

# Continued warming could transform Greater Yellowstone fire regimes by mid-21st century

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Contributed by Monica G. Turner, June 24, 2011 (sent for review May 28, 2011)

Climate change is likely to alter wildfire regimes, but the magnitude and timing of potential climate-driven changes in regional fire regimes are not well understood. We considered how the occurrence, size, and spatial location of large fires might respond to climate projections in the Greater Yellowstone ecosystem (GYE) (Wyoming), a large wildland ecosystem dominated by conifer forests and characterized by infrequent, high-severity fire. We developed a suite of statistical models that related monthly climate data (1972–1999) to the occurrence and size of fires >200 ha in the northern Rocky Mountains; these models were cross-validated and then used with downscaled (~12 km × 12 km) climate projections from three global climate models to predict fire occurrence and area burned in the GYE through 2099. All models predicted substantial increases in fire by midcentury, with fire rotation (the time to burn an area equal to the landscape area) reduced to <30 y from the historical 100–300 y for most of the GYE. Years without large fires were common historically but are expected to become rare as annual area burned and the frequency of regionally synchronous fires increase. Our findings suggest a shift to novel fire–climate–vegetation relationships in Greater Yellowstone by midcentury because fire frequency and extent would be inconsistent with persistence of the current suite of conifer species. The predicted new fire regime would transform the flora, fauna, and ecosystem processes in this landscape and may indicate similar changes for other subalpine forests.

Fire structures ecological systems across multiple scales and is an important component of the Earth system (1, 2). High-severity fire is characteristic of boreal and subalpine forests, including extensive conifer forests of western North America (3–6). High-severity fires are generally large, infrequent (i.e., fire return intervals are often 100–300 y), stand replacing, and driven by climatic effects on fuel flammability rather than by fuel quantity (5, 7–9). Fewer than 5% of fires account for >95% of area burned (3, 10). High-severity fires kill trees and initiate secondary succession, shifting stand age and structure and driving subsequent carbon storage, habitat patterns, and fuel loadings. Improved knowledge of fire dynamics is key to understanding Earth's coupled climate–carbon system (e.g., refs. 11–14). For residents and land managers of fire-prone regions, potential changes in fire dynamics have vast implications for vulnerability of future ecosystem services.

Fire regimes are shifting, and the tempo of change appears to be accelerating. With the warming of Earth's climate (15), fire frequency, extent, severity, and seasonality are expected to change profoundly in the future, with substantial increases in fire activity in many areas (9, 16–21). In the presence of a gradually changing driver such as climate, fire is a fast variable that triggers rapid and significant ecological change. However, there is substantial regional variation in climate–fire relationships (e.g., refs. 2 and 22–24), and a key challenge is translating broad-scale future fire predictions to scales relevant for anticipating ecological consequences and managing natural resources. Of central importance are the magnitude of anticipated changes in fire (e.g., annual area

burned and fire return interval) and whether rapid changes may occur soon (14, 18).

Ecosystem resilience may be compromised by novel disturbance regimes (9, 25, 26), and fire regimes may be sensitive indicators of tipping elements (*sensu* ref. 27) that exhibit threshold-like behavior and qualitatively change regional ecosystems. Lenton et al. (27) define tipping elements as subsystems that can be switched into qualitatively different states by small perturbations. The tipping point is the corresponding critical point—in forcing—beyond which the system is qualitatively altered. For example, successive fires in a relatively short time (i.e., compound disturbances) (25) may have synergistic effects, and thus the increased temperatures that drive more frequent fires could constitute a tipping point. Whether increased disturbance frequency will produce qualitative ecosystem changes will depend on the degree to which a community has recovered from the first disturbance when affected by a second. In fire-resilient plant communities, postfire successional trajectories typically lead to vegetation similar to the prefire community (28). Sequential fires could convert such forests to other plant communities if the interval between fires is less than that required to ensure postfire tree regeneration (e.g., to develop the canopy seedbank stored in serotinous cones that allows some conifer species to reestablish after high-severity fire) (29, 30).

