

Climate changes and wildfire alter vegetation of Yellowstone National Park, but forest cover persists

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Abstract. We present landscape simulation results contrasting effects of changing climates on forest vegetation and fire regimes in Yellowstone National Park, USA, by mid-21st century. We simulated potential changes to fire dynamics and forest characteristics under three future climate projections representing a range of potential future conditions using the FireBGCv2 model. Under the future climate scenarios with moderate warming ($>2^{\circ}\text{C}$) and moderate increases in precipitation (3–5%), model simulations resulted in 1.2–4.2 times more burned area, decreases in forest cover (10–44%), and reductions in basal area (14–60%). In these same scenarios, lodgepole pine (*Pinus contorta*) decreased in basal area (18–41%), while Douglas-fir (*Pseudotsuga menziesii*) basal area increased (21–58%). Conversely, mild warming ($<2^{\circ}\text{C}$) coupled with greater increases in precipitation (12–13%) suggested an increase in forest cover and basal area by mid-century, with spruce and subalpine fir increasing in abundance. Overall, we found changes in forest tree species compositions were caused by the climate-mediated changes in fire regime (56–315% increase in annual area burned). Simulated changes in forest composition and fire regime under warming climates portray a landscape that shifts from lodgepole pine to Douglas-fir caused by the interaction between the magnitude and seasonality of future climate changes, by climate-induced changes in the frequency and intensity of wildfires, and by tree species response.

Key words: Douglas-fir; fire regime; FireBGCv2; forest dynamics; landscape simulation model; lodgepole pine; *Pinus contorta*; *Pseudotsuga menziesii*; Yellowstone National Park.

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INTRODUCTION

Gradual changes in landscape composition and structure are predicted with shifting climate patterns (Hamann and Wang 2006, Rehfeldt et al. 2006, Danby and Hik 2007, Kelly and Goulden 2008, Crookston et al. 2010, Iglesias et al. 2015, Sheehan et al. 2015). However, climate-driven species shifts often occur in the context of increased landscape disturbance that can catalyze abrupt changes in composition, structure, and function

(Flannigan et al. 2000, Dale et al. 2001, Gavin et al. 2007). In particular, ecosystems across the globe are heavily influenced by the highly variable nature of fire disturbance (Turner et al. 1993, Bond et al. 2005, Krawchuk et al. 2009, Loehman et al. 2014). In fire-adapted, fire-prone systems, landscape patterns and vegetation distributions are determined primarily by reciprocal interactions with fire (Whitlock et al. 2003, Heyerdahl et al. 2008) and then by fine-scale interactions within and among species (e.g., competition and

dispersal) and their surrounding environment (e.g., climate and edaphic conditions; Falk et al. 2007).

An understanding of the interactions between climate and fire is especially critical for landscapes of the fire-prone western United States, as warmer and drier climate conditions are projected to cause more frequent, more severe, and larger fires than occurred historically (Flannigan et al. 2000, Giorgi and Mearns 2002, Bond et al. 2005, Krawchuk et al. 2009, Loehman et al. 2014). In Yellowstone National Park (YNP), fire has played a key role in shaping vegetation patterns and species adaptations (Romme 1982, Turner et al. 1994). YNP and surrounding Greater Yellowstone Ecosystem (GYE) have been the focus of decades of research on landscape ecological complexity, disturbance ecology, and paleoecological history (Taylor 1973, Romme 1982, Millspaugh and Whitlock 1995, Huerta et al. 2009). This rich body of research provides extensive evidence of the complex interactions among vegetation, wildfire, and climate, and the sensitivity of landscape patterns to changes in ecological drivers. Previous studies have suggested that climate-mediated shifts in fire patterns may result in dramatic changes in landscape vegetation composition in the park (Romme and Turner 1991, Westerling et al. 2011). For example, Romme and Turner (1991) developed a conceptual model of the response of vegetation to climate change, hypothesizing that a warmer and drier future would result in increased fire frequency, decreased forest extent, and shift in remaining forests toward younger age classes. Westerling et al. (2011) correlated the occurrence and size of contemporary wildfires with climate variables and projected that future warmer temperatures would lead to more frequent and larger fires than are present in the modern record, and subsequent potential changes in landscape composition and structure.

Given the complex, interacting, and potentially non-linear relationships between climate, fire, and vegetation (Allen 2007, Falk et al. 2007, Kitzberger et al. 2012), we hypothesized that a dynamic spatially explicit ecosystem process model—one capable of simulating reciprocal fire–vegetation interactions in response to climate drivers across space and time—could provide additional insight into potential, major changes in the landscape ecology of YNP and similar ecosystems. The simulation model used here, FireBGCv2, differs from models used in previous studies (Smithwick et al. 2010,

Westerling et al. 2011) because FireBGCv2 simulates complex and long-term interactions, dynamics, and feedbacks of the climate, vegetation, and wildfire system, including potential shifts in forest species composition and fire regimes. We used the FireBGCv2 model to evaluate three main questions: First, how might forest structure and composition change with changing climate? Second, do the interactions of climate and fire alter potential emerging vegetation patterns? Finally, how does variability in projected climate change, as represented by several different climate futures, affect vegetation and fire regimes in YNP?

METHODS

Study area

The central plateau (44.5° N, 110.6° W) of YNP is a high-elevation (2000–3000 m) forested region, approximately 162,000 ha in size, that is dominated by even-aged lodgepole pine (*Pinus contorta* ssp. *latifolia*) forests (Fig. 1). Lodgepole pine is particularly well adapted to crown fire regime (Brown 1973, Lotan et al. 1985, Despain 1990). Serotiny allows lodgepole pine to effectively store seeds for many years and to release large quantities of seed following a fire (Lotan et al. 1985). Lodgepole pine in YNP is capable of growing in high densities, and most stands have limited undergrowth (Despain 1990, Lotan and Critchfield 1990, Tinker et al. 1994).

