mean fire return interval < 25 years), often leading to open conditions and dominance by fire-adapted species (e.g., *Quercus spp.* and *Pinus spp.*; Flatley et al. 2013; Hanberry et al. 2020). Important exceptions included cove forests with longer fire return intervals (FRI; time between fire returning to an area) due topographic and fuel moisture limitations (Flatley et al. 2015; Mitchell et al. 2014). Following fire exclusion, the mean fire return interval increased to hundreds of years, favoring non-fire-adapted species (e.g., *Acer rubrum* L., *Liriodendron tulipifera* L.; Lafon et al. 2017). The Southern Appalachian WUI is also expanding (Thomas and Butry 2014) and suppressing wildfires that threaten life and property in the WUI has become a priority. In addition, accidental human ignitions now account for 82.4% of recent area burned by wildfire in the Southern Appalachians (Short 2021).

We assessed how interactions among climate, disturbance, and vegetation may change in a future with more frequent and severe droughts. We evaluated these changes at the broader landscape scale; the Southern Appalachians contain tremendous local variation in topography, climatic conditions, and vegetation. We focused on broad-scale, multi-decadal changes, recognizing that our results may be informative for understanding broad trends and could potentially inform landscape policy, yet may not be applicable to local planning or management.

To do so, we used a simulation modeling framework to estimate how climate will transform disturbance regimes and how disturbances would subsequently shape forested ecosystems (Scheller 2018). We deployed a process-based model of vegetation dynamics coupled to a fire model driven by fire weather conditions to capture the ecological response of wildfire (Scheller et al. 2019; Robbins et al. 2022). We selected climate projections representing divergent drought projections for the Southern Appalachians to capture future climate uncertainty.

Within this experimental framework, we tested the following hypotheses: (H1) an increase in climatic drought would increase the total area burned due to drier fuels, (H2) an increase in interannual variability of drought will increase the total burned area because wildfire disproportionately occurs under drought conditions (as witnessed in 2016), and (H3) any resulting increase in the burned area will favor historically fire-adapted species but will not restore their historic dominance because there will be insufficient burning to displace the mesic tree species that are now widely established.

Methods

Study area

Our study area was the Blue Ridge ecoregion of the Southern Appalachians (as defined by Omernik 1995) in North Carolina, South Carolina, Tennessee, and Georgia, USA (Fig. 1). The study area encompasses ~2.8 million ha of topographically diverse landscape (ranging from ~120 to ~2017 m, Fig. 1) with a heterogenous climate profile (Figs. 1, S.1-S.3). For the warmest areas, historic

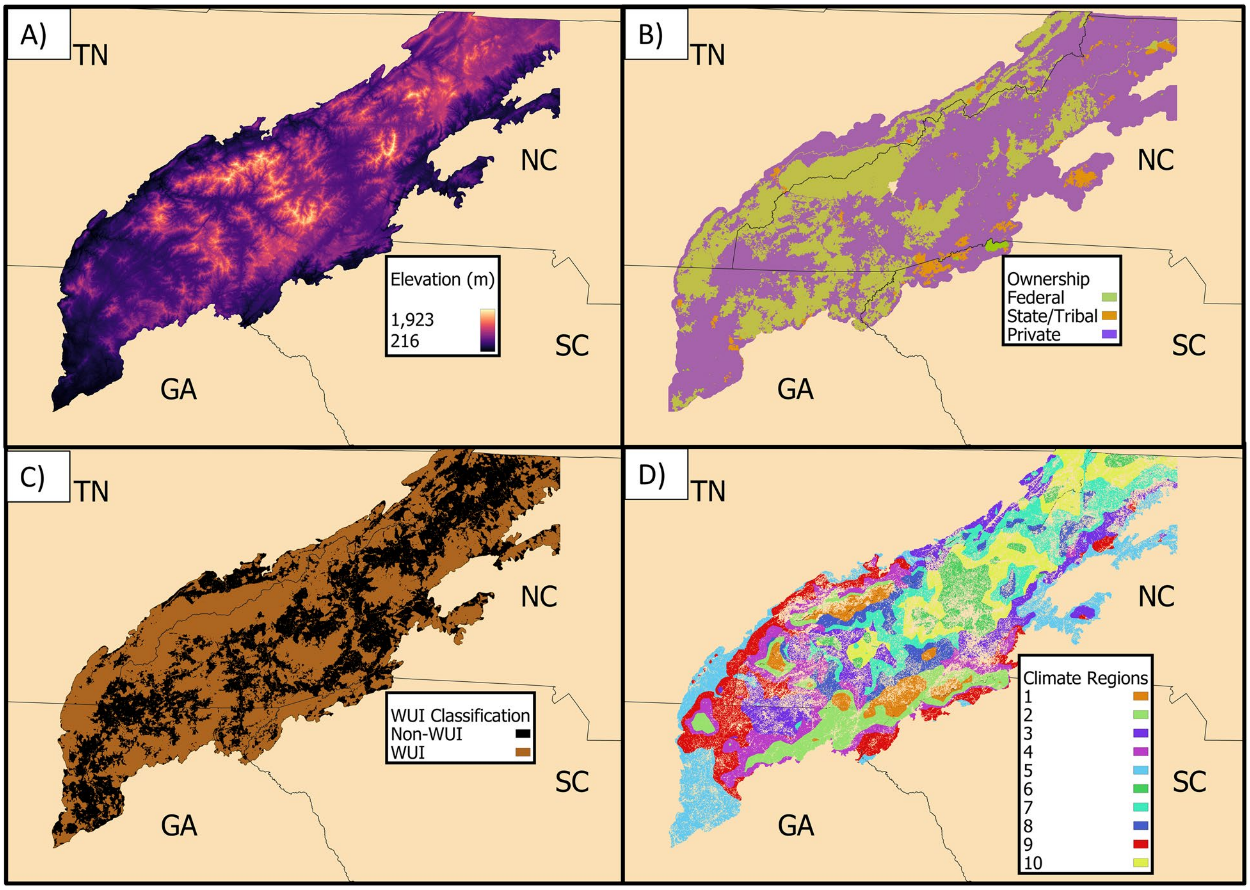

Fig. 1 Study area of the Southern Appalachians as defined by Omerik's (1995) blue ridge ecosystem. Here we show four separate maps of the study area which contains portions of Tennessee, Georgia, North Carolina, and South Carolina. The Southern Appalachians is a diverse and heterogeneous region as shown by **A** the wide ranging and complex elevation (Gesch et al. 2018), **B** the differing types of ownership (Noonan-Wright et al. 2021), **C** the wildland–urban interfaces (WUI: Radeloff et al. 2018), and **D** separate climate regions varying in precipitation and temperature profiles (Thornton et al. 2014; Figs. S1-S3). In this study, we used the LANDIS-II model to simulate the Southern Appalachians, USA, under four CMIP5 climate scenarios representing increased drought trend, increased drought variability, their combination, and a scenario with neither increase. These simulations were compared to the historical climate and each other to understand changes in fire patterns and landscape-scale changes in species composition and biomass

(1979–2019) summer mean temperature averaged 23 °C (June–August) and historic mean winter temperatures averaged 6 °C (November–January). Over the same period (1979–2019), mean daily temperature for November–January was ~6 °C for the warmest region and ~3 °C in the coolest region.

This area consists primarily of upland hardwood forests. Over 50 tree species are common (Bechtold and Patterson 2005). Ranked by aboveground biomass, the most common xeric deciduous tree species are chestnut oak (*Quercus montana* Willd), white oak (*Quercus alba* L.), northern red oak (*Quercus rubra* L.), scarlet oak (*Quercus coccinea* Muenchh.), and sourwood (*Oxydendrum arboreum* L.). Common mesic hardwood trees included red maple (*Acer rubrum* L.) and tulip-poplar (*Liriodendron tulipifera* L.). Common conifers included eastern white pine (*Pinus strobus* L.), Virginia pine (*Pinus virginiana*, Mill.), and loblolly pine (*Pinus taeda* L.). State abbreviations are TN: Tennessee, GA: Georgia, SC: South Carolina, NC: North Carolina

Climate scenarios

To understand future drought outcomes, we analyzed 20 downscaled global climate projections from the MACA database (Abatzoglou and Brown 2012) for the CMIP5 under Relative Concentration Pathway (RCP) 8.5 (Table S.2). We selected RCP 8.5 to maximize variability in model outcomes from which to select divergent scenarios. The climate models include forecasted data for daily relative humidity, temperature, precipitation, wind speed, and wind direction. For each model, we calculated the annual potential evapotranspiration (PET) for 2006–2100 using a Thornthwaite model (Thornthwaite 1948). We then calculated each climate drought trend (hence, T) via the model's annual precipitation (PPT) to PET ratio and used a linear trend with a fixed intercept to rank models by the slope in PPT:PET. Drought increased under all climate projections (Fig. S.4). We determined decadal variance in drought (hence, V) by calculating the decadal mean of PPT:PET and its squared variance. We then summed the squared variance for the study period and used this to rank each model (Figs. S.5 and S.6). We then selected four representative models (Table 1): (1) a minimal drought trend with low decadal variability (hence, LowT/LowV: MRI CGCM3 RCP 8.5), (2) a minimal drought trend with high decadal variability (LowT/HighV: CNRM CM5 RCP 8.5), (3) a maximal drought trend with low decadal variability (HighT/LowV: IPSL CM5A MR RCP 8.5), and (4) a maximal drought trend with high decadal variability (HighT/HighV: HadGEM2 ES365 RCP 8.5).