Recent evidence suggests that forests in the northern Rocky Mountains are close to a temperature threshold for fire vulnerability (29, 31). The Intermountain West is relatively arid, but dense conifer forests occur at higher elevations and more northerly latitudes where cool temperatures and snow-dominated precipitation support tree growth. Canopy fuels necessary to carry large fires are plentiful, but fuel flammability is controlled by climate. Throughout the West, forest area burned is most strongly associated with low precipitation, low moisture indexes (e.g., moisture deficit, Palmer drought severity) and high temperatures; numerous studies suggest that temperature and its effects on moisture are the most important controls on large fire occurrence and extent (e.g., refs. 18 and 32). Fire suppression, exclusion, and fuel treatment influences are detectable to varying degrees across forest types, but of secondary importance in most forests, especially at higher elevations (24, 33). Large fires have increased in the northern Rockies in recent decades in association with warmer temperatures, earlier snowmelt, and longer fire seasons (31). Midelevation Rocky Mountain forests with stand-replacing fire regimes have been most sensitive to climate warming, accounting for approximately two-thirds of recent west-wide increases in large forest fires (31). This change corresponds to increased spring

Author contributions: A.L.W., M.G.T., E.A.H.S., W.H.R., and M.G.R. designed research; A.L.W. performed research; A.L.W. analyzed data; and A.L.W. and M.G.T. wrote the paper.

The authors declare no conflict of interest.

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This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1110199108/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1110199108/-DCSupplemental).

and summer temperatures of  $<1\text{ }^{\circ}\text{C}$  and earlier spring snowmelt across a large area. However, what this portends for the timing and magnitude of future climate-driven changes in fire is not well understood.

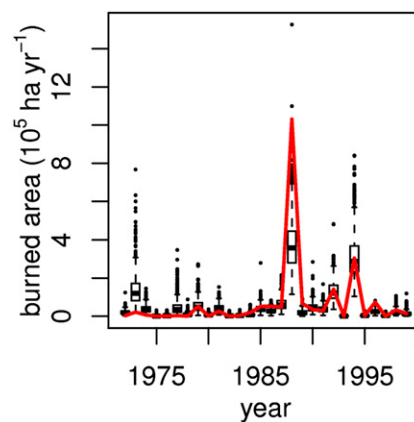
Here we consider how the occurrence, size, and spatial location of large fires ( $>200\text{ ha}$ ) in the Greater Yellowstone ecosystem (GYE) (Fig. S1) might change with climate change. The GYE is one of the most pristine and well-studied wildland ecosystems of temperate North America and an ideal natural laboratory for exploring climate–fire relationships. Fire return intervals of 100–300 y have characterized GYE forests for the past 10,000 y (34), and intervals of 75–100 y were documented in lower elevation forest–steppe vegetation (35, 36). We developed and cross-validated unique statistical models relating observed northern Rockies fires to land-surface characteristics, observed 1972–1999 climate, and hydrology simulated with the variable infiltration capacity (VIC) hydrologic model (37). We combined a logistic regression model to predict the probability of fire ( $>200\text{ ha}$ ) occurrence with a Poisson lognormal model to predict the number of fires given at least one occurred and a generalized Pareto distribution (GPD) model to predict fire size. The statistical models were then used with monthly output from three downscaled ( $\sim 12\text{ km} \times 12\text{ km}$  grid) global climate models (GCMs) and VIC to simulate 1,000 monthly fire occurrence and area burned histories for each scenario for the GYE through 2099 and to calculate expected fire rotations—the time to burn an area equal to the area of a landscape of interest (10). See *Methods* and *SI Text* for further details.

We used climate scenarios (Fig. S2) from three GCMs [National Center for Atmospheric Research (NCAR) CCSM 3.0, Centre National de Recherches Météorologiques (CNRM) CM 3.0, and Geophysical Fluid Dynamics Laboratory (GFDL) CM 2.1] from the Intergovernmental Panel on Climate Change (IPCC)'s Fourth Assessment (“AR4”) (14), forced with a medium-high emissions pathway (Special Report on Emissions Scenarios “SRES A2”) (38). These three GCMs are among a subset of AR4 models suitable for the western United States because of their depiction of seasonal variations in temperature and precipitation and multiyear variability in Pacific sea-surface temperature on the scale of El Niño/Southern Oscillation (39, 40). The A2 emissions scenario was selected as reasonably consistent with trends over recent decades in anthropogenic carbon emissions (41). Future emissions of greenhouse gases and their short-term feedbacks to climate are uncertain. However, most scenarios do not begin to differ meaningfully until midcentury, and our results for the next several decades should be somewhat robust to the choice of emissions scenario.