Climate on the plateau is characterized by long, cold winters and short, cool summers, with an average annual temperature near 0°C. Annual precipitation ranges from 50 to 120 cm. Drought conditions are common during the summer, as rains are rarely sufficient to replace water lost through evaporation and transpiration. Infrequent, high-intensity crown fires historically drove forest succession on the plateau, transforming lodgepole pine and late-successional spruce–fir (*Picea engelmannii*, *Abies lasiocarpa*) forests back to even-aged lodgepole pine seedling stands and pockets of aspen woodlands (Despain 1990, Turner et al. 1999). Fire history studies provide ample evidence of large stand-regenerating fires at long intervals of 200–400 years—accounting for most of the total area burned over the last several centuries—interspersed with few smaller fires, creating the current heterogeneous mosaic of species and structure (Romme 1982, Romme and Despain 1989, Whitlock 1993).

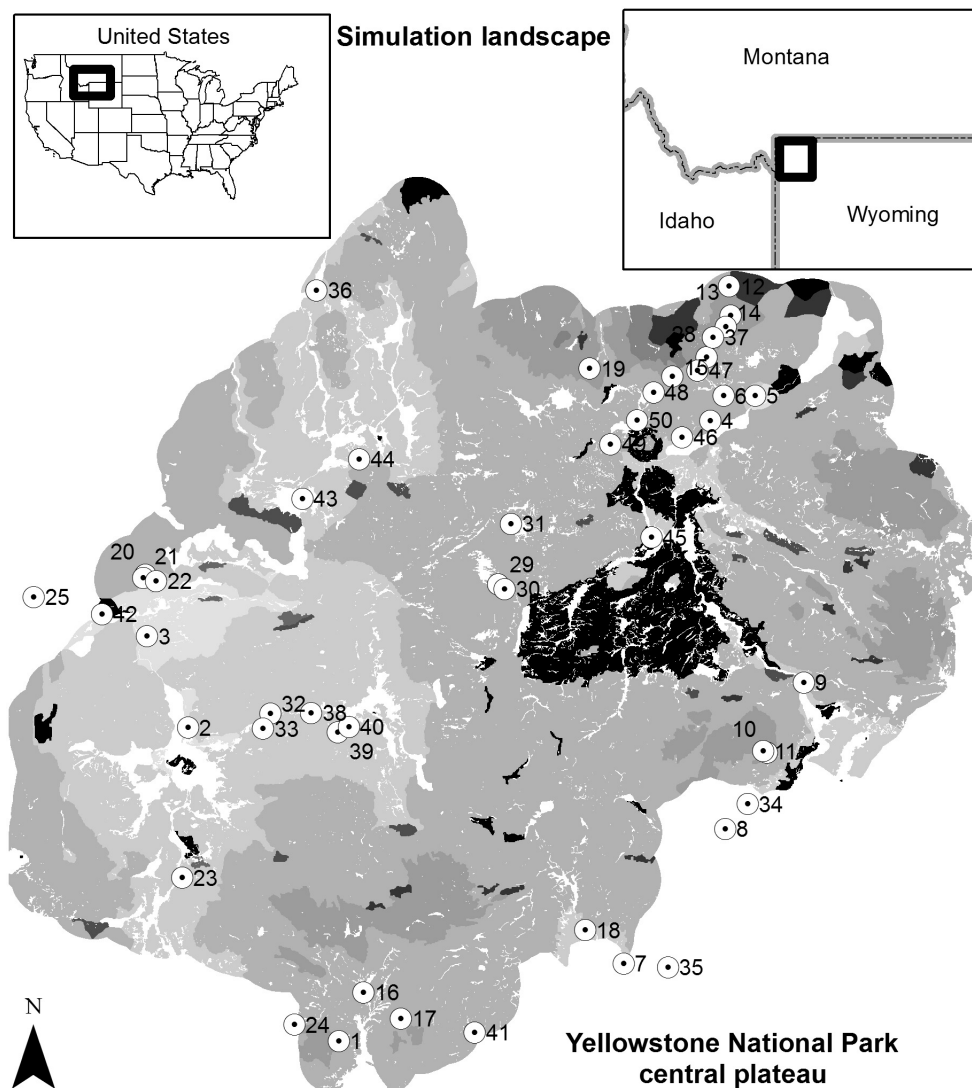


Fig. 1. Yellowstone National Park central plateau simulation landscape location. Field plot locations are indicated by solid white circles with black dots. Gray shading within the simulation landscape represents biophysical sites (see *Methods* section).

FireBGCv2 model

FireBGCv2 (Keane et al. 1996, 2011) is a cumulative effects model developed to assess long-term trends in landscape ecological regimes, and to simulate interactions of disturbance, climate, and vegetation across ecological timescales (centuries; Loehman et al. 2011). The FireBGCv2 platform incorporates a number of independent vegetation and fire modeling components from previously developed models (Running and Coughlan 1988, Keane et al. 1989, 1990, Running and Hunt 1993,

Finney 1998, Reinhardt et al. 1998, Thornton 1998) to simulate ecological processes.

The model integrates five hierarchical scales of spatial organization. From broad to fine, these scales are as follows: (1) coarse, fixed-boundary biophysical settings that are defined by similar topography, weather, soils, and potential vegetation which are held constant throughout the simulation; (2) dynamically created stands that differ by existing vegetation composition and structure; (3) simulation plots on which ecosystem processes

are modeled for computational efficiency; (4) individual species with well-defined physiological parameters; and (5) individual trees, each of which is explicitly represented with multiple attributes such as age, height, diameter at breast height (dbh), and leaf area.