Landscape change model

We simulated a dynamic wildfire regime and vegetation change using a landscape disturbance and change model, LANDIS-II (Scheller et al. 2007). LANDIS-II represents the landscape as an interconnected grid, simulating vegetation and disturbance processes within and between cells. Each grid cell represented a 250 m-by-250 m forest stand (6.25 ha). LANDIS-II simulates the establishment and succession of tree cohorts (cohorts are comprised of a single species and age class; each cell can contain multiple cohorts). LANDIS-II includes spatially explicit seed dispersal. We used the Net Ecosystem Carbon and Nitrogen succession ("NECN") extension (Scheller et al. 2011) and parameterized the growth and trait characteristics for 48 separate tree species (See supplemental, Fig S7). NECN simulates tree growth, regeneration, and mortality in each landscape cell; cohorts compete for light, nitrogen, and soil moisture, and regeneration is a function of species-specific seasonal temperature and moisture responses. To capture landscape heterogeneity, 10 climate regions were used both in the historical and future climate simulations (Figs. S1-S3). Finally, NECN calculates the exchange of carbon and nitrogen between living tissue, dead tissue, and soil pools following the logic of the CENTURY model (Parton 1996). NECN estimates fuel loads over time; the decay rates for fuels are a function of climate and leaf composition (lignin content, carbon to nitrogen ratio), and each cohort has a unique contribution to the fuel pool, creating a continuous and temporally dynamic fuel model.

We simulated the fire regime using the Social-Climate Related Pyrogenic Processes and their Landscape Effects (SCRPPLE) extension. SCRPPLE includes separate submodels for ignitions (e.g., lightning or accidental human ignition), fire spread, and tree mortality (Scheller et al. 2019; Robbins et al. 2022). The ignition sub-model calculates the likelihood of a successful accidental and lightning ignition based on the daily Canadian Fire Weather Index (FWI, an index that captures fine fuel moisture, Van Wagner 1987). The sub-model fits the estimated ignitions for the entire landscape from a zero-inflated Poisson model (Zuur et al. 2009). SCRPPLE spatially distributes the calculated number of ignitions using a probability distribution map for each ignition type. Each cell is weighted based on probability and then a weighted uniform draw is performed. SCRPPLE calculates the probability of adjacent, intercellular fire spread based on FWI, effective wind speed (wind speed adjusted by topography; Nelson 2002), and an index of fine fuel mass (g B m^{-2}). The fine fuel index is calculated by dividing the fine fuels in each cell by the maximum possible fine fuel mass (excluding disturbances); this adjustment maintains

Table 1 The CMIP 5 climate models (Abatzoglou and Brown 2012) selected to represent the four drought outcomes for the study area and used to project the influence of varying climate scenarios on potential shifts in the wildfire regime across the Southern Appalachians. The four models selected encompass a range of plausible future climate warming and drought variability. In this study, we used the LANDIS-II model to simulate the Southern Appalachians, USA, under four CMIP5 climate scenarios representing increased drought trend, increased drought variability, their combination, and a scenario with neither increase. These simulations were compared to the historical climate and each other to understand changes in fire patterns and landscape-scale changes in species composition and biomass

Climate model	Ranking in drought trend	Ranking in drought variability	Mean Warming by 2100	Labeled in this study
MRI CGCM3 RCP 8.5	20 of 20	20 of 20	~3° C	*Low T/ Low V*
CNRM CM5 RCP 8.5	19 of 20	4 of 20	~5° C	*Low T/ High V*
IPSL CM5A MR RCP 8.5	2 of 20	12 of 20	~6 °C	*High T/ Low V*
HaGEM2 ES365 RCP 8.5	1 of 20	2 of 20	~7° C	*High T/ High V*

model sensitivity to autumn leaf deposition and variable rates of foliar decay among tree species.

Notably, effective wind speed accounts for the effect of topography and aspect on fire behavior, as effective winds, and ultimately fire spread, increase with steeper slopes and on certain aspects. For each daily timestep, fire spreads to a new cell based on adjacent intercellular probabilities of spread until no more cells achieve the probability of spread or the daily maximum spread is reached (estimated from the observed maximum rate of possible spread modeled with FWI and effective wind speed). When fire passes through a cell, SCRPPLE calculates cohort mortality based on cohort bark thickness and site-level characteristics (potential evapotranspiration, climatic water deficit, soil composition) (Robbins et al. 2022).

We parameterized the SCRPPLE model based on wildfire occurrence data from our study area for 1992–2016 (Robbins et al. 2022) (Fig. 2). We fit the fire ignitions sub-model by comparing historic FWI to historical

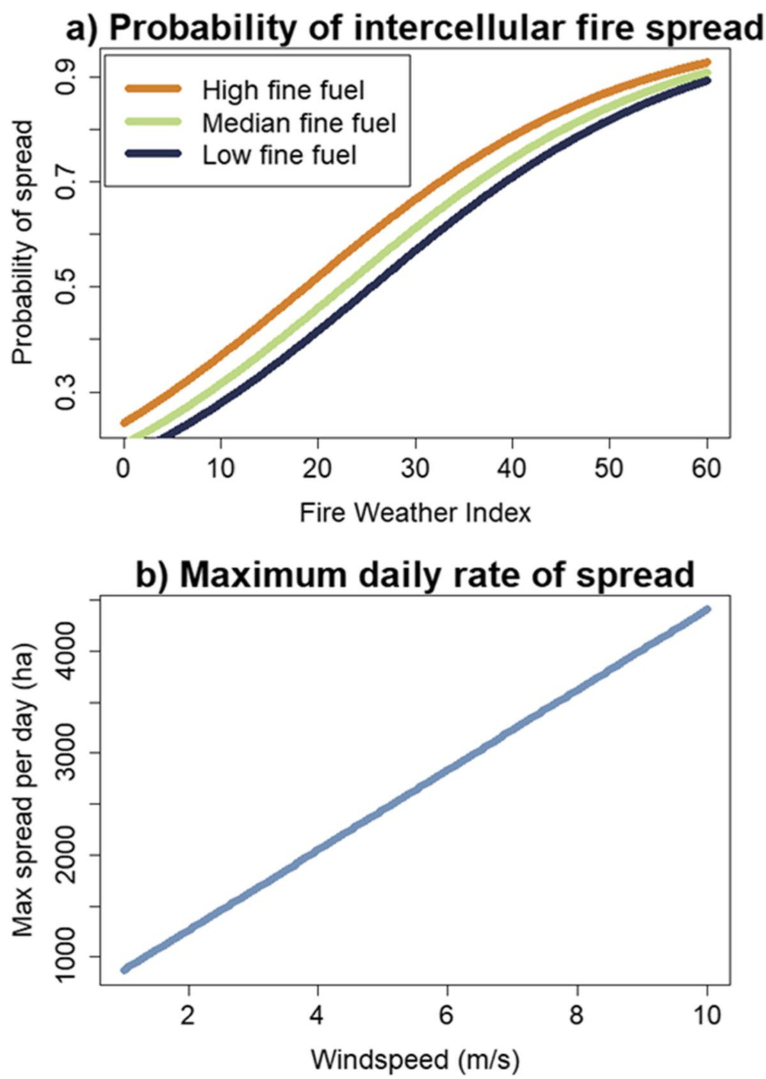

Fig. 2 The relationship within the model between fire variables (the index of fine fuel mass, fire weather index (accounting for fuel moisture), and effective windspeed) and modeled fire spread. **a** The intercellular fire spread probability as a function of the index of fine fuel mass and fire weather index. Colored lines represent different fine fuel indices (10th percentile, median, 90th percentile). **b** The maximum daily rate of spread (ha) as a function of effective daily wind speed. The model probabilistically calculates the likelihood of intercellular spread based on cellular conditions but is capped daily by the maximum daily rate of spread. In this study, we used the LANDIS-II model to simulate the Southern Appalachians, USA, under four CMIP5 climate scenarios representing increased drought trend, increased drought variability, their combination, and a scenario with neither increase. These simulations were compared to the historical climate and each other to understand changes in fire patterns and landscape-scale changes in species composition and biomass

ignitions from 1992 to 2016 (Table S3; Short 2021). We used separate processes to generate probability maps for each ignition type. For lightning, we used a climatology of lightning for the area (Albrecht et al. 2016), and for accidental human ignitions, we interpolated the spatial distribution from the wildfire record (Short 2021). We parameterized the fire spread function using fuel load, daily FWI, and topographically downscaled and effective wind speed. To model the probability of spread given the predictor variables, we identified the adjacent cells where a fire could spread using historic daily wildfire perimeters (Scheller et al. 2019; Walters et al. 2011). Finally, we used the combined data set to fit a generalized linear binomial fire spread model (Table 2a, b; Scheller et al. 2019).

We developed probabilistic prescribed fire ignition maps that use the spatial boundaries of different land ownerships to assign the relative probability for a prescribed burn (see Robbins et al. 2022). We parameterized prescribed fire on federal lands using the proposed prescribed burn sizes and frequencies in National Forest plans (Table S.4). To parameterize non-federal prescribed burning, we used records of known prescribed burns in other jurisdictions (private, tribal, state, and other). While prescribed fire is an integral part of this landscape (currently accounting for ~40% of the burned area), each future scenario represents the same total area burned by prescribed fire. Thus, we focus on the effects of drought on future wildfires. We spatially delineated three wildfire suppression levels using a combination of wildland-urban interface (WUI) definitions (Radeloff et al. 2018), distance from roads, slope, elevation, and USFS roadless wilderness designations (U.S. Forest Service 2001). To parameterize the three levels of wildfire suppression, we compared historical records of fire rotation period (time needed to burn an area of land equal to the landscape) for each of the three suppression zones to unsuppressed fire spread. We then calibrated suppression under three fire weather index scales (Table 2c).

Table 2 The resulting parameters from our calibration process controlling fire spread from the portion of the SCRPPLE fire model governing (a) fire spread probability and (b) the maximum daily rate of fire spread (ha) and (c) suppression probability for the three suppression ratings at three fire weather index level in our SCRPPLE fire model for the Southern Appalachians. In this study, we used the LANDIS-II model to simulate the Southern Appalachians, USA, under four CMIP5 climate scenarios representing increased drought trend, increased drought variability, their combination, and a scenario with neither increase. These simulations were compared to the historical climate and each other to understand changes in fire patterns and landscape-scale changes in species composition and biomass

Coefficient	Estimate	Std. Error	*P* value
(a) Fire spread probability			
Intercept	−1.740204	0.113415	< 0.0001
Fire weather index	0.725350	0.188870	< 0.0001
Fine fuel index	0.061306	0.003369	< 0.0001
b) Maximum rate of daily spread (ha)			
Intercept	477.60	55.70	< 0.0001
Mean effective wind-speed (m/s)	393.00	13.28	< 0.0001
(c) Fire suppression values			
Suppression class	FWI < 20	20 < FWI < 28	FWI > 28
Low (1)	0.30	0.12	0.05
Medium (2)	0.50	0.25	0.03
High (3)	0.70	0.35	0.20

Scenario analysis

To test the influence of drought trends and variability, we simulated seven replicates for each climate projection for 80 years (using the parameterized landscape from Robbins et al. 2022 with the addition of climate change). In addition, we included a baseline historical-random (HR) climate scenario randomly assigning climate years from 1972 to 2016 to future years.

