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Wildfire, climate, and invasive grass interactions negatively impact an indicator species by reshaping sagebrush ecosystems

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Iconic sagebrush ecosystems of the American West are threatened by larger and more frequent wildfires that can kill sagebrush and facilitate invasion by annual grasses, creating a cycle that alters sagebrush ecosystem recovery post disturbance. Thwarting this accelerated grass–fire cycle is at the forefront of current national conservation efforts, yet its impacts on wildlife populations inhabiting these ecosystems have not been quantified rigorously. Within a Bayesian framework, we modeled 30 y of wildfire and climatic effects on population rates of change of a sagebrush-obligate species, the greater sage-grouse, across the Great Basin of western North America. Importantly, our modeling also accounted for variation in sagebrush recovery time post fire as determined by underlying soil properties that influence ecosystem resilience to disturbance and resistance to invasion. Our results demonstrate that the cumulative loss of sagebrush to direct and indirect effects of wildfire has contributed strongly to declining sage-grouse populations over the past 30 y at large spatial scales. Moreover, long-lasting effects from wildfire nullified pulses of sage-grouse population growth that typically follow years of higher precipitation. If wildfire trends continue unabated, model projections indicate sage-grouse populations will be reduced to 43% of their current numbers over the next three decades. Our results provide a timely example of how altered fire regimes are disrupting recovery of sagebrush ecosystems and leading to substantial declines of a widespread indicator species. Accordingly, we present scenario-based stochastic projections to inform conservation actions that may help offset the adverse effects of wildfire on sage-grouse and other wildlife populations.

alternate ecosystem state | cheatgrass | resilience | resistance | sage-grouse

Wildfire is a common disturbance whose effects on ecosystem processes vary spatiotemporally and are mediated by climate, soil, and resulting vegetation (1, 2). These effects influence thresholds that govern shifts to alternative ecological states post disturbance that have new functional and possibly hysteretic properties compared with the predisturbed state (3, 4). Invasion by nonnative species following disturbance can then promote additional strong feedbacks that drive an ecosystem further from its original state (5), and may ultimately yield a novel ecosystem that has no historical analog (6, 7).

In conservation planning, fragile ecosystems have a defining characteristic of high species turnover following disturbance (8), and altered fire regimes in these ecosystems can act as a disturbance driving state transitions across multiple spatiotemporal scales (2). The Great Basin of North America is a 541,727-km^2 cold desert dominated by sagebrush (*Artemisia* spp.) shrubland in the American West that provides a timely example of how altered wildfire regimes fueled by invasive species can drive rapid changes within fragile ecosystems at enormous spatial scales (9). The Great Basin intersects six states and is larger than 75% of countries worldwide; hence, perturbations to this ecoregion have significant ecological and sociopolitical ramifications that are at the forefront of national conservation and fire management policy (10). Wildfire frequency and size have increased significantly in the majority of this ecoregion since the 1980s (11) due, in large part, to synergistic interactions with invading cheatgrass (*Bromus tectorum*), an annual grass native to Eurasia (9, 12). Incipient risks of degradation of sagebrush by transition to cheatgrass-dominated grasslands that readily burn were recognized by Aldo Leopold over half a century ago (13), and the positive feedback loop between wildfire and cheatgrass invasion is now recognized as the primary mechanism altering contemporary sagebrush ecosystems of the Great Basin (14). Wildfire kills individuals of nearly all subspecies of big sagebrush (*Artemisia tridentata*), which have inherently slow growth rates and do not resprout (15); thus, cheatgrass can dominate burned landscapes and spread wildfire to sagebrush that would otherwise be less prone to burning (9, 12, 16).

Evaluating population or community response to state transitions, especially within ecologically meaningful time frames, is an important component for monitoring the effectiveness of conservation actions aimed at mitigating or thwarting these changes (17). In the case of the cheatgrass–fire cycle, rangeland

Significance

The Great Basin of western North America is larger than 75% of countries worldwide and is comprised mostly of a "sagebrush sea" threatened by a novel disturbance cycle of wildfire and annual grass invasion. The greater sage-grouse is a sagebrush-obligate species whose populations generally track declines in sagebrush, and is highly influential in shaping state and national land-use policy. Using three decades of sage-grouse population count, wildfire, and climate data within a modeling framework that allowed for variable postfire recovery of sagebrush, we provide quantitative evidence that links long-term declines of sage-grouse to chronic effects of wildfire. Projected declines may be slowed or halted by targeting fire suppression in remaining areas of intact sagebrush with high densities of breeding sage-grouse.