In the FireBGCv2 model, wildland fire processes are reckoned at multiple scales. Fire ignitions are simulated at the site scale using functions that relate the climate variable, Keetch-Byram Drought Index (KBDI), calculated from daily weather, to input fire return intervals (Catchpole 2002). Fire occurs when fine fuel loadings are sufficient ($>0.05 \text{ kg/m}^2$) and fuel moistures are sufficiently dry ($<10\%$), as determined by dynamic, stand-level characteristics. Fires spread across the landscape via cell percolation techniques where fire growth follows gradients of slope and wind direction; growth is terminated when fuels are too wet or too sparse to sustain spread, or when cumulative annual area burned reaches an area stochastically determined from input average fire size. Fire behavior characteristics such as flame length, scorch height, and intensity are calculated at the stand scale using algorithms from BURNUP, a model that calculates heat transfer to fuels (Albini 1994). Individual fire-caused tree mortality is modeled as a function of bark thickness (a user-defined parameter) and scorch height, and can be used to assess fire severity. The degree of crown scorch and cambial kill depends on fire intensity and duration, as empirically determined in Ryan and Reinhardt (1988). As implemented, fire strongly affects regeneration and landscape composition and structure through controls on mortality and post-fire environmental context (e.g., residual duff, available seed sources). As model simulations progress, vegetation patterns influence fire dynamics via rate of production and type of fuels and tree and stand characteristics that influence fire behavior, such as bark thickness, crown base height, and canopy closure.

Simulation landscape development

We created 18 biophysical sites within our YNP landscape (Fig. 1) based on a classification of slope, aspect, elevation, and soils to capture topographic, solar radiation, and precipitation gradients and soil types important for determining species composition and productivity. We

developed an initial stand map, representative of current vegetation within each biophysical site, by intersecting a forest cover layer (Yellowstone National Park, *unpublished data*) with the site layer described above. The forest cover layer is based on a 40-class vegetation layer (Despain 1990) which was updated with wildfire perimeters and burn severities through 2003. Stands with areas less than 100 ha were merged with similar nearby stands. We used a total of 747 stands to initialize the simulations (Appendix S1: Table S1).

Field data collection

To initialize and parameterize important state variables in FireBGCv2, we collected field data across the YNP central plateau in 2010 and 2011. These data were gathered from 50 plots representative of the model biophysical sites described above, using methods developed for other FireBGCv2 projects (Keane et al. 1996, 1999, Loehman et al. 2011; Fig. 1). At each plot, we collected data estimating forest and undergrowth (non-tree species) biomass and characterized structure and composition of the forest canopy by recording individual tree species, height, diameter at breast height, crown ratio, canopy position, and health status within circular plots of 11.3 m radii (Lutes et al. 2006). At each plot, we also measured surface fuel loadings (kg/m^2) for shrubs, herbaceous plants, litter, duff, and 1-, 10-, 100-, and 1000-h fuels using visual techniques detailed in Keane and Dickinson (2007), as these data are important for simulating fire behavior. Plot data were used to initialize stands and trees on the simulation landscape and to quantify some model parameters. Because FireBGCv2 dynamically alters stand perimeters every year as fire activity, tree mortality, and physiologically determined vegetation responses to resource availability occur, model results from multi-century simulations are not strongly determined by stand-level initial conditions. Thus, 50 plots provided sufficient stand variability for model initialization and parameterization.

Model parameterization

The FireBGCv2 model requires a daily weather data stream for each site to simulate ecological processes, fuel dynamics, and fire behavior. To represent contemporary conditions in the model, we obtained a weather data record from a 98-year

instrumental record (1910–2008) of daily temperature and precipitation, from the National Climatic Data Center cooperative weather station located at Lake Yellowstone (NCDC 2011). We used the Mountain Climate Simulator (MT-CLIM) to extrapolate this weather stream to individual sites using elevation, slope, and aspect corrections for temperature and precipitation, and to calculate required inputs of vapor pressure deficit, solar radiation, and day length (Hungerford et al. 1989, Thornton and Running 1999). MT-CLIM provides a flexible weather extrapolation technique that can be matched to any spatial resolution with high accuracy (Thornton et al. 1997). The MT-CLIM calculations require baseline precipitation, derived for each site based on a PRISM Climate Group spatial grid of historical precipitation for the period 1981 to 2010 (Prism Precipitation Norm 1981–2010 2012). The 98-year contemporary climate data and daily weather streams representing future climate, described below, were repeated end to end for the duration of the 600-year simulations (see *Discussion*).

As parameterized, fire frequency and size interact in the model with weather, climate, vegetation, and surface fuels to determine where and when fires burn on the simulation landscape. Historical fire frequency and size were parameterized using available fire history studies (Romme 1982, Schoennagel et al. 2003) and lake sediment studies dating back ~10,000 years (Millspaugh and Whitlock 1995, Millspaugh et al. 2000, Higuera et al. 2011). To calibrate the FireBGCv2 model, we adjusted fire size and frequency parameters until the model simulated an average landscape fire return interval of 328 years (SD 127 years) under the contemporary weather record, consistent with the available fire history record for the region (Romme 1982, Schoennagel et al. 2003).