Our approach assumes that the fundamental relationships between climate and fire are stationary, but changes in the frequency and location of climatic conditions conducive to large fires will influence fire activity. Because this stationarity assumption will be violated once climate shifts beyond the conditions that sustain the current ecosystem and fire regime, our approach is most useful for determining responses to climate change in the coming decades and identifying when the climate–vegetation system might not be sustained in its present form.

## Results

Our combined statistical models predicted fire and characterized extreme fire years in the Northern Rockies more effectively than has been done previously (Fig. 1 and *SI Text*). Temperature, precipitation, and moisture deficit were all important for predicting fire occurrence and number; given that a fire occurred, cumulative water year moisture deficit was key for estimating fire size distributions (*SI Text*). The models explained 83% of interannual variation in large fire occurrence and 73% of the variation in burned area for the calibration dataset. For the model estimation period in the Northern Rockies, 33% of fires

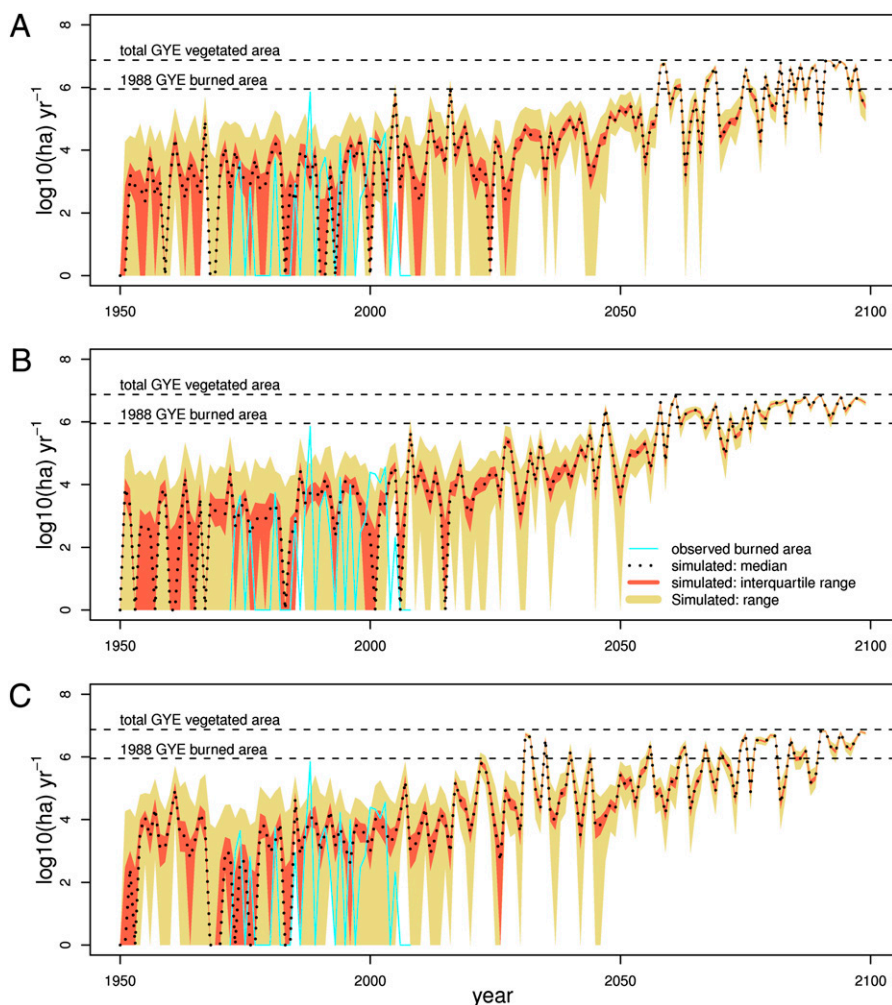


**Fig. 1.** Annual area burned by large fires in the Northern Rockies: observed (line) versus predicted from 1,000 simulations per month, aggregated across 2,309 grid cells (boxes show interquartile range; whiskers, 1.5 $\times$  interquartile range; and points, extremes). Results are a composite of simulations for fire presence/absence using probabilities from cross-validated logistic regressions, simulations for fire size from cross-validated Poisson lognormal distributions conditional on fire presence and the linear estimator from the cross-validated linear regression, and fire size estimated using a generalized Pareto distribution conditional on fire occurrence and moisture deficit (see also Figs. S6–S9). The generalized Pareto is validated elsewhere (*SI Text* and Figs. S7 and S8).

and 66% of burned area occurred during the two largest fire years (1988 and 1994); 30% of fires and 45% of burned area in our simulation also occurred during those two years (*SI Text* and Fig. S3). High fire activity always occurred during warmer-than-average years, and this pattern was clear within the GYE (Fig. S4). The relationship between temperature and fire was non-linear, and only  $\sim 0.5\text{ }^{\circ}\text{C}$  above the 1961–1990 average spring and summer temperature (March–August) distinguished large-fire years from most other years in the GYE (Fig. S4). Warmer-than-average temperatures were a necessary but not sufficient condition for predicting extreme fire years; in addition to temperature, moisture deficit and summer precipitation (July–August) also influenced fire during warm years (Fig. S6). Our methods captured broad-scale topographic variability in climate (e.g., cooler temperatures at higher elevations), which is necessary for regional fire projections. The probabilistic models enabled robust estimates of fire response to changing climate, including extreme fire years, by running large numbers of simulations (*SI Text*).