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ecologists increasingly emphasize management practices that understand factors driving resilience to wildfire and resistance to cheatgrass (hereinafter, R&R), which are influenced strongly by soil moisture and temperature regimes in semiarid ecosystems such as the Great Basin (14, 18). However, responses of vertebrate populations inhabiting sagebrush ecosystems have not been linked empirically to altered disturbance regimes (e.g., the cheatgrass–fire cycle) or underlying factors influencing sagebrush ecosystem R&R across large spatiotemporal scales despite their obvious importance from a conservation perspective (10, 19).

The greater sage-grouse (*Centrocercus urophasianus*; hereinafter, sage-grouse) is a large gallinaceous bird that can be an indicator for ecological health in sagebrush ecosystems because it requires distinct ecological states to fulfill its diverse life-history requirements (20). Hence, population dynamics of the species are an ideal metric for assessing linkages to specific sagebrush disturbances. Populations of this sagebrush obligate have declined concomitantly with the overall loss and fragmentation of sagebrush following settlement of the American West, and the species now occupies approximately one-half of its historic distribution (21). Accordingly, the species has undergone multiple evaluations for protection under the Endangered Species Act, the most recent of which stimulated unprecedented amendments to land management policy (with an emphasis on R&R) across millions of acres of federally managed land (10, 19). Critical to these large-scale efforts is a sound understanding of how sage-grouse populations respond to spatiotemporal variation in wildfire, while accounting for modeled postwildfire recovery times and R&R-dependent probability of state transition to cheatgrass, as well as complex relationships with climatic and demographic processes (22, 23). Direct and indirect effects of wildfire have been identified qualitatively as a threat to sage-grouse persistence in the western portion of their range (11). However, we lack rigorous and long-term evaluations that quantify mechanisms (e.g., wildfire) driving prevailing trends in sage-grouse population size and can identify populations most at risk. Long-term evaluations are needed because sage-grouse populations can cycle over periods of less than ∼10 y (24), thus studies with durations shorter than the typical cyclical period may reveal population growth patterns running counter to actual long-term trajectories.

Species using central-placed breeding strategies, such as lek breeding sage-grouse (25), are especially well-suited for spatially explicit and large-scale analyses of the effects of environmental and demographic stochasticity on population rate of change (26). In this study, we used a Bayesian analytical framework (Fig. S1) to link sage-grouse annual population rate of change (λ, as measured from yearly counts of male sage-grouse attending leks; *Materials and Methods*) to different measures of wildfire and seasonal precipitation while accounting for R&R-related recovery processes and density-dependent effects over a 30-y period (1985–2013) across the Great Basin (Fig. 1 and Fig. S2). Spatially explicit estimates of wildfire deemed severe enough to drive a change in vegetation were generated from the Monitoring Trends of Burn Severity Database (27) (MTBS; *Materials and Methods*). Spatially explicit estimates of sagebrush recovery, defined as 20% of prefire sagebrush cover that can fulfill partial life-history requirements for sage-grouse (28), were modeled by calculating cumulative burned area (CBA) within 5–10 km of leks on an annual basis (26, 29). Recovery times were based on three index classes for R&R (high, moderate, and low) extracted from a recently published map of spatially explicit soil moisture and temperature regimes (18) that strongly influence R&R in sagebrush ecosystems (14) (*SI Materials and Methods*, Fig. S3, and Table S1). Burned areas within high and moderate R&R index classes (cool and moist soils) were assigned to respective fast-track and slow-track recovery rates, based on a meta-analysis of sagebrush postfire recovery (30), whereas burned areas within the low R&R index class (warm and dry soils) were assumed to reflect a permanent state transition to invasive grassland (31) (Table S2). We also considered interactions with