Species parameters, used in model algorithms to simulate phenology, establishment, growth, and mortality, were taken from the literature and previous FireBGCv2 projects (Loehman et al. 2011, Holsinger et al. 2014). Many tree and stand initial conditions, such as leaf, stem, and root carbon, were calculated within the model using our field data (Keane et al. 2011). Field data provided the tree species and understory species present on the modeled landscape. Field measurements of individual understory species' biomass, height, and cover provided understory plant biomass

parameters and biomass maxima. Species' growing degree-day minima and maxima, parameters that influence tree productivity and mortality, were calculated from climatic envelopes produced by Climate-FVS, a tool that incorporates climate change impacts into the forest growth simulation model Forest Vegetation Simulator (FVS; Crookston et al. 2010). Tree-ring widths from collections taken in YNP were used to calibrate the modeled diameter growth increment of each species under the historical (1903–2008) climate. These were obtained from the World Data Center for Paleoclimatology (Briffa et al. 1992, Evans et al. 2010, King and Evens 2008, King and Tercek 2010).

Serotiny, the long-term storage and fire-triggered release of seeds, is an important fire adaptation in lodgepole pine, the dominant contemporary tree species in YNP (Schoennagel et al. 2003). The FireBGCv2 model can simulate species-specific levels of serotiny (proportion of cones per tree that are serotinous), and we set the serotiny level for lodgepole pine at 20% following data from Tinker et al. (1994); in other words, 20% of the cones on every tree are serotinous (see *Discussion: Model limitations*).

Simulating climate changes

Climate futures are represented in the FireBGCv2 model using a “delta” or “offset” method, which applies projected changes in temperature and precipitation as offsets derived from a global climate model (GCM) to daily observed weather records (Snover et al. 2003). The delta method represents the most straightforward method for downscaling global-scale model projections to local regions and has a high level of climate realism that is desirable in future impact studies (although the method only accounts for changes to the mean climate signal; Ekström et al. 2015).

We incorporated a range of potential climate futures from three climate models to assess the response of vegetation and fire regimes. We chose two climate models that bracketed the range of potential extremes (Littell et al. 2011) and one ensemble average. Ensemble averaging minimizes model error and bias and provides more comprehensive climate predictions than single-model simulations (Giorgi and Francisco 2000, Murphy et al. 2004, Solomon 2007) because magnitude, direction, and seasonality of

Table 1. Annual climate offsets used in simulations.

Climate	Temperature offset (°C)	Precipitation offset (%)
Historic	+0	+0
A2-low	+1.6	+13
A2-avg	+2.7	+5
A2-high	+4.0	+3

Notes: A2-avg is the ensemble average from 13 GCMs. A2-high is from the MIROC3.2 GCM. A2-LOW is from the NCAR-PCM GCM. All values are projections for the study area in 2050.

GCM-derived temperature and precipitation projections may vary widely for a given region (Dai 2006). Our three models were as follows: (1) an ensemble average (A2-avg) of 13 GCMs; (2) the NCAR-PCM (A2-low) model (Washington et al. 2000), which projects the coolest mid-century climate for the study area (i.e., lower bound); and (3) the MIROC3.2 (A2-high) model (K-1 Model Developers 2004) that projects the warmest mid-century climate (i.e., upper bound; Table 1). For each of the climate models, we used the A2 emission scenario (Nakicenovic et al. 2000), which represents a high-emission future (850 parts per million by volume by 2100). The A2 scenario is similar to the Stocker et al. (2013) RCP8.5 scenario. We selected these older Nakicenovic and Swart (2000) scenarios because fine-scale (8 km) extrapolations for the GYE at the time of this study were unavailable for the newer RCP4.5 or RCP8.5 Stocker et al. (2013) scenarios.

We acquired ensemble global climate model temperature and precipitation projections from the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 3 (CMIP3) multi-model dataset (Meehl et al. 2007). The data were downscaled to a 0.5° grid, based on the 1950–1999 gridded observations of Adam and Lettenmaier (2003) as described by Maurer et al. (2009) using the bias-correction/spatial downscaling method (Wood et al. 2004). These data were accessed via the Climate Wizard online tool (Maurer et al. 2007, Climate Wizard 2012).

Offsets for all three climate scenarios by seasons were annually warmer (1.6–4.0°C) and wetter (3–13%) than those for the historical climate (Table 1). As the lower bound, the A2-low scenario had the least amount of warming and the greatest increase in precipitation. As a measure of central tendency in GCMs, the A2-avg scenario had slightly more warming and more modest

precipitation increase than the A2-low scenario. Finally, as the upper bound, the A2-high scenario had the greatest amount of warming and generally the smallest precipitation increase. End-of-century temperature offsets are more extreme (2.5–6.2°C) than the mid-century offsets used here (1.6–4.0°C), and may produce more dramatic changes on the Yellowstone landscape. We simulated a “ramp-up period” of 100 years to obtain the highest values in the offsets and then applied these maximum values for the remaining 500 years of simulation. Our intent was not to simulate 600 years into the future, but rather simulate 500 years of change to assess possible shifts in vegetation dynamics and fire regimes.

Simulation design

We produced 10 replicate 600-year model runs for each of the three future climate simulations (A2-low, A2-avg, A2-high) and the historical climate (Historic). We used several model outputs as response variables in our analysis. To track fire regime shifts, we analyzed two variables: *annual area burned* and *fire rotation*. Area burned was calculated as the average annual area burned over the 600-year simulation period over the entire landscape. Fire rotation, the amount of time to burn an area equivalent to the entire 162,000-ha simulation landscape, was calculated as landscape area divided by average annual area burned across the landscape over the 600 years.