Fire simulations for three downscaled GCM scenarios for the recent historical period (1950–1990) in the GYE produced realistic interannual variation in area burned and no directional trends (Fig. 2). Predicted area burned was  $<10,000\text{ ha}$  ( $<1.25\%$  of the GYE) in most years and agreed well with observed variability; however, no simulated fire years were as extreme as 1988 before the first decade of the 21st Century. This result is not unexpected; 1988-scale events in the GYE are necessarily very rare (otherwise historical fire rotations would be less than the observed  $>120\text{ y}$ ). In addition, our hydrologic simulations cannot incorporate extremes in day-to-day variability in wind speed because downscaled wind fields are not yet available. Because extreme dry conditions in the recent historical record resulted from climate (high temperature and low precipitation) and weather (high winds), the simulated dry extremes in moisture deficit using climatological winds are likely underestimated.

Post-1990 simulations projected substantial increases in GYE fire (Fig. 2). Notably, by 2020 projected increases in burned area over a 1951–1990 reference period were detectable with 95% confidence over 100% of simulations using one-sided Mann–



**Fig. 2.** The range (light shading), interquartile range (dark shading), and median (dotted line) of predicted area burned for 1,000 gridded monthly simulations, aggregated over the GYE by year, and the observed annual area burned (solid line) for three downscaled GCM SRES A2 climate scenarios: NCAR CCSM 3.0 (A), CNRM CM 3.0 (B), and GFDL CM 2.1 (C).

Whitney tests. Fire seasons comparable to 1988 became more frequent, with between one (for NCAR) and five (for GFDL) such events occurring between 2011 and 2050. After 2050, all models predicted that annual area burned would exceed 100,000 ha during most years. Years with no large fires—common in the historical record—became extremely rare by 2050 and did not occur in 1,000 simulations after 2050 for either the CNRM or GFDL scenarios and occurred only three times in the 1,000 NCAR simulations. This increase in average annual “background” area burned in years without 1988-scale events is also apparent in observed fires for the last two decades (Fig. S5). By about 2075, potential annual area burned regularly exceeds the signature 1988 event, often by a large margin. By then, forest ecosystems in the GYE, and the fuels and fire responses they support, would likely have been transformed by changing climate and disturbance and moved outside the bounds of the modeled climate–fire relationship.