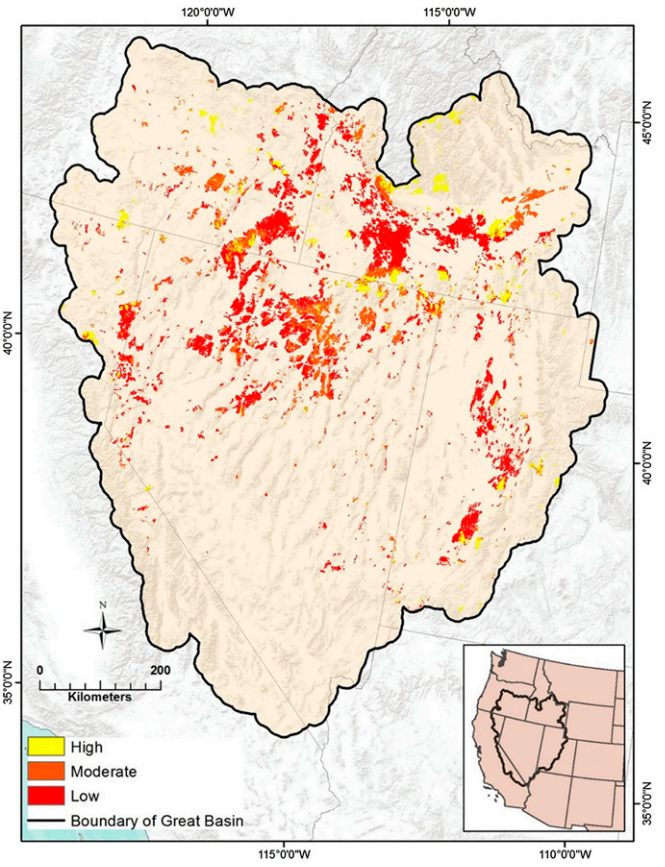


Fig. 1. Map of CBA by R&R (high, moderate, and low) index class across the Great Basin of western North America over three decades as of 2013. High and moderate areas were predicted as undergoing recovery to sagebrush, whereas low areas were predicted as undergoing a state transition to areas dominated by annual invasive grass. For each year of the analysis, a CBA surface was created and values were extracted to 5-km and 10-km lek buffers as predictor variables for sage-grouse λ. This surface represents the CBA extracted to leks for 2013.

precipitation because water availability is integral to ecosystem productivity in cold deserts like the Great Basin (32), and can drive sage-grouse population dynamics independent of wildfire (22, 33). Using model-derived parameters of fire effects on λ, we then projected sage-grouse populations 30 y into the future and identified a fire suppression strategy that may slow or halt projected declines.

Results and Discussion

We used count surveys of male sage-grouse attendance at leks (n = 1,770) (*Materials and Methods* and Table S3) to calculate λ, and then regressed the log-transformed rate [instantaneous rate of change (r)] on a suite of environmental predictors within a Bayesian mixed-effects modeling framework, whose convergence and evidence were evaluated in a stepwise fashion using the R-hat statistic and deviance information criteria (DIC), respectively (*Materials and Methods* and Tables S4–S6). We first identified a significant Gompertz-type (34) density-dependent effect that was carried to all subsequent models, followed by a positive effect of precipitation within 10 km of a lek during the previous spring, summer, and fall. We then identified the most parsimonious wildfire predictor to include in a model that accounted for effects of density dependence and seasonal precipitation on an annual basis (Table S5).

Parameters from posterior distributions indicated that declines in sage-grouse populations over the past 30 y occurred

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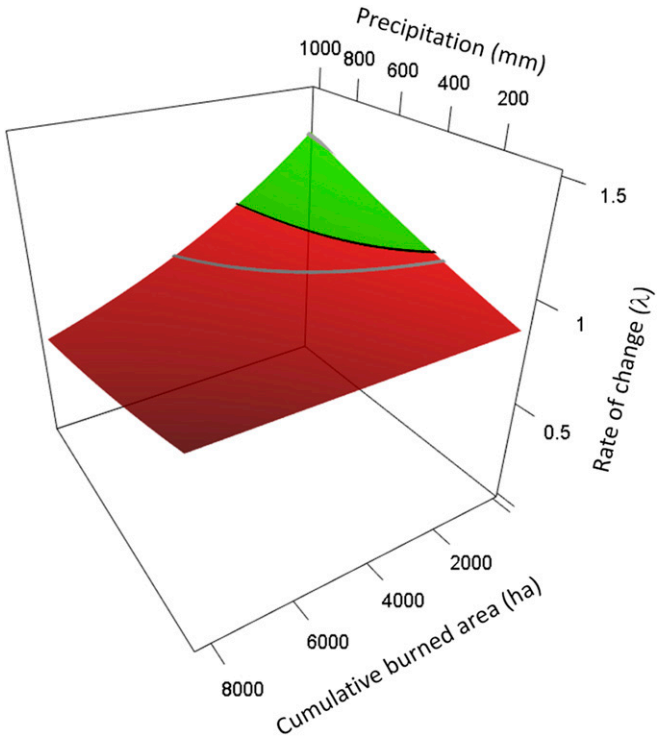