To monitor vegetation abundance and composition, we used three variables: *total basal area* (m²/ha), *forest cover* (%), and *basal area by tree species* (m²/ha). Total basal area is a sum of basal area for all tree species and is a proxy for total forest biomass on the landscape. Forest cover tracks the percentage of the landscape covered in forest (greater than 25% canopy cover) vs. non-forest vegetation (<10% tree cover). To assess forest composition, we used *basal area by species*. For basal area and forest cover variables, we report landscape values at the end of the 600-year simulation to capture the cumulative effects of climate and fire.

Statistical analysis

Two-way analysis of variance was used to compare total basal area, basal area by species, fire rotation, area burned, and forest cover from each of the three climate simulations to the contemporary simulations. The landscape was used

Table 2. Landscape means of total basal area, forest cover, fire rotation, and area burned.

Climate scenario	Basal area (m ² /ha)	Forest cover (%)	Fire rotation (yr)	Area burned (ha)
Historic	24.4 (6.8)	65.0 (15.3)	401.4 (91.1)	401.5 (92.8)
A2-low	29.8 (4.7)ns	72.5 (11.9)ns	336.1 (114.7)ns	500.9 (152.9)ns
A2-avg	9.8 (7.7)***	21.2 (21.2)***	147.9 (45.0)***	1116.2 (287.0)***
A2-high	12.0 (7.8)**	31.0 (20.4)***	97.7 (29.5)***	1666.2 (358.2)***

Notes: Values in parenthesis are SDs. Statistically significant differences from the historic values are bolded and denoted as * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, and ns (not significant). See Fig. 3 for maps of forest cover and average fire return interval.

as the unit of analysis (calculated as an area-weighted sum of stand values); end-of-simulation values (basal area and forest cover) and averages over simulation period (area burned and fire rotation) were used for analysis. All statistical analyses were performed using the R statistical software package (R Development Core Team 2012). Linear models were fit using the “nlme” package and a correlation structure (corAR1) to account for temporal autocorrelation (Pinheiro et al. 2013). Assumptions of normality were checked for each response variable, and a power transformation (0.44) was applied to the species basal area variable. Hypothesis testing was carried out using the “glht” function and the multiple comparisons package (Hothorn et al. 2008). P -values from the analysis of variance were adjusted to account for multiple comparisons using the BH method (Benjamini and Hochberg 1995, Benjamini and Yekutieli 2001).

RESULTS

The effects of climate change on forest structure and composition varied by climate scenario. Our model results suggest that moderate 21st-century warming (1.6°C) may decrease forest cover and basal area (Table 2) and alter species composition from lodgepole pine- to Douglas-fir-dominated stands (Fig. 2). Simulations incorporating A2-avg and A2-high climate futures resulted in decreased forest cover (by 34–44%) and basal area (by 51–60%) while increasing the relative amount of Douglas-fir (by 23–59%) and decreasing the amount of lodgepole pine (by 18–43%) relative to the historic simulations. Interestingly, the A2-low climate simulations, which had a warming of <2°C and greater increased precipitation, actually resulted in increased forest cover (8%), basal area (12%), and subalpine fir and Engelmann spruce (22%).

Fire regimes

Fire rotations were shorter for all future climates than the simulated contemporary rotation of 400 years, with A2-high and A2-avg climates producing significantly different values of 98 and 148 years, respectively (Table 2). Annual area burned increased for all climate simulations and a significantly larger area burned under A2-high (1666 ha) and A2-avg (1116 ha) as compared with simulated historical burned area. The most extreme departure from modeled historical values for both fire rotation (303 years shorter, or 24% of historical) and area burned (increase of 1265 ha burned per year, or 4.1 times more than historical simulation values) occurred for the warmest climate scenario (A2-high). The least departure in fire rotation (65 years shorter or 83% of historical simulation values) and area burned (increase of 100 ha burned per year or 1.3 times more than historical simulation values) occurred for the coolest climate scenario (A2-low). Over time, area burned varied widely in all simulations (Fig. 2b). Warmer simulations showed both greater average area burned per year and larger individual fires. Spatially, average fire return interval followed patterns of elevation, with shorter return intervals at lower elevations and longer return intervals at higher elevations, and prevailing wind direction spreading fires to the northeast (Fig. 3a). Changes in fire regime altered vegetation patterns, as reflected in the model results.

Vegetation

The A2-avg and A2-high simulations resulted in both reduced basal area and forest cover compared to historic simulations, while the A2-low simulations resulted in non-significant increases in basal area and forest cover (Table 2). Simulated total basal area ranged from 9.8 m²/ha (A2-avg) to 29.8 m²/ha (A2-low) representing a