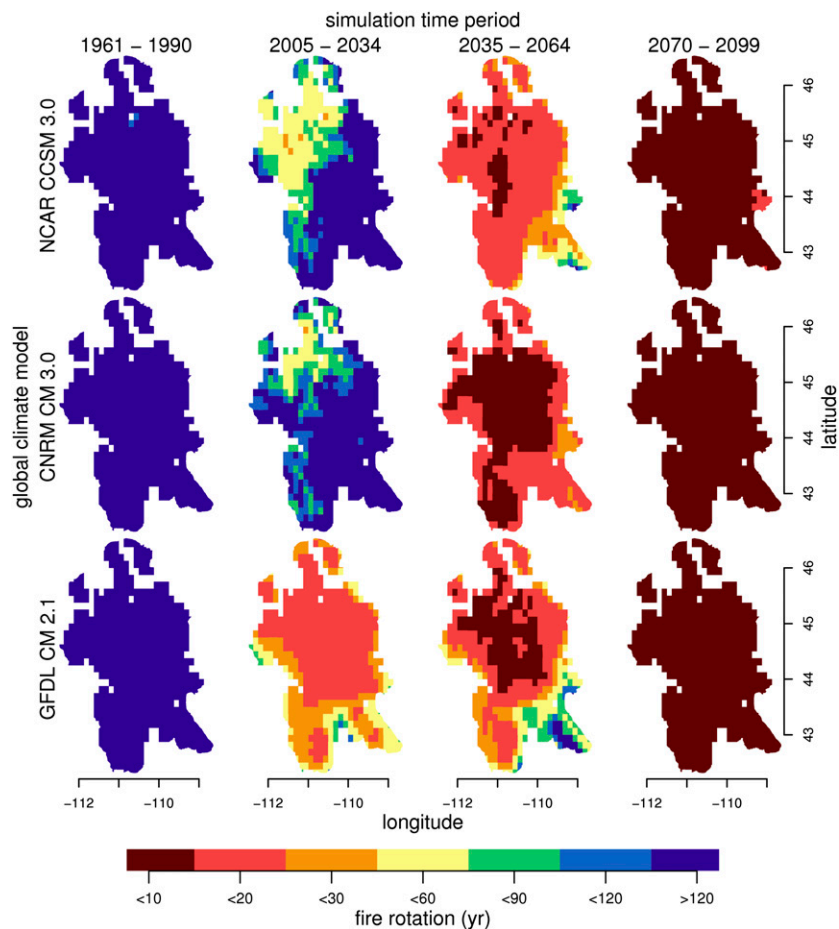
Fire rotations (FRs), which exceed 120 y throughout most of the GYE before 1990, are in transition to shorter periods across all scenarios by the first decades of the 21st century (Fig. 3). Downscaled climate predictions from all three GCMs were qualitatively similar but differed somewhat with respect to mid-century timing of fire-regime shifts. For 2005–2034, FRs begin to fall below 60 y in portions of the landscape for all scenarios, although the rate of change varies; differences in precipitation among scenarios have greater influence on fire early on, whereas effects of high temperatures dominate late in the century. Spatial patterns are similar across scenarios, with FRs decreasing sooner

and to a greater extent in the northwestern areas of the GYE. By midcentury, FRs are <20 y throughout the majority of the GYE, except for small portions to the southeast (Fig. 3). By end of century, climatic conditions associated with large fires are the norm (Fig. S2), and FRs <10 y are projected across the GYE for all three GCMs (Fig. 3); however, by the time such short fire rotations could be driven by climate, fuel limitations would be expected to constrain fire occurrence and area burned.

### Discussion

Our findings indicate that GYE forests are rapidly approaching a threshold beyond which fire occurrence and extent are likely to change the ecosystem qualitatively. Recent history shows that a shift in spring and summer temperature (March–August) of just over 0.5 °C above the 1961–1990 average distinguished extreme fire years from most others in the Northern Rockies, and increases in average spring and summer temperatures predicted by 2099 are ~4.5–5.5 °C for the GCM scenarios explored here (Fig. 2 and Fig. S2). The projected changes in temperatures and fire are not consistent with persistence of the suite of conifer species that have dominated the Yellowstone landscape throughout the Holocene. Rather, the projected climate–fire regime is consistent with lower montane woodland or nonforest vegetation and implies a shift from a climate-limited to a fuel-limited system (24) by midcentury. Climate conditions conducive to large fires in the current system would occur in most years, but less biomass would be available to burn because recovery times between successive fires would be shorter. Thus, we might expect novel fire–climate–





**Fig. 3.** Projected fire rotations calculated for 1,000 monthly gridded simulations for four 30-y periods across three downscaled GCM SRES A2 climate scenarios.

vegetation relationships, suggesting that the GYE is approaching a tipping point (i.e., critical change in temperature and moisture deficit) that could be exceeded by mid-21st century.