Fig. 2. Three-dimensional illustration of the interactive effects of precipitation (spring through fall) and CBA (within a 5-km circular buffer of lek centers) on λ of sage-grouse in the Great Basin using annual data from 1985 to 2014. The population trend is stable at $\lambda = 1$, declining at $\lambda < 1$ (red), and increasing at $\lambda > 1$ (green). The black line represents the median estimated effect, and gray lines represent 95% credible limits.

primarily as a function of chronic wildfire effects (i.e., different recovery processes and long-lasting impacts from R&R-estimated CBA) with normal recovery times within 5 km of leks, rather than acute wildfire effects (i.e., immediate impact of annual burns) or chronic effects with accelerated or decelerated recovery times (Tables S2 and S5). The chronic effect from CBA yielded a decline in λ of 2.1% [95% credible interval (CI): 1.2–3.1%] with every 1,000-ha increase in CBA. Because over 50% of the Great Basin is dominated by low R&R conditions (i.e., warm and dry; Fig. S3) conducive for cheatgrass, the chronic effect of CBA on λ was driven strongly by the lack of modeled recovery within low R&R areas. Accordingly, large swaths of sagebrush ecosystems and sage-grouse habitat are at high risk of wildfire if cheatgrass expansion continues at its unfettered pace (11, 31). Fig. 1 further illustrates the broad spatial extent of CBA (derived using the normal R&R-based recovery rate) for wildfires across the Great Basin (irrespective of proximity to lek) over three decades as of 2013, whereby a total of 36,467 km^2 of low R&R had cumulatively burned compared with 14,774 km^2 of moderate R&R and 8,332 km^2 of high R&R.

We then asked if wildfire effects on λ varied by precipitation by fitting a multiplicative model, which had more support than the additive model (Table S5). In the absence of fire, a 100-mm increase in precipitation from spring through fall predicted an increase in λ of 4.4% (95% CI: 1.4–7.4%) (Fig. 2). However, positive effects of precipitation on λ decreased as CBA increased, and populations declined ($\lambda < 1.0$) at leks associated with relatively large amounts of CBA even during years with high precipitation. Specifically, our model estimated that ~35% of CBA within 5 km of leks nullified positive effects of any precipitation (Fig. 2). Precipitation supports moisture recharge of upland mesic sites, where forbs and invertebrates are a critical food source for young grouse (35). Accordingly, periods of above-average precipitation typically boost sage-grouse survival and population recruitment, and can act as a population-level buffer against subsequent periods of prolonged drought, which can have deleterious impacts on population persistence, independent of wildfire (22, 33). When wildfire is introduced, however, our results indicate that the positive climatic effect of precipitation is decoupled from λ, and periods of population decline similar to declines that occur during drought conditions ensue. Wildfire appears to negate the positive effects of precipitation across multiple spatial scales, given that our broad-scale findings corroborate similar findings at local scales within the Great Basin (22).

We then regressed CBA against time over a 30-y period (1984–2013) and predicted future (2014–2044) CBA within 5 km of leks to forecast wildfire effects on sage-grouse. By 2013, our model estimated that 10.9% and 10.3% of burned areas within 5 km of leks were in various states of postfire sagebrush recovery within the high and moderate R&R classes, whereas 15.8% occurred in the low R&R class that our model assumed to have transitioned to cheatgrass (Fig. 3). By 2044, the median CBA was projected to increase to 22.2%, 20.9%, and 32.2% in the high, moderate, and low R&R classes, respectively (Fig. 3). We then took each sample of the posterior probability distribution for the projected CBA for each year and multiplied it by the effect of CBA on λ to project proportional changes in population size separately by R&R index class over the next 30 y. Because the effect of CBA on λ was confounded with precipitation, we generated population projections under typical (50th percentile), low (25th percentile), and high (75th percentile) levels of precipitation. These levels bracket a range of climate model predictions in the Great Basin from south to north (15, 36, 37), which is important, given model uncertainties and scale dependency (38). By 2044, we projected a decrease in sage-grouse populations to 43% (95% CI: 23–64%) of their current size when averaged across all R&R classes and assuming no change in precipitation (Fig. 4*A*). Deviations from current conditions to drought and high precipitation conditions resulted in variable projections (Fig. 4 *B* and *C*), yet most projections indicated significant negative impacts to long-term persistence of sagebrush ecosystems and sage-grouse populations, especially in areas of low R&R. Our projections are similar to the projections of another recent study conducted for sage-grouse in the Great Basin,