We analyzed the relative fire regimes by looking at the pattern of fire return interval for each model in each of the suppression areas and in the WUI. Finally, we examined how tree species composition (by biomass) changed under each climate scenario. To understand changes in the forest composition under each FRI, we compared all climate model scenarios and assessed the mean biomass density across all sites of that FRI; we also analyzed the mean biomass density across all sites of a given FRI for all individual models. SCRPPLE also calculates mean fire severity (the sum of severity in individual cells divided by the number of cells in the fire). We tracked changes in severity over time and across climate scenarios, with a specific interest in events that had with a fire severity greater than > 300 at 250 m (measured as relative delta in normalized burn ratio in Robbins et al. 2022 and included within the model as severity) for comparison in the relative occurrence of high severity fires.

Results

Parameterizing the wildfire regime

In our statistical fitting of the fire spread model (see Supplemental), we found both FWI (representing fine fuel moisture) and the index of fine fuel mass were significant predictors of the probability of intercellular fire spread (Table 2). Visual interpretation of the effects of FWI and the fine fuel index suggests that FWI is the dominant control of fire spread (Fig. 2). However, increasing fine fuel mass will increase the probability of intercellular fire spread by as much as

~10%. Our ecological interpretation of this statistical fitting is that for this area, fire weather is the primary contributor to high fire spread between forested cells, but the location of available fuels may determine where a fire is most likely to spread. Due to directional error, wind speed was removed from predicting intercellular spread probability. Wind speed, however, was the predictor used in calculating the maximum daily rate of spread within the model (Fig. 2). This may reflect the limitations of downscaled wind speed in weather records (i.e., at a large-scale wind speed affects fire spread rates, but this cannot be captured at relevant scales for modeling intercellular fire spread.) Both lightning and accidental human ignitions simulated by our fire model were sensitive to changes in FWI (Table S3, Fig. S8). For the lightning ignition sub-model, the likelihood of an excess zero increased with increasing FWI; however, so did the predicted daily lightning (S.3). The accidental human ignition sub-model was not sensitive to FWI for the probability of excess zeros (S.3); however, the daily ignition count was positively correlated with FWI. Therefore, accidental ignition likelihood increased slightly with increasing FWI. For additional information on the influence of FWI on ignition likelihoods, please see the Supplemental.

Validating the wildfire regime

The SCRPPLE fire model reproduced the expected number of accidental human-ignited fires (1623 (95% CI: 1598–1649) compared to 1709 observed) and lightning-ignited fires (160 (95% CI: 153–177) compared to 174 observed) from 1992 to 2016 (Fig. S.9). The mean total area burned in the simulations between 1992 and 2016 was 140,316 (95% CI: (119,067–161,564)) ha, compared to 147,367 ha observed by Short (2021) (a mean underestimation of ~2%; Fig. S.10). The SCRPPLE fire model generally captured the fire size distribution; the model slightly overestimated the proportion of small (0–50 ha)

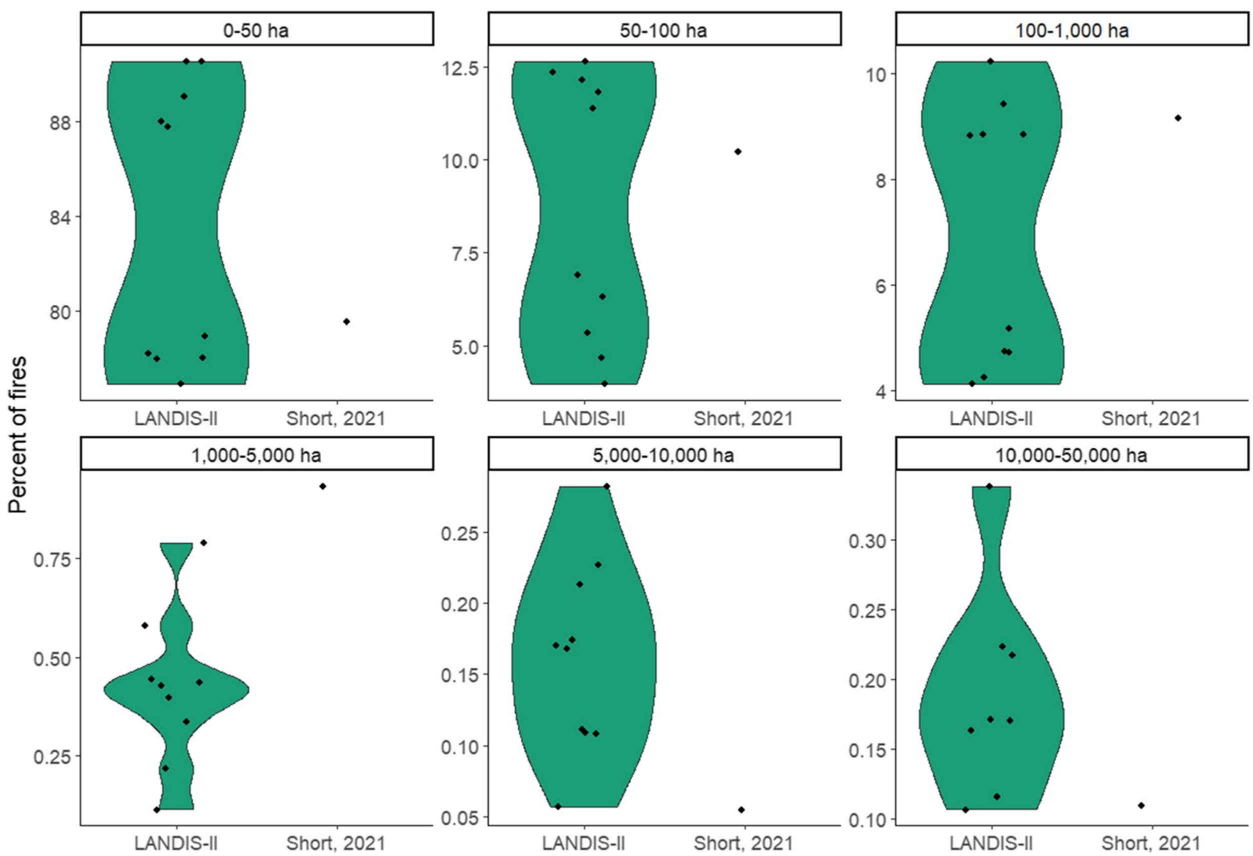

Fig. 3 The distribution of binned fire sizes for ten LANDIS-II model replicates compared to historical fire size observations by Short (2021). For each fire size class, the LANDIS-II values show the proportions of fire sizes for the modeled years in the final validations (1992–2016), which correspond with the observation period for Short (2021). Note the varied *y*-axis. In this study, we used the LANDIS-II model to simulate the Southern Appalachians, USA, under four CMIP5 climate scenarios representing increased drought trend, increased drought variability, their combination, and a scenario with neither increase. These simulations were compared to the historical climate and each other to understand changes in fire patterns and landscape-scale changes in species composition and biomass

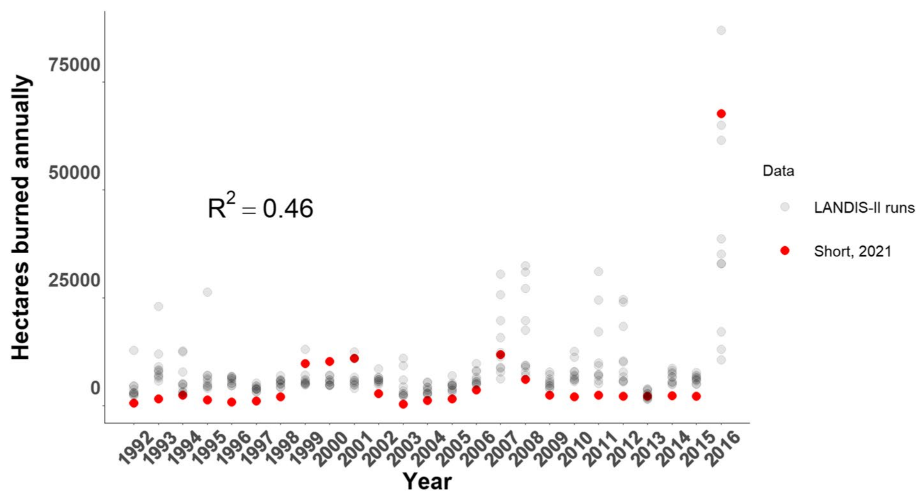

Fig. 4 The interannual variability in the simulated annual burned area (ha/year) and the total area burned (ha) generated by the SCRPPLE fire model, compared to the observed historical burned area. Transparent gray dots represent individual replicates, solid red dots represent the observed data (Short 2021). R^2 represents the predictive power of the combined replicates in explaining the annual variation in the observed data. In this study, we used the LANDIS-II model to simulate the Southern Appalachians, USA, under four CMIP5 climate scenarios representing increased drought trend, increased drought variability, their combination, and a scenario with neither increase. These simulations were compared to the historical climate and each other to understand changes in fire patterns and landscape-scale changes in species composition and biomass

and large (5000 ha and above) fires and underestimated fires of intermediate size (50–5000 ha) (Fig. 3; Short 2021). Comparing the annual area burned shows that the model captured about 46% of interannual variability in the burned area (Fig. 4). The model tended to overestimate burned area, even if by only a few hundred ha, with the largest overestimates occurring in the same years across replicates (1992–1994, 2008, 2011–2012). Simulations of the peak fire year in 2016 (observed ~67,000 ha burned) yielded highly variable modeled values of burned area (13,112–87,043 ha) (Fig. 4).