Our results are consistent with predictions for increased temperature-driven fire activity in other regions (20, 21, 23, 42, 43) but also suggest that future climate–fire dynamics may differ from those observed in the past. Numerous studies demonstrate that climate and fire have varied substantially in the GYE throughout the past 10,000 y. During the early Holocene, increased summer temperature was associated with increased fire frequency on the central plateau in Yellowstone National Park, and the fire return interval declined to 75–100 y for several millennia (44). During the past 1,300 y, large fires on the central plateau occurred in decades including the driest years, and widespread burning (>10,000 ha) occurred at 150- to 300-y intervals (45). During the past 2,650 y in forest–steppe vegetation of northern Yellowstone, fire intervals averaged 75 y, but fire-free intervals of several centuries were detected twice (35). Thus, climate and fire regimes have varied considerably in the past. Nonetheless, our models indicate that, by the middle of the 21st century, forests of the GYE may regularly experience climatic conditions that exceed the most extreme years in the instrumental and paleoecological record. Our models also predicted geographic differences in the timing of predicted transitions in fire regimes, notably an earlier onset of shorter fire rotations in the northwestern portions of the region. Other studies have noted spatial variation in precipitation and fire regimes in the GYE (e.g., refs. 34 and 46–49), and geographic differences in fire regimes are likely to be observed in the future.

Uncertainty in predicted climate–fire relationships increases as climate conditions move outside the historical range of vari-

ability, and predictions for the latter 21st century must be interpreted with care. Our fire models will become increasingly poor guides as current and future climates—and the fuel conditions that support current climate–fire relationships—diverge. This is true to some extent for any statistical model given the lack of recent historical analogs and the currently highly nonlinear climate–fire relationship in the study area, and predicted fire activity (especially beyond 2050) must be interpreted in the context of key assumptions. First, the statistical models of fire occurrence and area burned are based primarily on fires in conifer forests (which dominate the vegetated area) given present-day climate and vegetation; predicted future climate diverges substantially from that used for model development. Second, the nature of feedbacks from vegetation to future fire activity is a critical unknown. Area burned cannot increase indefinitely because changing fuels will eventually limit fire occurrence (50). This feedback is not included in our models but will become an increasingly important influence on fire in the latter half of the century. Following severe fire, subsequent fire activity is reduced for some time because fuels are sparse. Younger forests will burn readily in extreme fire weather, as observed during the 1988 Yellowstone fires when regenerating saplings in *Pinus contorta* stands <10 y old carried crown fire (4, 51). However, fuel quantity will diminish as the time for vegetation recovery between fires declines. Third, our study used average conditions within 12-km × 12-km grid cells and cannot predict variation in fire dynamics (e.g., effects of local topography or subgrid cell FRs) at finer spatial scales. Finally, our study did not consider variation in fire severity, and we have not considered potential interactions with other disturbances, such as outbreaks of native bark beetles (*Dendroctonae*) (52, 53).

Anticipating vegetation shifts in the GYE under altered climate–fire regimes is complex and beyond the scope of this study. However, fire can catalyze rapid shifts in plant communities when climate conditions change sufficiently to favor postfire establishment of different species (e.g., ref. 54), and such dynamics have already been observed elsewhere (55–57). Warming temperatures alone are expected to cause declines in suitable habitat for some conifers now common in the GYE, even if precipitation also increases (58–60). In the GYE, projected changes in temperature reach the historical differences in temperature between subalpine forest (with an historical fire rotation >100 y) and lower montane forest (with an historical fire rotation <30 y) by the end of the century. Following fire, tree species that currently occupy lower elevations in the GYE (e.g., *Pseudotsuga menziesii*, *Populus tremuloides*) could potentially expand upslope on suitable substrate, as documented for andesite substrates in the GYE during the early Holocene (61). Although the paleoecological record has revealed remarkable resilience of GYE vegetation to a wide range of climate and fire regimes (e.g., refs. 44 and 61), our study suggests that future changes in climate and fire rotations could preclude conifer regeneration and convert currently forested areas to woodland or nonforest. Future research should prioritize understanding potential postfire successional trajectories.