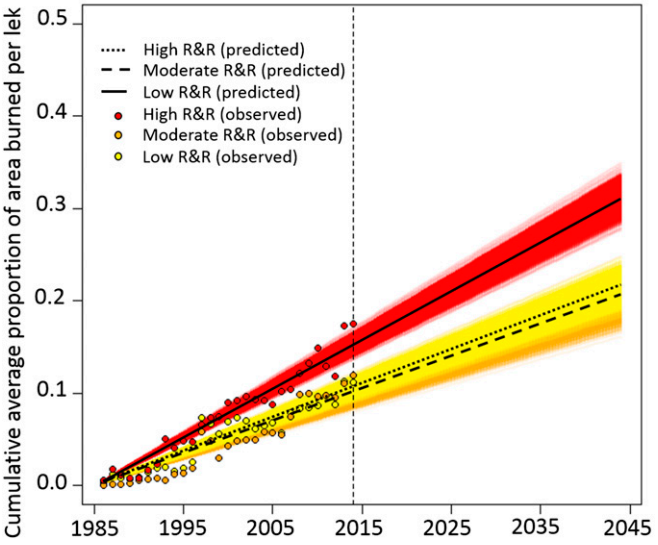


Fig. 3. Observed and model-predicted changes in CBA from 2015 to 2045 by R&R class (high = yellow, moderate = orange, low = red). The *y*-axis values represent the average annual proportion of CBA within a 5-km circular buffer from lek centers.

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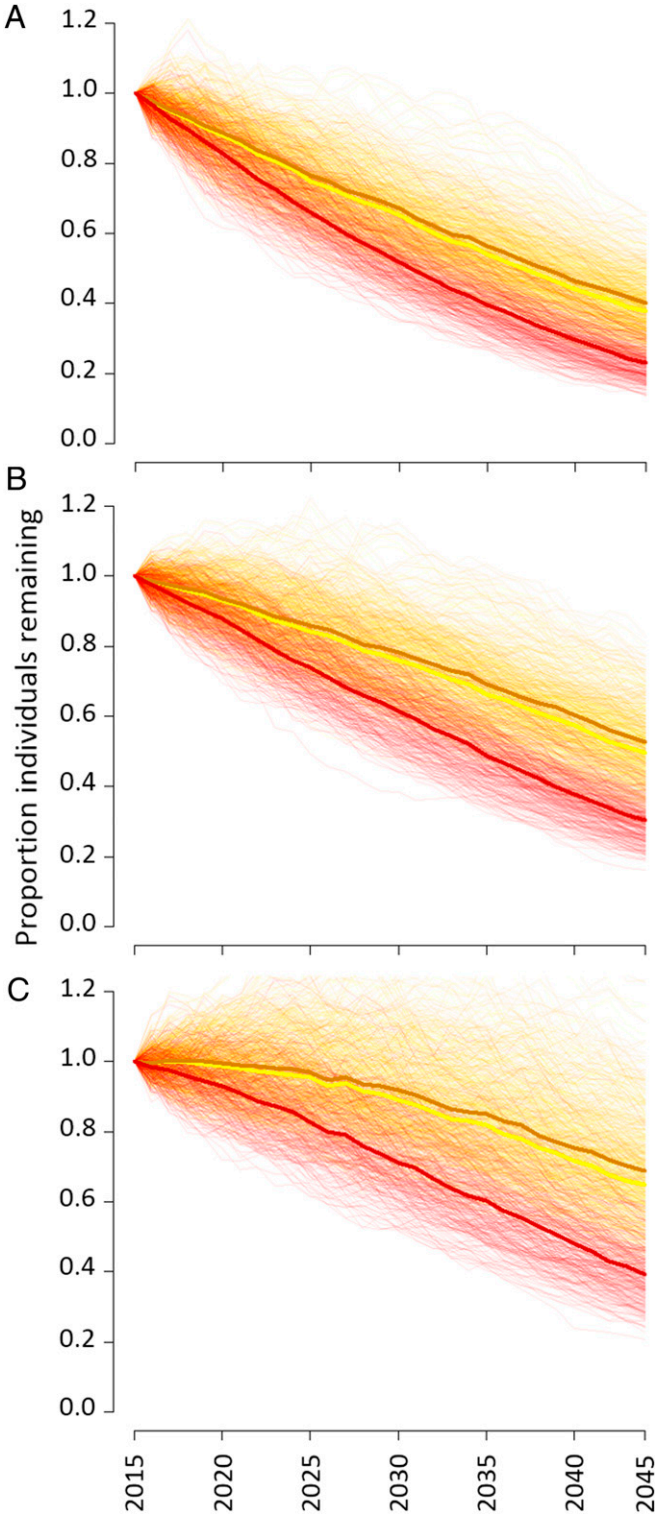