Climate simulations

The modeled burned area of the historical-random (782,302.7, model range: (716,655.0–847,950.3) ha) and LowT/LowV (707,858.0 (684,478.3–731,237.8) ha) scenarios were similar (Fig. 5a). The burned area of the HighT/LowV scenario (high drought trend, low variability: 1,602,085.7 (1,511,837.5–1,692,334.0) ha) was 104.8% higher than the historical-random simulation. The burned area of the LowT/HighV scenario (increased drought-variability, 1,134,888.4 (1,067,437.2–1,202,339.6) ha) was 42.3% higher than the historical-random simulation. The burned area for the HighT/HighV scenario (high drought trend and drought variability, 4,573,925.0 (4,434,910.5–4,712,939.5) ha) increased nearly 500% from the historical-random scenario (Fig. 5a). The LowT/LowV model showed similar temporal patterns to the random historical simulations oscillating around ~60,000 hectares burned per decade (Fig. 5b). The LowT/HighV scenario forecasted increasing hectares burned during the middle part of this century and eventually returned to the burned interval range seen in the historic-random scenario. This tracks the pattern in FWI (Fig S.13a), rather than a pattern in fuel availability (S.13b). The HighT/LowV scenario forecasted a similar burned area to the historical-random simulation until the middle of the century, when the burned area rose and remained elevated for the rest of the century. The HighT/HighV scenario began with an elevated burned area (~2×the historical-random) and increased throughout the simulation, forecasting a burned area ~9×higher than the random historical scenario during the last decade of the century (Fig. 5b).

Modeled fire severity remained similar throughout the simulation, generally low with a minimal increase in the proportion of higher severity fires or an increase in the gross number of higher severity fires (Fig S.14). In scenarios with more burned area (HighT/LowV and HighT/HighV), mean fire severity per individual forested cell fell slightly through time. Lower severity is likely due to the prior removal of the most susceptible cohorts.

The modeled mean landscape fire rotation period for the historic climate scenario was ~284 years, in the LowT/LowV scenario ~314 years, in the LowT/HighV scenario ~200 years, in the HighT/LowV scenario ~139 years, and in the HighT/HighV scenario ~48 years. In forecasts using the LowT/LowV, LowT/HighV, and HighT/LowV scenarios, the largest percentage of the landscape either had an FRI over 200 years or experienced no fire

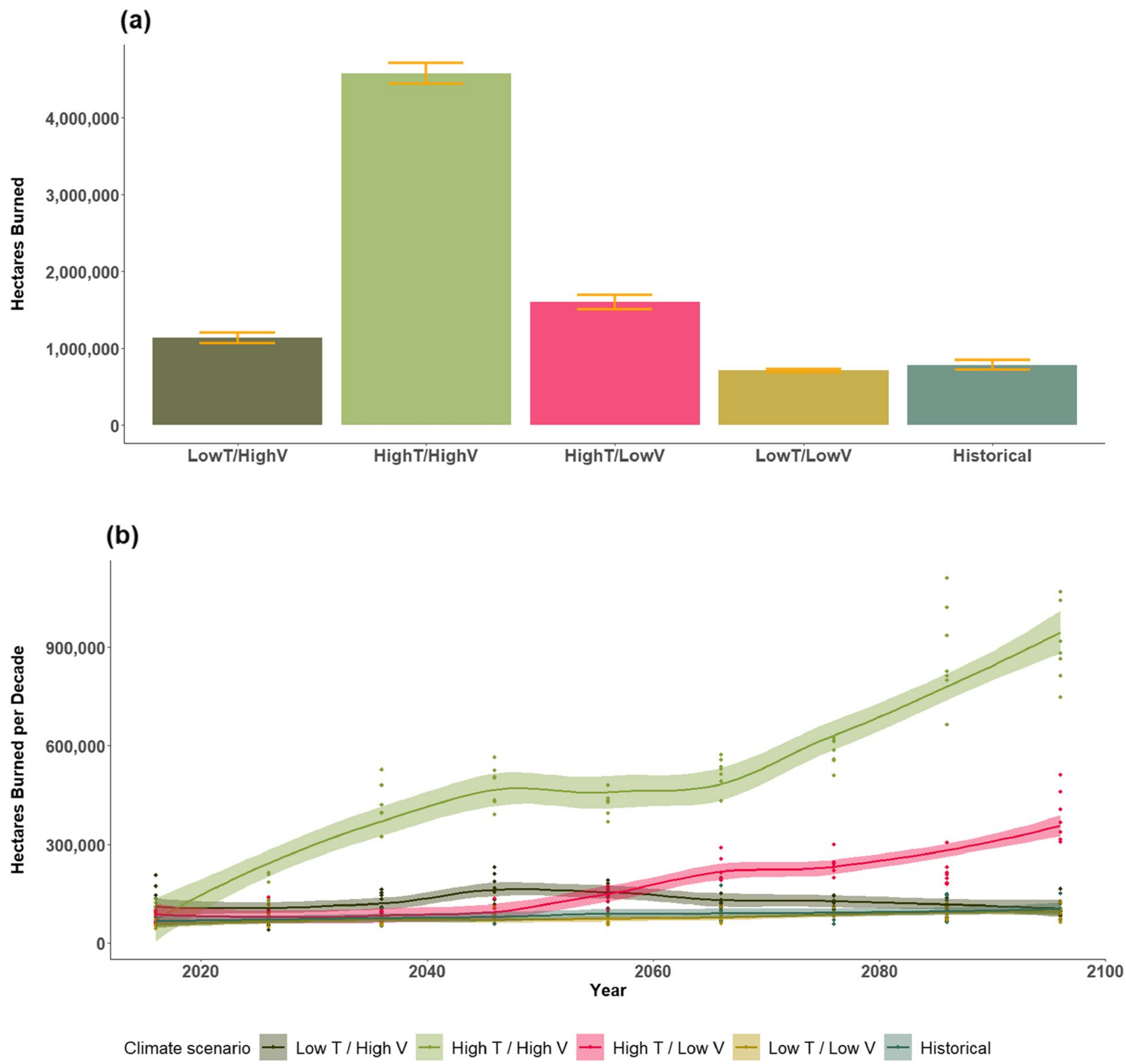

Fig. 5 The change in the burned area attributed to drought and drought variability. **a** The total area burned during a 90-year simulation in our process-based, paired fire, and landscape change models for four selected climate models that represent a range of future drought conditions. Error bars represent the 95% CI across models. **b** Hectares burned per decade under the four selected climate models. Dots represent individual model runs and the trend line represents a LOESS smoothed model. High T represents a major drought trend, while Low T represents a minor drought trend. High V represents high variability, while Low V represents low variability. The historical simulation's climate is years drawn randomly from the years 1979–2016. In this study, we used the LANDIS-II model to simulate the Southern Appalachians, USA, under four CMIP5 climate scenarios representing increased drought trend, increased drought variability, their combination, and a scenario with neither increase. These simulations were compared to the historical climate and each other to understand changes in fire patterns and landscape-scale changes in species composition and biomass

(Table 3). However, under the HighT/HighV scenario, only ~22% had an FRI longer than 200 years or experienced no fire. The modeled spatial distribution showed lower fire rotation period in the non-WUI areas (Fig S.7), and in areas with a lower suppression classification (Fig. 6, Fig S.6). The northwestern and southwestern areas where fires are most concentrated across scenarios represent the boundaries of the Chattahoochee–Oconee and the Cherokee National Forests (Fig. 1). Areas that experienced a FRI less than 50 years expanded under all climate scenarios that increased burned area, including more frequent fire in the WUI and high suppression area

Table 3 The distribution of simulated FRI intervals across the southern Appalachians for each climate model in our study, based on the mean of all seven model replicates. The fire return intervals represent the time between fires in an individual cell on the landscape for each modeled climate scenario. In this study, we used the LANDIS-II model to simulate the Southern Appalachians, USA, under four CMIP5 climate scenarios representing increased drought trend, increased drought variability, their combination, and a scenario with neither increase. These simulations were compared to the historical climate and each other to understand changes in fire patterns and landscape-scale changes in species composition and biomass

FRI	Low T/Low V	Low T/High V	High T/Low V	High T/High V
0–25	0.00%	0.00%	0.01%	15.07%
25–50	0.00%	1.87%	5.52%	28.62%
50–100	3.70%	12.27%	20.26%	21.17%
100–200	17.01%	23.82%	26.71%	13.00%
200–Inf	79.21%	62.01%	47.37%	22.13%

(Table 3, Tables S.5 and S.6). Increased burned area suggests that fire frequency will increase and fire, with its potential ecological benefits and possible hazards, will impact a larger portion of the future landscape.

Modeled mean total biomass decreased in sites with an FRI of < 5 years (79.95 Mg/ha) as compared to 25–50 years (104.46 Mg/ha), 50–80 (119.73 Mg/ha), or sites that experienced no fire (131.03 Mg/ha). Sites with FRIs of 0–25 years and 25–50 years had lower biomass than the initial landscape average (106.24 Mg/ha). Percent total biomass of xeric white oaks increased for all FRIs, but the maximum biomass increase (45.4%) occurred with the shortest FRI (Fig. 7). Biomass of xeric red oaks held constant in all scenarios. The percent of maple biomass declined by half under the scenario with the shortest FRI (from 13.1% of landscape biomass to ~8%). Mesic hardwood biomass remained relatively stable in all FRI, although the proportion declined with decreasing FRI. Yellow pine declined in all scenarios (from 1.0% to ~0.5%). Non-oak xeric hardwoods declined in all scenarios from (~5% to around 0.3%, Fig. 7). Comparing the relative biomass in each FRI class between models showed minimal differences (S.20-S.23).