## Conclusions

Continued warming could completely transform GYE fire regimes by the mid-21st century, with profound consequences for many species and for ecosystem services including aesthetics, hydrology, and carbon storage. The conditions associated with extreme fire seasons are expected to become much more frequent, with fire occurrence and area burned exceeding that observed in the historical record or reconstructed from paleoproxy records for the past 10,000 y. Even in years without extreme fire events, average annual area burned is projected to increase, and years with no large fires—common until recently—are projected to become increasingly rare. The timing and spatial location of such changes varied somewhat among the three GCMs used in this study, but the models converged by the latter part of the century. The magnitude of predicted increases in fire occurrence and area burned suggests that there is a real likelihood of Yellowstone’s forests being converted to nonforest vegetation during the mid-21st century because reduced fire intervals would likely preclude postfire tree regeneration. A change in dominant vegetation would also cause the GYE to shift from a climate- to a fuel-limited fire regime (24). We suggest that the climate–fire system is a tipping element that may qualitatively change the flora, fauna, and ecosystem processes in this landscape and could be indicative of similar changes in other subalpine or boreal forests.

## Methods

**Spatial and Temporal Domain.** The spatial domain for developing the climate–fire statistical models is a 1°/8° latitude/longitude grid for the Northern Rocky Mountains ( $n = 2,309$  grid cells,  $\sim 12\text{-km} \times 12\text{-km}$  cell size; Fig. S1). We used this larger region because it encompasses the GYE and includes multiple fire occurrences across a broad range of representative climate conditions. Statistical models were estimated for the entire domain and then applied and evaluated for the subsample comprising the GYE ( $n = 578$ ). The temporal domain for model estimation included monthly data from 1972 to 1999, defined by the overlap in availability of high-quality gridded historical observed climate datasets and a comprehensive gridded fire history for the region. Thus, the statistical models were fit for 775,824 data points ( $2,309$  grid cells  $\times 28$  y  $\times 12$  mo/y). See SI Text for study area description and data sources.

**Statistical Models of Climate–Fire Relationships.** We developed three probabilistic statistical models relating observed fires to climatic conditions for 1972–1999. Logistic regression was used to predict the probability of a fire >200 ha (henceforth “fire”) occurrence in each grid cell by month. Conditional Poisson lognormal models were then estimated to predict the number ( $\geq 1$ ) of fires given that fire occurred, with a covariate derived from the lo-

gistic regression. Finally, the area burned in each fire was predicted using a GPD fit to observed fires, using a climatic covariate. The overall statistical modeling approach is summarized as

$$\text{Expected Area Burned} = P(\theta(X)) \times \hat{C}(\theta | \text{fire} > 0) \times \hat{A}(X | \text{fire} = 1),$$

where  $\theta$  is the linear estimator from a logistic regression on variables  $X$  for a given grid cell and month,  $P$  is the probability of fire where

$$P = \exp(\theta) / (1 + \exp(\theta)),$$

$\hat{C}(\theta | \text{fire} > 0)$  is the expected number of fires given that fire occurs ( $\geq 1$ ) estimated by a set of Poisson lognormal models conditioned on  $\theta$ , and  $\hat{A}$  is the expected burned area per fire estimated by a GPD model as a function of variates  $X$ . See SI Text for full model descriptions and cross-validation results.

**Projected 21st Century Forest Fire Regimes in the GYE.** Three AR4 GCMs (NCAR CCSM 3.0, CNRM CM 3.0, and GFDL CM 2.1) forced with a medium-high emissions pathway (SRES A2) (38) were used for climate predictions. For current and future climate, we used GCM runs downscaled to the North American Land Data Assimilation System (LDAS) (62) 1°/8° latitude/longitude grid (henceforth grid) to force hydrologic simulations using VIC, providing a suite of hydroclimatic variables (37).