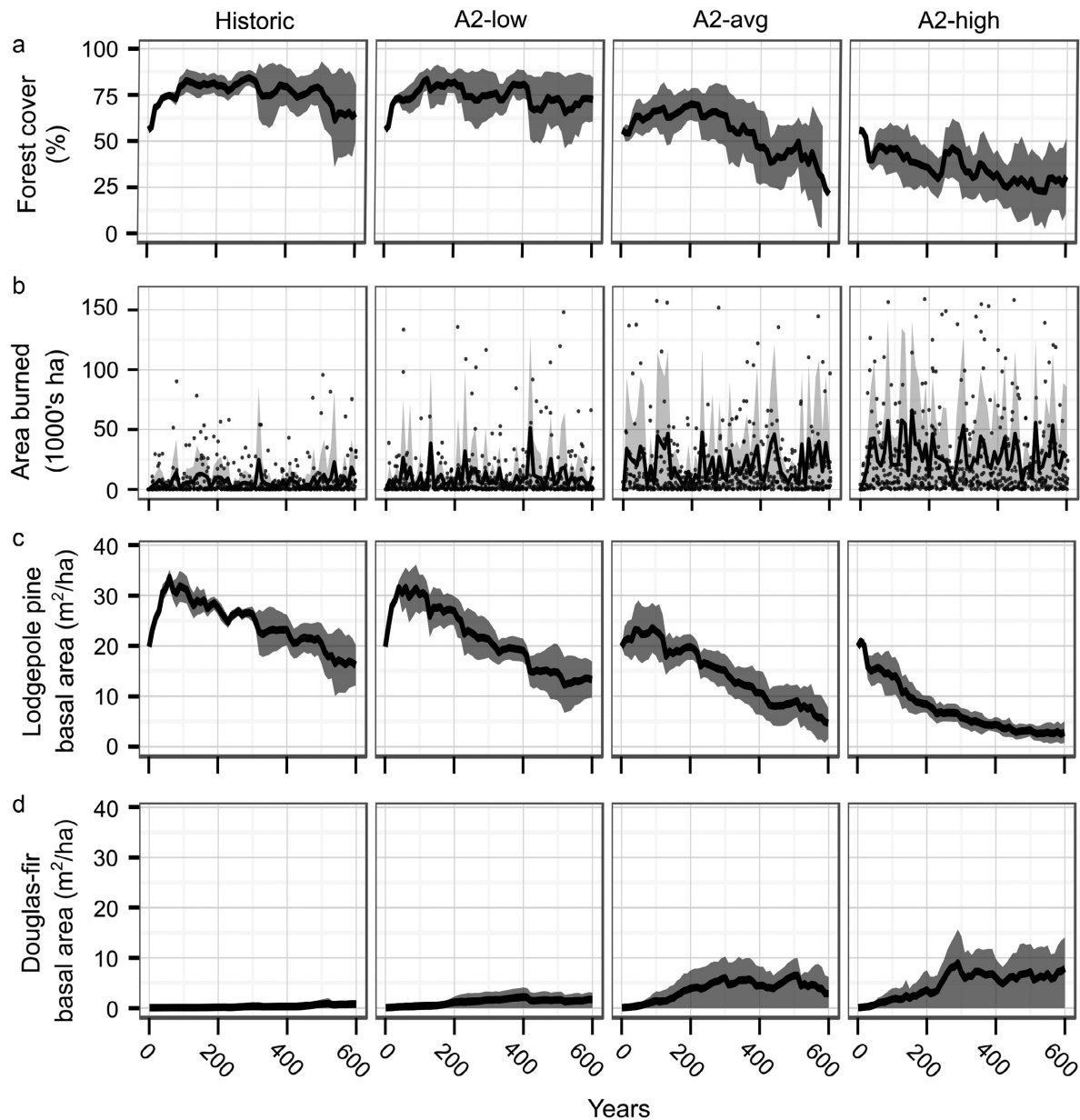


Fig. 2. Time series of simulation landscape variables: forest cover (a), area burned (b), lodgepole pine basal area (c), and Douglas-fir basal area (d). Black lines represent means of replicate model simulations, gray-shaded areas represent ± 1 SD, and black dots in (b) represent total area burned for a given year.

decrease of 60% to an increase of 22% over historic simulations. Similarly, forest cover ranged from 21% (A2-avg) to 73% (A2-low) representing a decrease of 68% to an increase of 12% over historic simulations (Fig. 2a). Spatially, there was large variability in forest cover and basal area, which was largely controlled by fire history and

underlying biophysical site properties (see *Methods* for site details; Fig. 3d).

Species composition also varied among climate scenarios. In historic simulations, the landscape was dominated by lodgepole pine (71%), with lesser amounts of Engelmann spruce (14%), sub-alpine fir (11%), Douglas-fir (3%), and whitebark