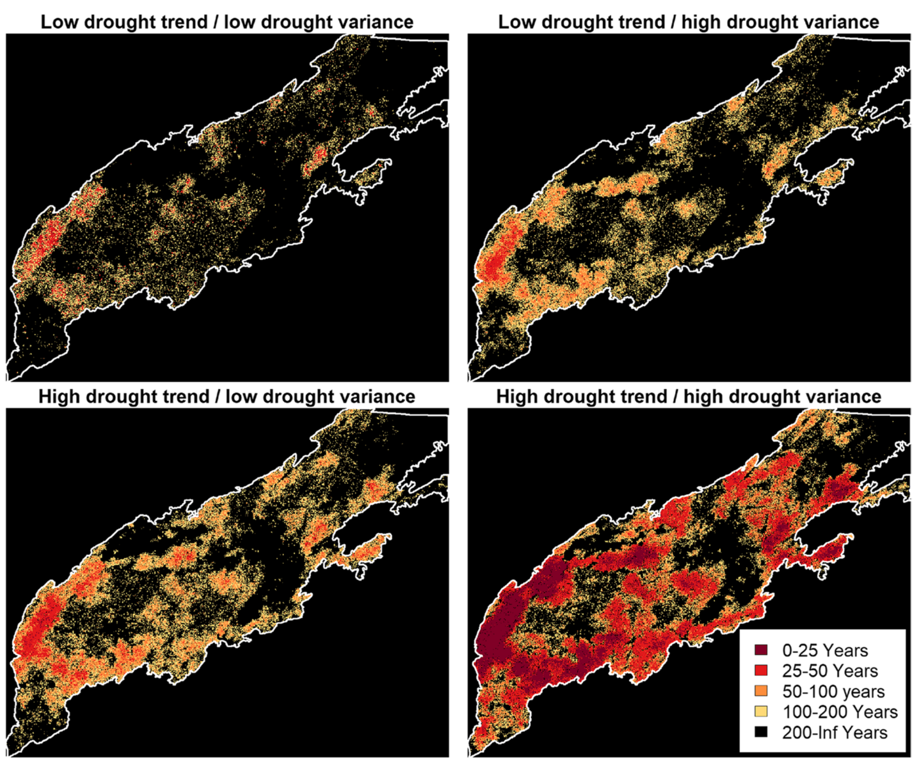

Fig. 6 Spatial distribution of the fire return interval (FRI: years simulated/fires that occurred) simulated by the SCRPPLE fire model across the Southern Appalachian landscape under four climate scenarios. Each map represents the combined FRI of seven simulations (wildland fire plus prescribed fire). The white outline denotes the study boundary. Climate models are LowT/LowV (MRI CGCM3 RCP 8.5), LowT/HighV (CNRM CM5 RCP 8.5), HighT/LowV (IPSL CM5A MR RCP 8.5), and HighT/HighV (HadGEM2 ES365 RCP 8.5). In this study, we used the LANDIS-II model to simulate the Southern Appalachians, USA, under four CMIP5 climate scenarios representing increased drought trend, increased drought variability, their combination, and a scenario with neither increase. These simulations were compared to the historical climate and each other to understand changes in fire patterns and landscape-scale changes in species composition and biomass

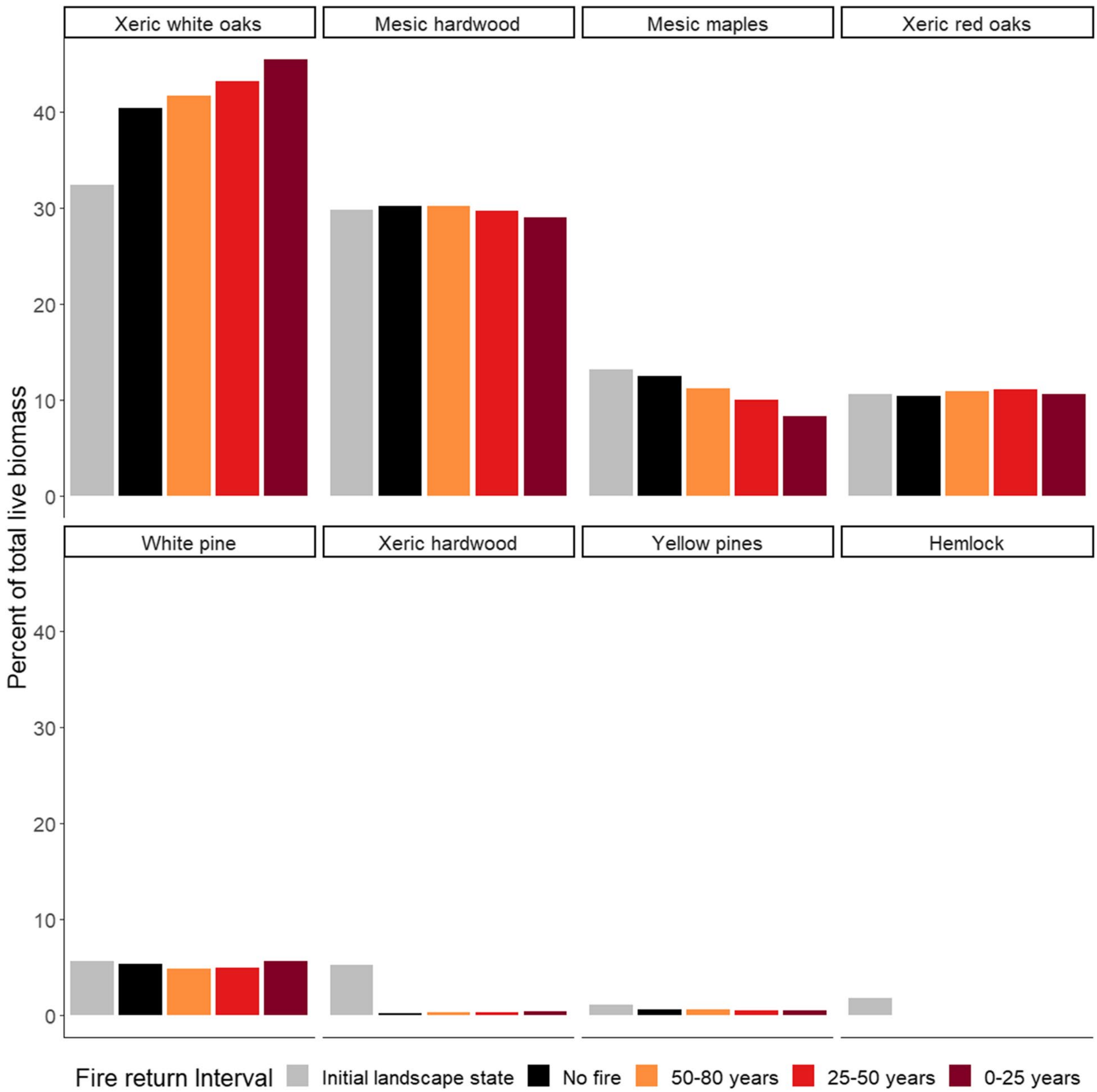

Fig. 7 Landscape proportions of the functional groups represented in each fire return interval (FRI: years simulated/fires that occurred) in our model of fire regime and vegetation change in the Southern Appalachians. Each bar represents the mean percent of total live biomass of each functional group across all locations that experience that FRI across the landscape in all simulations under all climate models. Functional groups are defined in Table S.1. In this study, we used the LANDIS-II model to simulate the Southern Appalachians, USA, under four CMIP5 climate scenarios representing increased drought trend, increased drought variability, their combination, and a scenario with neither increase. These simulations were compared to the historical climate and each other to understand changes in fire patterns and landscape-scale changes in species composition and biomass

Discussion

We found that both increasing annual drought trends and greater drought variability could increase the area burned across the Southern Appalachians, validating our first two hypotheses (H1 and H2). Furthermore, the increase in the modeled burned area due to a high drought trend and high drought variability suggests multiplicative non-linear interactions (Fig. 5) and represents the threshold-driven nature of the wildfire regimes in mesic forested systems (Young et al. 2017; Abatzoglou et al. 2021). The historical data and our simulations suggest that drought years (particularly those containing months with fire weather indices > 22) will contribute most to future burned area. Because strong drought years account for a disproportionate amount of area burned by wildfire, an increase in drought variability has a substantial effect on the modeled area burned even without an overall increase in the projected drought trend. The non-linear interaction is driven disproportionately by the most drought prone years, (i.e., the 2016 fire season); therefore the combination of decreasing annual PPT/ET ratios and greater interannual variability results a greater number of years with widespread fire. The difference in modeled area burned between the four climate scenarios used in this study was determined by their divergent forecasts. The HADGEM-ES 365 (High T / High V) model predicted the most drastic changes in future climate, with mean temperatures 7 °C higher and a decrease in precipitation of 180 mm annually by the end of the century (Table 1). The ISPL CM5A-LR (High T/ Low V) and CNRM-CM5 (Low T/ High V) models predicted 5–6 °C of warming, with slight increases in annual precipitation (Table 1). However, future precipitation patterns for the southern USA should be interpreted with caution because global climate model projections derived from the Coupled Model Intercomparison Project Phase 5 (CMIP5) fail to simulate observed fall precipitation patterns (Bishop et al. 2019). For context, Rupp (2016) analyzed the MACA downscaling of these GCMs (among others) in the southeastern USA and compared historic minimum, maximum, and average monthly temperature, and surface precipitation to weather data to characterize inherent bias. Overall, the highest-ranking model (according to a normalized error score of 22 metrics) was the CNRM-CM5 (Low T/ High V), and the HADGEM-ES 365 (High T / High V) was ranked 10th of 41. The MRI.CGCM3 (Low T/ Low V) and the IPSL CM5A-LR (High T/ Low V) both scored near the 25th percentile in normalized error score. As is common in GCMs, models reproduced temperature more accurately than precipitation.