We used our statistical models to simulate fire occurrence for the GYE ( $n = 578$  grid cells) for 1951–2099, using downscaled hydroclimate for each GCM run. We estimated fires and area burned for 1,000 simulations per grid cell and month and then compared predictions with the historical record (Fig. 2). The actual historical record is only one possible outcome of a complex system, and the models will not reproduce the historical record exactly. However, observed fire should be within the range of outcomes represented by the simulations. The ability to generate an arbitrary number of simulations allowed us to estimate changes in extremes as well as mean fire activity and to estimate quantiles of expected fire activity.

As noted above, climate–fire interactions in GYE forests are such that small changes in model specifications can produce divergent outcomes in fire activity, especially for climate that exceeds the historic range of variability. To produce conservative future estimates of fire activity, we constrained our models by assuming that historically observed fire–climate relationships within Northern Rockies forests describe the most extreme scenarios possible at any point in space and time within the GYE. Thus, for our GCM-driven fire projections, we required that  $P(\theta)$  never exceed the maximum calculated using historical climate (24%), Poisson lognormal distributions never exceed the extremes calculated for historic climate (i.e., the probability of observing multiple large fires does not increase for  $\theta$  above the historic maximum), the maximum number of fires burning in a single grid cell can never exceed the historic maximum (5), the GPD scale parameter never exceeds the historic maximum (i.e., scale does not increase with normalized cumulative water–year moisture deficit greater than the 1972–1999 maximum), fires never exceed the observed historic maximum area burned per fire (173 kha), and total area burned by multiple fires ignited in the same year and grid cell can never exceed the observed historic maximum (211 kha). These constraints require that, for any point in space and time, the number and size of fires simulated cannot exceed the maximum observed in the recent record and the probability of observing extremes in fire number and size cannot increase as climate exceeds historically observed extremes. Only increases in the frequency and spatial extent of extreme climate conditions are allowed to drive increases in fire.

In addition, whereas available unburned vegetated area is seldom a binding constraint on GYE burned area, we anticipate that it will become so in the future. Many simulated fires burn only a portion of a cell, but some fires burn all of the vegetated area within a cell or are larger than the cell itself. For each fire simulation, we allocate the burned area of fires starting in a grid cell to the vegetated area in that grid cell first and then to immediately adjacent cells. Where multiple fires would burn together, the total burned area is limited to the available vegetated area. Fire rotations were then estimated for simulated fire histories following Baker (10):

$$FR = t \times A \times \left( \sum_{i=1}^n a_i \right)^{-1},$$

where  $t$  is the simulation period in years,  $A$  is total landscape area, and  $a_i$  is the area of fire  $i$  of  $n$  total fires observed over period  $t$ . For each climate scenario, FR was estimated for each grid cell over 1,000 simulations for each of four 30-y periods (1961–1990, 2005–2034, 2035–2064, and 2070–

2099), so that  $t = 30,000$  for each 30-y period. Some fire was always present for each period  $t$ . Total landscape area was estimated to be the average per-grid cell vegetated area using LANDFIRE vegetation data ( $0.89 \times$  cell area) (63).

**ACKNOWLEDGMENTS.** We thank A. Keyser, K. Lubetkin, T. Das, F. Munoz-Arriola, and D. Lettenmaier for assistance with data processing, visualization, hydrologic simulations, and historical gridded climate data. We acknowledge the Program for Climate Model Diagnosis and Intercomparison

and the World Climate Research Program's Working Group on Coupled Modeling for their roles in making available the World Climate Research Program Coupled Model Intercomparison Project phase 3 multimodel dataset, supported by the US Department of Energy. We thank C. D. Allen, F. S. Chapin, D. C. Donato, C. Whitlock, and M. D. Dettinger for comments that improved this manuscript. This research was funded by Joint Fire Science Program Project 09-3-01-47, US Forest Service Southern Research Station Joint Venture Agreement 07-CA-11330143-129, and National Oceanic and Atmospheric Administration Grant NA10OAR4310217.

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