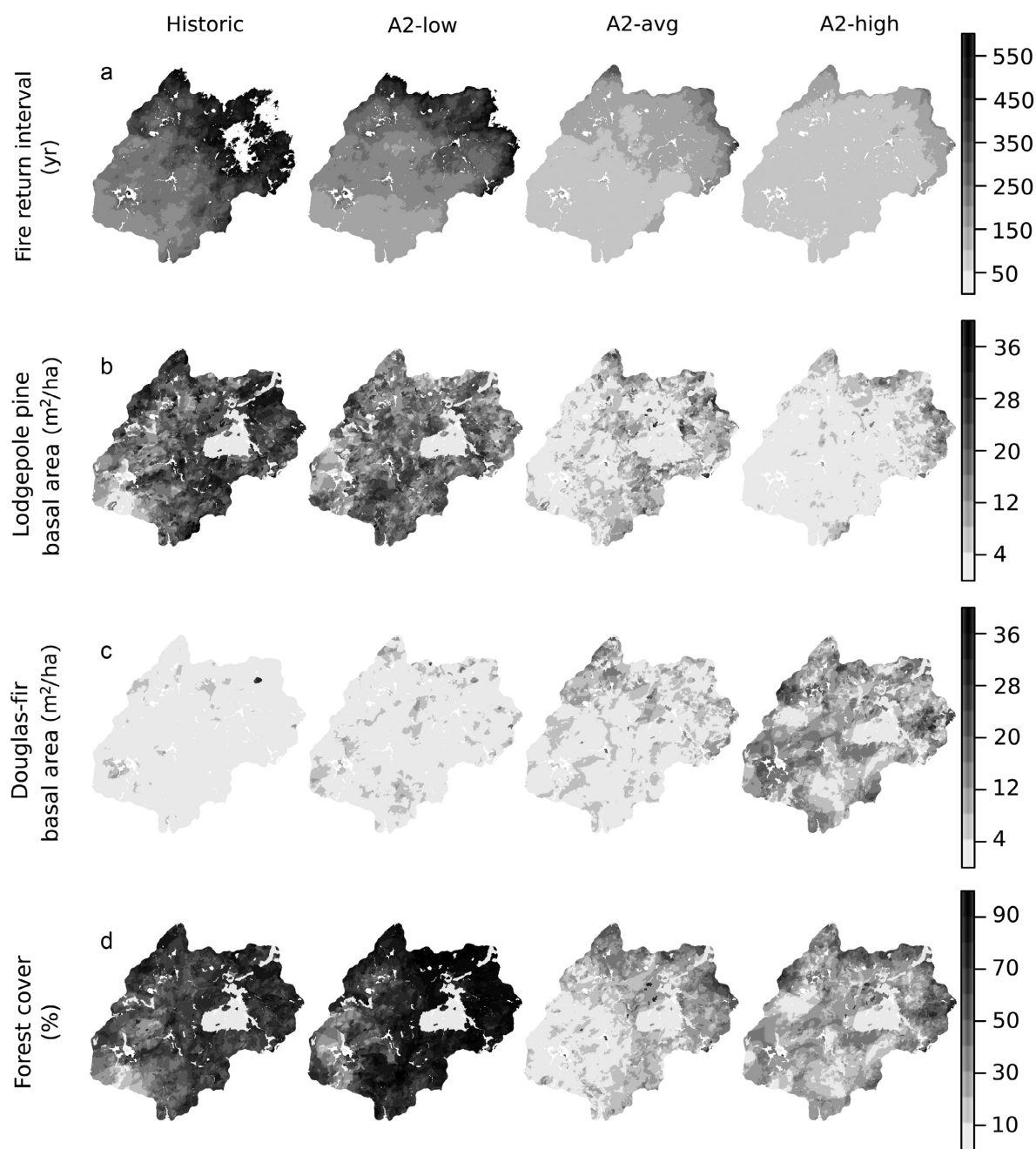


Fig. 3. Maps of simulation landscape variables: fire return interval (a), lodgepole pine basal area (b), Douglas-fir basal area (c), and forest cover (d). Maps represent the average of model replicates for each climate scenario at year 600. Lighter grays represent lower values, while darker grays represent higher values. Scaling of gray values varies by panel.

pine (2%; Table 3). In both the A2-avg and A2-high simulations, composition shifted from lodgepole pine dominance toward a more equal mix with Douglas-fir (Fig. 2c, d). Under the

hottest scenario (A2-high), Douglas-fir basal area surpassed lodgepole pine basal area albeit at low densities (Fig. 3b, c). The A2-low scenario maintained lodgepole pine basal area at levels close to

Table 3. Forest species composition.

Climate scenario	Basal area (m ² /ha)			Basal area (% of total)		
	Lodgepole pine	Douglas-fir	Other	Lodgepole pine	Douglas-fir	Other
Historic	17.1 (4.2)–	0.8 (0.9)–	6.6 (2.5)–	71.1 (–)	3.0 (–)	25.9 (–)
A2-low	14.0 (3.8)ns	1.8 (1.5)ns	14.0 (2.8)**	46.6 (–24.6)	6.0 (+2.9)	47.5 (+21.6)
A2-avg	4.9 (3.3)***	3.0 (3.5)ns	1.9 (1.8)ns	53.5 (–17.6)	26.0 (+23.0)	20.5 (–5.3)
A2-high	3.1 (2.3)***	8.4 (6.5)**	0.6 (0.2)*	27.7 (–43.4)	61.8 (+58.8)	10.4 (–15.4)

Notes: Basal area (m²/ha) is presented with SDs in parenthesis. Statistically significant differences from the historic values are bolded and denoted as * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, and ns (not significant). All percentage values are mean percentages of total basal area. Values in parenthesis are the percentage difference from the historic simulation (i.e., under the A2-low climate simulation, lodgepole pine is 46.6% of total basal area, which is 24.6% less than the 71.1% lodgepole pine in the historic simulation). Other includes whitebark pine (*Pinus alba*), subalpine fir, and Engelmann spruce. See Fig. 2 for changes in species basal area over time. See Fig. 3 for maps of basal area.

the historic scenario, but increased the basal area of subalpine fir and Engelmann spruce.

DISCUSSION

The size and intensity of wildfires, major drivers of forest structure (Flannigan et al. 2000), will be critical in determining the future landscape of YNP. We found that warmer future climates, especially $>2^{\circ}\text{C}$, increased the amount of fire on the landscape and caused major changes in vegetation composition (Tables 2 and 3). Similar to Westerling et al. (2011), we modeled a decrease in fire rotation and increase in annual area burned; however, in contradiction to their findings that suggested that amplified fire activity could result in a shift from forest to grasslands, we found an alternative pathway toward a more fire-resistant species, Douglas-fir. Thus, our model results suggest that climate changes and wildfire can alter the vegetation of YNP, but forest cover persists.

The mechanisms driving the conversion from lodgepole pine to Douglas-fir in FireBGCv2 are related to both fire activity and species' fire tolerance. Douglas-fir is more fire-resistant than lodgepole pine because mature Douglas-fir develops thick bark that can protect trees from low-intensity fires that occur after repeated fire cycles reduce fuels (Agee 1996). In contrast, lodgepole pine has relatively thin bark and may be easily killed by low-intensity fires (our simulations showed over 70% fire-caused mortality in lodgepole pine). Moreover, as fires increase on the YNP landscape, there are more areas that reburn before lodgepole pine can reach reproductive maturity (>15 yr), thereby eliminating the species from the reburned

area and reducing off-site seed dispersal because of serotiny. This can result in a conversion to non-forest cover or, if Douglas-fir is present, the encroachment of Douglas-fir into the reburned area. Douglas-fir may also be better adapted to the potential future climate of YNP than lodgepole pine as it grows in warmer, drier locations and can tolerate successive low to moderate-intensity fires (Ryan and Reinhardt 1988). Lodgepole pine may be able to tolerate predicted temperature increases, but its ability to remain on the landscape will depend on the frequency of fire and associated changes in precipitation, while genetic adaptation and redistribution necessary may take centuries (Rehfeldt et al. 2001).