Our findings reflect the complex, non-linear interactions between fire frequency due to climate coupled with changes in fire behavior due to human management of fuels and fire (Balch et al. 2017; Pausas and Keeley 2021; Krawchuk et al. 2009). Our results suggest more area burned under increased drought trend and drought variability, even where a high level of fire suppression was modeled (Table 3, Table S.6). Our inclusion of fire suppression and patterns of human ignition indicate that the current pace of wildfire management may not be sufficient to maintain current levels of burned acres or limit burning in the WUI under a more arid future climate with more wildfire activity (Tables S.6 and S.7). However, this effect is most prominent in areas away from housing development and population centers (Table S.7). As such, fuel reduction efforts that target the WUI, particularly under drier future conditions, may be most effective in this region (Sturtevant et al. 2009; Krofcheck et al. 2019). In other forested systems, however, land management and human interaction with the landscape have been projected to play a more prominent role in increasing fire activity than the role projected by the warming climate (Creutzburg et al. 2017), at least in the near term (Maxwell et al. 2022). Our results are similar to those of Moritz et al. (2012), who found that climate trends could exceed the influence of land management. Our results differ in that our model suggests short-term drought patterns (as represented by drought variability) also had a large effect on total burned area. Other factors to consider include that fuel loads can increase due to rural abandonment and long periods of fire suppression, and ignitions can increase in previously remote areas via increased access through fragmentation (Pausas and Keeley 2014). It is also possible that future fire suppression could increase to meet wildfire management needs to combat increased fuel loads and more accidental human ignitions (Andela et al. 2017; Driscoll et al. 2021).

Our results run contrary to prior projections of area burned under climate change in the Southern Appalachians (Prestemon et al. 2016; James et al. 2020). These studies suggested that the total area burned would likely decline over the next 50 years under the CMIP3 models, MIROC32, CSIROMK35, and CGCM31 (scenarios AB1, A2, and B2). A decline in burned area was attributed to denser populations and rising wealth resulting in increased wildfire suppression efforts that could negate any increase in fire size associated with future temperatures. However, these studies were parameterized with data from 1992 to 2010 and did not capture the 2016 fire year that had monthly FWIs > 22. Our findings suggest that failing to capture such exceptionally dry years will severely underestimate landscape-level wildfire activity as these drought years account for a disproportionate amount of burned area. In the context of all three studies, including ours, the level of fire suppression could ultimately drive the fire regime across this landscape, but increased levels of high drought variability will challenge suppression efforts (Prestemon et al. 2016; James et al. 2020).

Our results suggest that the species composition change has passed a threshold and is unlikely to revert to pre-fire suppression and exclusion composition in the Southern Appalachians in the next century. Even under drastic climatic and fire regime shifts, we see only minor variation in species composition, supporting the idea of an ecological hysteresis (Nikanorov and Sukhorukov 2008). Based on these conclusions, we support our third hypothesis (H3) that the amount of area burned is unlikely to restore the majority of the landscape to more fire-adapted conditions, as even the most frequent FRI maintained near current levels of non-fire adapted mesic hardwoods. These results suggest an alternative stable state and that consistent reintroduction of fire, without additional land management restoration actions, may not restore the landscape to a more fire-adapted state (Beisner et al. 2003; Alexander et al. 2021).

Under a modeled shift to a much more frequent FRI, stands were able to maintain both fire-adapted and non-fire-adapted tree species throughout the century, unlike more arid areas in the Western USA, where more permanent state shifts are expected to occur (Davis et al. 2019). Continued fuel availability will likely differentiate fire activity in areas that experience increases in drought under future warming (Abatzoglou et al. 2018). Our succession sub-model (NECN) calculates the fuel load as surficial detrital biomass (reflecting annual foliage turnover and recent disturbance, not including large wood material); our simulations indicated that the fuel load would not decline to the point of limiting fire at the landscape scale, even under an increase in fire frequency and resulting mortality.

While increased area burned did not yield a complete reduction in mesic species or restoration of *Quercus spp.*, our simulations suggest that white oak (*Leucobalanus*: *Q. montana* Willd and *Q. alba*) will remain the dominant canopy species and will not be replaced by other species within the next century, regardless of the climate scenario. While oaks are currently less prevalent in the mid and understory, larger and older oak trees will make up an increasing fraction of the overstory biomass in the future because of their continued growth potential and ability to survive low–moderate intensity fires. Many oaks in the Southern Appalachians were established during early industrial harvesting and before fire suppression and exclusion (1890–1930) and generally can live between 200–400 years (Loehle 1988). Essentially, the larger oaks still have considerable growth potential, maintaining their successional legacy into the next century. While more frequent fires may favor oaks under the hotter and drier climate projections, this was accompanied by lower regeneration rates in all species due to increasing drought stress (higher frequency and intensity, Figs. S.15-S.19). Including oak decline (Greenberg et al. 2014) or disturbances beyond fire (Clinton et al. 1993) in future simulation studies could provide further insight into these dynamics.

Our study presents a novel approach to simulating the spatio-temporal interactions of fire suppression, management, and increased and more variable drought conditions and quantifies how these interactions affect wildfire activity in the Southern Appalachians. Future work should quantify the effects of varied fire suppression and ignition reduction tactics coupled with other management strategies, such as changes in the number and size prescribed fires, to balance ecosystem resilience with human community safety.

Limitations to our forecasts must be considered. Anomalous events in wildfire records, such as those of the 2016 fire season, are difficult to model as they have no replicates and are outliers from preceding wildfire patterns. However, our fire spread model is centered around fire behavior metrics (fuel load, FWI, windspeed), which should allow some extrapolation to future annual weather conditions. Additionally, our model of interactive fire spread, and suppression is non-adaptive, meaning that while the effect of fire suppression does scale with fire weather conditions, it does not consider the reorganization of fire suppression resources, as might be expected if the wildfire regime radically shifts. Nor did we consider a future reduction in fire suppression resources created by national-scale wildfires that compete for firefighting labor (Belval et al. 2020). Our simulations represented the cumulative effects of climate-wildfire interactions over the entire Southern Appalachians (3.4 M ha area simulations), not the efficacy of individual prescriptions on specific stands or areas. Given the broad variation in climatic trends and the high stochasticity introduced by wildfire, localized uncertainty (at the small watershed or stand scale, for example) is high and therefore the information produced should not be used to inform local management or to infer local ecological trends. It should be noted that fire occurrence is not uniform across the landscape. Areas with greater fire frequency may be more predisposed to xeric species or other adaptations not captured in this fire analysis. Further, our analysis focuses on the landscape at large; future analysis will examine fine-scale trends in specific management-relevant outcomes, including smoke and bird habitat. Finally, fire severity was parameterized primarily from current stands in areas where fire events were rare (Robbins et al. 2022). While the mortality parameterization included areas that had been burned twice, a shift in fire frequency may change the mortality profile. Increased fire frequency may reduce fire severity by removing trees that are more susceptible to subsurface burning due to the buildup of duff or by altering the mycorrhizal environment (Waldrop et al. 2016; Carpenter et al. 2021).

Conclusion

Increased future drought severity and variability may generate a much greater area burned in the Southern Appalachian region than has recently been experienced, even when accounting for wild fire suppression. In ecosystems where fuel moisture (and not load) is the standard limitation to fire spread, increased pulses of drought may provide the conditions for more fire activity, regardless of effects on fuel loading. Furthermore, while fire suppression and other disturbances have altered this landscape's vegetation composition for over a century, the future projected increases in wildfire will likely not revert the landscape to pre-suppression conditions, owing to the establishment of non-fire-adapted species. However, oak canopy dominance will likely continue into the next century because of continued growth potential of the current oak population, but oak regeneration is more questionable. Thus, the future fire regime of the Southern Appalachians (and other fuel moisture-limited systems) may be neither like the past nor the present but a novel ecosystem state governed by climate and human activities.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-023-00231-1.

Additional file 1. Supplementary material.

Acknowledgements
We would like to thank Joe O'Brien, Matt Reilly, Derrick Wallace, Steve Flannigan and Steve Norman for their feedback and support.

Authors' contributions
ZR, TM, and KJ parameterized the LANDIS-II and SCRPPLE models. ZR, LL, KJ, and RS designed the study. ZR conducted the computational analysis. ZR, LL, TM, KJ, and RS analyzed results and wrote the manuscript.

Funding
We acknowledge the support provided by the USDA Forest Service Southern Research Station, the Center for Forest Disturbance Science, the Athens Prescribed Fire Laboratory, in Athens, GA, and the Oak Ridge Institute for Science and Education. This work was additionally funded by the NCSU Chancellor's Faculty Excellence Program.

Availability of data and materials
The models used in this analysis and their crucial outputs will be published openly on Github at https://github.com/LANDIS-II-Foundation/Project-Southern-Appalachians/tree/master/Research_Projects/Future_fire. Other data is denoted where publicly available.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
None

Author details
[1]Forestry and Environmental Resources Department, North Carolina State University, Raleigh, NC, USA. [2]Southern Research Station, Center for Forest Disturbance Science, Athens Prescribed Fire Science Laboratory, U.S.D.A. Forest Service, Athens, GA, USA. [3]Conservation Science Partners, Truckee, CA, USA. [4]Center for Geospatial Analytics, North Carolina State University, Raleigh, NC, USA.

Received: 30 May 2023 Accepted: 30 October 2023
Published online: 12 January 2024

References

Abatzoglou, J.T., and T.J. Brown. 2012. A comparison of statistical downscaling methods suited for wildfire applications. *International Journal of Climatology* 32: 772–780. https://doi.org/10.1002/joc.2312.

Abatzoglou, J.T., and A.P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western US forests. *PNAS* 113: 11770–11775. https://doi.org/10.1073/pnas.1607171113.

Abatzoglou, J.T., A.P. Williams, L. Boschetti, M. Zubkova, and C.A. Kolden. 2018. Global patterns of interannual climate–fire relationships. *Global Change Biology* 24: 5164–5175. https://doi.org/10.1111/gcb.14405.

Abatzoglou, J.T., D.S. Battisti, A.P. Williams, W.D. Hansen, B.J. Harvey, and C.A. Kolden. 2021. Projected increases in western US forest fire despite growing fuel constraints. *Communications Earth & Environment* 2: 1–8. https://doi.org/10.1038/s43247-021-00299-0.

Albrecht, Rachel I., Steven J. Goodman, Dennis E. Buechler, Richard J. Blakeslee, and Hugh J. Christian. 2016. LIS 0.1 Degree Very High Resolution Gridded Lightning Annual Climatology (VHRAC). https://doi.org/10.5067/LIS/LIS/DATA304.

Alencar, A.A., P.M. Brando, G.P. Asner, and F.E. Putz. 2015. Landscape fragmentation, severe drought, and the new Amazon forest fire regime. *Ecological Applications* 25: 1493–1505. https://doi.org/10.1890/14-1528.1.

Alexander, H.D., C. Siegert, J.S. Brewer, J. Kreye, M.A. Lashley, J.K. McDaniel, A.K. Paulson, H.J. Renninger, and J.M. Varner. 2021. Mesophication of oak landscapes: Evidence, knowledge gaps, and future research. *BioScience* 71: 531–542. https://doi.org/10.1093/biosci/biaa169.

Andela, N., D.C. Morton, L. Giglio, Y. Chen, G.R. van der Werf, P.S. Kasibhatla, R.S. DeFries, G.J. Collatz, S. Hantson, S. Kloster, D. Bachelet, M. Forrest, G. Lasslop, F. Li, S. Mangeon, J.R. Melton, C. Yue, and J.T. Randerson. 2017. A human-driven decline in global burned area. *Science* 356: 1356–1362. https://doi.org/10.1126/science.aal4108.

Balch, J.K., B.A. Bradley, J.T. Abatzoglou, R.C. Nagy, E.J. Fusco, and A.L. Mahood. 2017. Human-started wildfires expand the fire niche across the United States. *Proceedings of the National Academy of Sciences* 114: 2946–2951. https://doi.org/10.1073/pnas.1617394114.

Bechtold, W.A., and P.L. Patterson, ed. 2005. The enhanced forest inventory and analysis program - national sampling design and estimation procedures. In *Gen. Tech. Rep. SRS-80*, vol. 85, 080. Asheville: U.S. Department of Agriculture, Forest Service, Southern Research Station. https://doi.org/10.2737/SRS-GTR-80.

Beisner, B., D. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* 1: 376–382. https://doi.org/10.1890/1540-9295(2003)001[0376:ASSIE]2.0.CO;2.

Belval, E.J., C.S. Stonesifer, and D.E. Calkin. 2020. Fire suppression resource scarcity: Current metrics and future performance indicators. *Forests* 11: 217. https://doi.org/10.3390/f11020217.

Bishop, D.A., A.P. Williams, R. Seager, A.M. Fiore, B.I. Cook, J.S. Mankin, D. Singh, J.E. Smerdon, and M.P. Rao. 2019. Investigating the causes of increased twentieth-century fall precipitation over the Southeastern United States. *Journal of Climate* 32: 575–590. https://doi.org/10.1175/JCLI-D-18-0244.1.

Carpenter, D.O., M.K. Taylor, M.A. Callaham, J.K. Hiers, E.L. Loudermilk, J.J. O'Brien, and N. Wurzburger. 2021. Benefit or liability? The ectomycorrhizal association may undermine tree adaptations to fire after long-term fire exclusion. *Ecosystems* 24: 1059–1074. https://doi.org/10.1007/s10021-020-00568-7.

Clinton, B.D., L.R. Boring, and W.T. Swank. 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. *Ecology* 74: 1551–1558. https://doi.org/10.2307/1940082.

Creutzburg, M.K., R.M. Scheller, M.S. Lucash, S.D. LeDuc, and M.G. Johnson. 2017. Forest management scenarios in a changing climate: Trade-offs between carbon, timber, and old forest. *Ecological Applications* 27: 503–518. https://doi.org/10.1002/eap.1460.

Davis, K.T., S.Z. Dobrowski, P.E. Higuera, Z.A. Holden, T.T. Veblen, M.T. Rother, S.A. Parks, A. Sala, and M.P. Maneta. 2019. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. *PNAS* 116: 6193–6198. https://doi.org/10.1073/pnas.1815107116.

Driscoll, D.A., D. Armenteras, A.F. Bennett, L. Brotons, M.F. Clarke, T.S. Doherty, A. Haslem, L.T. Kelly, C.F. Sato, H. Sitters, N. Aquilué, K. Bell, M. Chadid, A. Duane, M.C. Meza-Elizalde, K.M. Giljohann, T.M. González, R. Jambhekar, J. Lazzari, A. Morán-Ordóñez, and T. Wevill. 2021. How fire interacts with habitat loss and fragmentation. *Biological Reviews* 96: 976–998. https://doi.org/10.1111/brv.12687.

Flannigan, M.D., B.M. Wotton, G.A. Marshall, W.J. de Groot, J. Johnston, N. Jurko, and A.S. Cantin. 2016. Fuel moisture sensitivity to temperature and precipitation: Climate change implications. *Climatic Change* 134: 59–71. https://doi.org/10.1007/s10584-015-1521-0.

Flatley, W.T., C.W. Lafon, H.D. Grissino-Mayer, and L.B. LaForest. 2013. Fire history, related to climate and land use in three southern Appalachian landscapes in the eastern United States. *Ecological Applications* 23: 1250–1266.

Flatley, W.T., C.W. Lafon, H.D. Grissino-Mayer, and L.B. LaForest. 2015. Changing fire regimes and old-growth forest succession along a topographic gradient in the Great Smoky Mountains. *Forest Ecology and Management* 350: 96–106. https://doi.org/10.1016/j.foreco.2015.04.024.

Greenberg, C.H., C.E. Keyser, L.C. Rathbun, A.K. Rose, T.M. Fearer, and W.H. McNab. 2014. Forecasting long-term acorn production with and without oak decline using forest inventory data. *Forest Science* 60: 222–230. https://doi.org/10.5849/forsci.12-106.

Gesch, D.B., G.A. Evans, M.J. Oimoen, and S. Arundel. 2018. The national elevation dataset (American Society for Photogrammetry and Remote Sensing). 83–110. available at: http://pubs.er.usgs.gov/publication/70201572.

Hanberry, B.B., D.C. Bragg, and H.D. Alexander. 2020. Open forest ecosystems: An excluded state. *Forest Ecology and Management* 472: 118256. https://doi.org/10.1016/j.foreco.2020.118256.

James, N.A., K.L. Abt, G.E. Frey, X. Han, and J.P. Prestemon. 2020. Fire in the Southern Appalachians: Understanding impacts, interventions, and future fire events. In *Gen. Tech. Rep. SRS-249*, 249, 1–34. Asheville: U.S. Department of Agriculture Forest Service, Southern Research Station.

Johnstone, J.F., C.D. Allen, J.F. Franklin, L.E. Frelich, B.J. Harvey, P.E. Higuera, M.C. Mack, R.K. Meentemeyer, M.R. Metz, G.L. Perry, T. Schoennagel, and M.G. Turner. 2016. Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment* 14: 369–378. https://doi.org/10.1002/fee.1311.

King, K.J., G.J. Cary, R.A. Bradstock, and J.B. Marsden-Smedley. 2013. Contrasting fire responses to climate and management: Insights from two Australian ecosystems. *Global Change Biology* 19: 1223–1235.

Krawchuk, M.A., and M.A. Moritz. 2011. Constraints on global fire activity vary across a resource gradient. *Ecology* 92: 121–132. https://doi.org/10.1890/09-1843.1.

Krawchuk, M.A., M.A. Moritz, M.-A. Parisien, J.V. Dorn, and K. Hayhoe. 2009. Global pyrogeography: The current and future distribution of wildfire. *PLoS One* 4: e5102. https://doi.org/10.1371/journal.pone.0005102.

Kreye, J.K., J.M. Varner, J.K. Hiers, and J. Mola. 2013. Toward a mechanism for eastern North American forest mesophication: Differential litter drying across 17 species. *Ecological Applications* 23: 1976–1986. https://doi.org/10.1890/13-0503.1.

Krofcheck, D.J., E.L. Loudermilk, J.K. Hiers, R.M. Scheller, and M.D. Hurteau. 2019. The effects of management on long-term carbon stability in a southeastern U.S. forest matrix under extreme fire weather. *Ecosphere* 10: e02631. https://doi.org/10.1002/ecs2.2631.

Lafon, C.W., A.T. Naito, H.D. Grissino-Mayer, S.P. Horn, and T.A. Waldrop. 2017. Fire history of the Appalachian region: A review and synthesis. In *Gen. Tech. Rep. SRS-219*, 219, 1–97. Asheville: U.S. Department of Agriculture, Forest Service, Southern Research Station. https://doi.org/10.2737/SRS-GTR-219.

Lindenmayer, D.B., E.J. Bowd, C. Taylor, and G.E. Likens. 2022. The interactions among fire, logging, and climate change have sprung a landscape trap in Victoria's montane ash forests. *Plant Ecology* 223: 733–749. https://doi.org/10.1007/s11258-021-01217-2.

Loehle, C. 1988. Tree life history strategies: The role of defenses. *Canadian Journal of Forest Research* 18 (2): 209–222. https://doi.org/10.1139/x88-032.

Ma, W., L. Zhai, A. Pivovaroff, J. Shuman, P. Buotte, J. Ding, B. Christoffersen, R. Knox, M. Moritz, R.A. Fisher, C.D. Koven, L. Kueppers, and C. Xu. 2021. Assessing climate change impacts on live fuel moisture and wildfire risk using a hydrodynamic vegetation model. *Biogeosciences* 18: 4005–4020. https://doi.org/10.5194/bg-18-4005-2021.

Maxwell, C., R. Scheller, J. Long, and P. Manley. 2022. Forest management under uncertainty: the influence of management versus climate change and wildfire in the Lake Tahoe Basin, USA. *Ecology and Society* 27: 15.

McLauchlan, K.K., P.E. Higuera, J. Miesel, B.M. Rogers, J. Schweitzer, J.K. Shuman, A.J. Tepley, J.M. Varner, T.T. Veblen, S.A. Adalsteinsson, J.K. Balch, P. Baker, E. Batllori, E. Bigio, P. Brando, M. Cattau, M.L. Chipman, J. Coen, R. Crandall, L. Daniels, N. Enright, W.S. Gross, B.J. Harvey, J.A. Hatten, S. Hermann, R.E. Hewitt, L.N. Kobziar, J.B. Landesmann, M.M. Loranty, S.Y. Maezumi, L. Mearns, M. Moritz, J.A. Myers, J.G. Pausas, A.F.A. Pellegrini, W.J. Platt, J. Roozeboom, H. Safford, F. Santos, R.M. Scheller, R.L. Sherriff, K.G. Smith, M.D. Smith, and A.C. Watts. 2020. Fire as a fundamental ecological process: Research advances and frontiers. *Journal of Ecology* 108: 2047–2069. https://doi.org/10.1111/1365-2745.13403.