Climate-induced shifts from lodgepole pine to Douglas-fir have been projected for other ecosystems. Hamann and Wang (2006), using a climate envelope model, predicted habitat decreases for lodgepole pine and large increases for Douglas-fir through 2085 in British Columbia, Canada, in the absence of wildfire. While Douglas-fir cannot compete successfully under the current climate on YNP's rhyolitic soils, there is paleo-evidence for a greater abundance of Douglas-fir ~9000 years ago (Whitlock 1993). Climate warming during the late-glacial period (20,000–11,000 years before present [YBP]) and earlier in the Holocene (11,000–7000 YBP) caused drastic changes in vegetation and fires (Millsaugh et al. 2000, Huerta et al. 2009). Historical reconstructions from pollen core analysis revealed that warming of $4\text{--}5^{\circ}\text{C}$ allowed for *Picea* forest to develop in what was previously a meadow shrub community. *Abies* and *Pinus* (*albicaulis* or *flexilis*) established throughout the region except on the central plateau where *Pinus contorta* and *Pseudotsuga* were prevalent, eventually giving

rise to the *Pinus contorta*-dominated forest of today. Analyses of charcoal in lake sediments revealed that an increase in fire frequency during middle to late Holocene was due to warming (Millsbaugh et al. 2000, Huerta et al. 2009). The forest changes simulated using FireBGCv2, while representing a dramatic change from current conditions, are similar in magnitude to recorded type shifts in the paleo-assemblages.

Model limitations, assumptions, and uncertainties

Algorithms, parameters, and assumptions in FireBGCv2 represent our limited understanding of the complex interactions among biotic and abiotic ecosystem components, and these are certainly not all-inclusive. Model results are influenced by stochastic elements of fire spread and tree regeneration (Keane et al. 2011), as well as parameter settings and simulation design. For example, we set serotiny at a fixed level of 20% for all simulations, although variable levels of serotiny from 4% to 65% have been measured on pre- and post-fire landscapes in the GYE (Tinker et al. 1994, Schoenagel et al. 2003). The FireBGCv2 model does not currently allow for variable levels of serotiny within species, although future modeling experiments could use a sensitivity testing approach to address the effects of varying serotiny levels on post-fire regeneration and landscape composition.

Model results are influenced by our method of repeating weather records in sequence for multiple cycles over the 600-year simulation. In our historic simulations, large-fire years show a weak tracking of historic hot and dry, large-fire years (e.g., 1988) in cyclical patterns. However, in the future climate simulations large fires occur in many years and the cyclical pattern of large-fire years is not apparent. It is also important to understand that the model is used here to simulate changes in vegetation and fire regimes, and not to predict what will happen over the next 600 years.

The fire regimes used in this study were produced by adjusting the size and frequency of fires from the historic scenario based on the KBDI (Keane et al. 2011). This is an assumption in modeling future fire regimes, as little work has been done linking landscape-scale fire regime with daily-to-yearly weather records (Clark 1989, Rorig and Ferguson 1999). Previous work has demonstrated there is a strong link between

weather and fire (Westerling et al. 2006), and the strong link of KBDI to fire activity (Catchpole 2002, Dolling et al. 2005, Liu et al. 2010). Absent data and simulation resources to model ignition mechanisms explicitly, our method represents an acceptable approximation that aggregates the many processes involved in ignition, and evaluations from previous FireBGCv2 modeling efforts indicate that this technique provides realistic correlations with observed fire statistics (Holsinger et al. 2014).

CONCLUSION

Although forest cover persisted on the central plateau of YNP under all of the six simulated climate futures, the composition and structure of the forest varied by climate simulation and were heavily influenced by the frequency of wildfires. Our results indicate that lodgepole pine forest may persist on the YNP landscape with as much as a 76% reduction in the historical fire rotation (1.2–4.2 times more area burned), providing the species can tolerate the local shifts in temperature and precipitation associated with climate change. Douglas-fir is predicted to increase under warmer climates because of its tolerance to increased fire activity, but also because the species is physiologically better adapted to warmer, drier conditions.

The interactions and feedbacks of climate and fire, over both short and long timescales, are critically important in determining the growth, distribution, and structure of YNP's forests, so it is equally critical that ecosystem models represent these interactions, preferably in a mechanistic approach (Keane et al. 2015). Wildfire regimes are sensitive to climate and are likely to change more rapidly than vegetation via immediate responses of fuel moistures and availability of ignitable fuels (Renkin and Despain 1992). Over longer timescales, climate-driven shifts in vegetation composition and structure (i.e., fuels) strongly influence fire regimes, which in turn influence vegetation (Loehman et al. 2014). The exact nature and strength of these feedbacks is uncertain but depends on emergent patterns of climate, the ability of forest species to adapt to new climatic conditions, and resulting fire and other disturbance regimes. Our results highlight the importance of understanding and testing species responses to novel environmental

and climate conditions, and explicitly modeling reciprocal fire–vegetation interactions across landscape scales and decades to centuries.

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SUPPORTING INFORMATION

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