Mitchell, R.J., Y. Liu, J.J. O'Brien, K.J. Elliott, G. Starr, C.F. Miniat, and J.K. Hiers. 2014. Future climate and fire interactions in the southeastern region of the United States. *Forest Ecology and Management* 327: 316–326. https://doi.org/10.1016/j.foreco.2013.12.003.

Moritz, M.A., M.-A. Parisien, E. Batllori, M.A. Krawchuk, J.V. Dorn, D.J. Ganz, and K. Hayhoe. 2012. Climate change and disruptions to global fire activity. *Ecosphere* 3: art49. https://doi.org/10.1890/ES11-00345.1.

Nelson, R.M.J. 2002. An effective wind speed for models of fire spread. *International Journal of Wildland Fire* 11: 153–161. https://doi.org/10.1071/wf02031.

Nikanorov, A.M., and B.L. Sukhorukov. 2008. *Ecological hysteresis*. *Doklady Earth Sciences* 423 (1): 1282–1285. https://doi.org/10.1134/S1028334X08080229.

Noonan-Wright, E., and C.A. Seielstad. 2021. Patterns of wildfire risk in the United States from systematic operational risk assessments: How risk is characterised by land managers. *International journal of wildland fire* 30 (8): 569–584.

Nowacki, G.J., and M.D. Abrams. 2008. The demise of fire and "mesophication" of forests in the Eastern United States. *BioScience* 58: 123–138. https://doi.org/10.1641/B580207.

Nowacki, G.J., and M.D. Abrams. 2015. Is climate an important driver of post-European vegetation change in the Eastern United States? *Global Change Biology* 21: 314–334. https://doi.org/10.1111/gcb.12663.

Omernik, J.M. 1995. Ecoregions: A framework for managing ecosystems. *The George Wright Forum* 12: 35–50.

Parton, W.J. 1996. *"The CENTURY model." Evaluation of soil organic matter models: Using existing long-term datasets*, 283–291. Berlin, Heidelberg: Springer Berlin Heidelberg.

Pausas, J.G., and J.E. Keeley. 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist* 204: 55–65. https://doi.org/10.1111/nph.12921.

Pausas, J.G., and J.E. Keeley. 2021. Wildfires and global change. *Frontiers in Ecology and the Environment* 19: 387–395. https://doi.org/10.1002/fee.2359.

Prestemon, J.P., U. Shankar, A. Xiu, K. Talgo, D. Yang, E. Dixon, D. McKenzie, K.L. Abt, J.P. Prestemon, U. Shankar, A. Xiu, K. Talgo, D. Yang, E. Dixon, D. McKenzie, and K.L. Abt. 2016. Projecting wildfire area burned in the south-eastern United States, 2011–60. *International Journal of Wildland Fire* 25: 715–729. https://doi.org/10.1071/WF15124.

Radeloff, V.C., D.P. Helmers, H.A. Kramer, M.H. Mockrin, P.M. Alexandre, A. Bar-Massada, V. Butsic, T.J. Hawbaker, S. Martinuzzi, A.D. Syphard, and S.I. Stewart. 2018. Rapid growth of the US wildland-urban interface raises wildfire risk. *PNAS* 115: 3314–3319. https://doi.org/10.1073/pnas.1718850115.

Robbins, Z.J., E.L. Loudermilk, M.J. Reilly, J.J. O'Brien, K. Jones, C.T. Gerstle, and R.M. Scheller. 2022. Delayed fire mortality has long-term ecological effects across the Southern Appalachian landscape. *Ecosphere* 13: e4153. https://doi.org/10.1002/ecs2.4153.

Rupp, D. E. 2016. An evaluation of 20th century climate for the Southeastern United States as simulated by Coupled Model Intercomparison Project Phase 5 (CMIP5) global climate models. In *Open-File Report (2016–1047)*. U.S. Geological Survey. https://doi.org/10.3133/ofr20161047.

Scheller, R.M. 2018. The challenges of forest modeling given climate change. *Landscape Ecology* 33: 1481–1488.

Scheller, R.M., J.B. Domingo, B.R. Sturtevant, J.S. Williams, A. Rudy, E.J. Gustafson, and D.J. Mladenoff. 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological Modelling* 201: 409–419. https://doi.org/10.1016/j.ecolmodel.2006.10.009.

Scheller, R.M., D. Hua, P.V. Bolstad, R.A. Birdsey, and D.J. Mladenoff. 2011. The effects of forest harvest intensity in combination with wind disturbance on carbon dynamics in Lake States Mesic Forests. *Ecological Modelling* 222: 144–153. https://doi.org/10.1016/j.ecolmodel.2010.09.009.

Scheller, R., A. Kretchun, T.J. Hawbaker, and P.D. Henne. 2019. A landscape model of variable social-ecological fire regimes. *Ecological Modelling* 401: 85–93. https://doi.org/10.1016/j.ecolmodel.2019.03.022.
Serra-Diaz, J.M., C. Maxwell, M.S. Lucash, R.M. Scheller, D.M. Laflower, A.D. Miller, A.J. Tepley, H.E. Epstein, K.J. Anderson-Teixeira, and J.R. Thompson. 2018. Disequilibrium of fire-prone forests sets the stage for a rapid decline in conifer dominance during the 21st century. *Science and Reports* 8: 6749. https://doi.org/10.1038/s41598-018-24642-2.
Short, K.C. 2021. *Spatial wildfire occurrence data for the United States, 1992–2018 [FPA_FOD_20210617] (5th Edition)*. https://doi.org/10.2737/RDS-2013-0009.5.
Stewart, S.I., V.C. Radeloff, R.B. Hammer, and T.J. Hawbaker. 2007. Defining the wildland–urban interface. *Journal of Forestry* 105: 201–207. https://doi.org/10.1093/jof/105.4.201.
Sturtevant, B.R., B.R. Miranda, J. Yang, H.S. He, E.J. Gustafson, and R.M. Scheller. 2009. Studying fire mitigation strategies in multi-ownership landscapes: Balancing the management of fire-dependent ecosystems and fire risk. *Ecosystems* 12: 445–461. https://doi.org/10.1007/s10021-009-9234-8.
Syphard, A.D., H. Rustigian-Romsos, M. Mann, E. Conlisk, M.A. Moritz, and D. Ackerly. 2019. The relative influence of climate and housing development on current and projected future fire patterns and structure loss across three California landscapes. *Global Environmental Change* 56: 41–55. https://doi.org/10.1016/j.gloenvcha.2019.03.007.
Thomas, D.S., and D.T. Butry. 2014. Areas of the US wildland–urban interface threatened by wildfire during the 2001–2010 decade. *Natural Hazards* 71: 1561–1585.
Thornthwaite, C.W. 1948. An approach toward a rational classification of climate. *Geographical Review* 38: 55–94. https://doi.org/10.2307/210739.
Thornton, P.E., M.M. Thornton, B.W. Mayer, N. Wilhelmi, Y. Wei, R. Devarakonda, and R.B. Cook. 2014. *Daymet: Daily surface weather data on a 1-km grid for North America, Version 2 315612.646437 MB*. https://doi.org/10.3334/ORNLDAAC/1219.
Turner, M.G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91: 2833–2849. https://doi.org/10.1890/10-0097.1.
United States Forest Service. 2001. S_USA.RoadlessArea_2001. https://www.fs.usda.gov/detail/roadless/2001roadlessrule/maps/?cid=stelprdb5382437.
Van Wagner, C.E. 1987. *Development and Structure of the Canadian Forest Fire Weather Index System. Canadian Forestry Service*, 37. Ottawa: Forestry Technical Report 35.
Waldrop, T.A., D.L. Hagan, and D.M. Simon. 2016. Repeated application of fuel reduction treatments in the Southern Appalachian Mountains, USA: Implications for achieving management goals. *Fire Ecology* 12: 28–47. https://doi.org/10.4996/fireecology.1202028.
Walters, S.P., N.J. Schneider, and J.D. Guthrie. 2011. Geospatial Multi-Agency Coordination (GeoMAC) Wildland Fire Perimeters, 2008. *US Geological Survey Data Series* 612 (6). https://doi.org/10.3133/ds612.
Wei, F., S. Wang, B. Fu, M. Brandt, N. Pan, C. Wang, and R. Fensholt. 2020. Nonlinear dynamics of fires in Africa over recent decades controlled by precipitation. *Global Change Biology* 26: 4495–4505. https://doi.org/10.1111/gcb.15190.
Williams, A.P., B.I. Cook, J.E. Smerdon, D.A. Bishop, R. Seager, and J.S. Mankin. 2017. The 2016 Southeastern U.S. drought: An extreme departure from centennial wetting and cooling. *Journal of Geophysical Research: Atmospheres* 122: 10888–10905. https://doi.org/10.1002/2017JD027523.
Yang, J., H. Tian, B. Tao, W. Ren, J. Kush, Y. Liu, and Y. Wang. 2014. Spatial and temporal patterns of global burned area in response to anthropogenic and environmental factors: Reconstructing global fire history for the 20th and early 21st centuries. *Journal of Geophysical Research: Biogeosciences* 119: 249–263.
Young, A.M., P.E. Higuera, P.A. Duffy, and F.S. Hu. 2017. Climatic thresholds shape northern high-latitude fire regimes and imply vulnerability to future climate change. *Ecography* 40: 606–617. https://doi.org/10.1111/ecog.02205.
Zuur, A.F., E.N. Ieno, N. Walker, A.A. Saveliev, G.M. Smith. 2009. *Mixed effects models and extensions in ecology with R, Statistics for biology and health*. New York: Springer. https://doi.org/10.1007/978-0-387-87458-6.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.