Fig. 4. Thirty-year (2015–2045) predictions for proportion of sage-grouse populations remaining in the Great Basin, given modeled effects of cumulative fire on population rates of change under projected median (*A*; 50th percentile), low (*B*; 25th percentile), and high (*C*; 75th percentile) amounts of precipitation during spring, summer, and fall. Thin and thick lines represent single posterior samples and median effects, respectively, for high (yellow), moderate (orange), and low (red) R&R.

which utilized a maximum likelihood-based approach using time as a predictor (rather than an environmental covariate, such as fire) and projected a 50% reduction (range: 32–60%) in carrying capacity (a surrogate for population size) by 2043 (39). Similar projections among studies support wildfire and precipitation as environmental predictor variables that explain temporal patterns in sage-grouse population size in the Great Basin, and are not spurious artifacts of a specific modeling technique.

Spatially explicit indices reflecting high ecological function can provide proxy-based measures (40) to guide resource allocation strategically for agencies tasked with managing wildfire. Hence, we derived sage-grouse concentration areas (SGCAs) that consist of areas where wildfire management actions would likely be most effective for sage-grouse (*SI Materials and Methods* and Fig. S4). Boundaries for SGCAs represent <10% of the Great Basin but capture nearly 90% of sage-grouse populations, thereby allowing fire suppression and restoration to be targeted in the most important landscapes to sage-grouse. To model the efficacy of this approach and provide additional decision support, we created management scenarios by reducing the 30-y averaged annual rate of CBA by 25%, 75%, and 99% within SGCAs and applied our stochastic model to project sage-grouse population trajectories under median, low, and high precipitation levels across the Great Basin over the next 30 y. Reducing the rate of CBA by 25% for those leks defined SGCAs under all three precipitation conditions slowed but did not halt declines (Fig. 5 *A*–*C*). However, reducing the rate of CBA by 75% substantially slowed declines under low precipitation (Fig. 5*D*) and either stabilized or increased populations with typical or high precipitation (Fig. 5 *E* and *F*). Near-complete reduction of rate of CBA (99%) resulted in either stabilized or increased population numbers under all precipitation conditions (Fig. 5 *G*–*I*).

Conclusion

We recognize that other landscape disturbances, such as energy extraction and production, livestock and wild equid grazing, and woodland expansion, have been identified as threats to sage-grouse populations in parts or all of their range (41). However, our analysis focused on threats from an accelerated grass–fire cycle that is at the center of national rangeland conservation policy and widespread throughout the Great Basin (10). Our results illustrate that current trends in wildfire pose nontrivial risks to sage-grouse and sagebrush ecosystem persistence in the Great Basin. Although wildfire is a natural process in sagebrush ecosystems and other perturbations exist that influence wildfire, burn frequency and size of wildfires within the boundaries of the hydrographic Great Basin have increased artificially in large response to the dominance of invasive annual grasses (9), particularly in areas of low R&R (14). This increase has resulted in a cheatgrass–fire cycle with no analog for comparison in ecological time. If left unabated, the current modeled estimate of 15.8% of sagebrush habitat lost to cheatgrass in low R&R habitats is projected to double over the next 30 y. This habitat loss is functionally influencing sage-grouse population dynamics by decoupling the otherwise positive relationship between precipitation and population growth, leading to steady and long-term declines. Paradoxically, high precipitation in the Great Basin may have long-term adverse effects on sage-grouse populations because wet years produce fine fuels (e.g., cheatgrass) that contribute significantly to wildfire size in subsequent dry years in fuel-limited semiarid environments (42). Another important result for contemporary management is the projected long-term decline for sage-grouse inhabiting moderate and high R&R habitats. Although areas of increased resilience may recover relatively quickly (i.e., decades) and passive restoration efforts are likely more effective in high R&R compared with low R&R habitats (14), ecosystem recovery even in high R&R areas appears asynchronous with recovery of sage-grouse population growth rates, given the increases in wildfire frequency and size.

Our research supports ecosystem conservation that strategically targets areas for wildfire prevention and suppression versus

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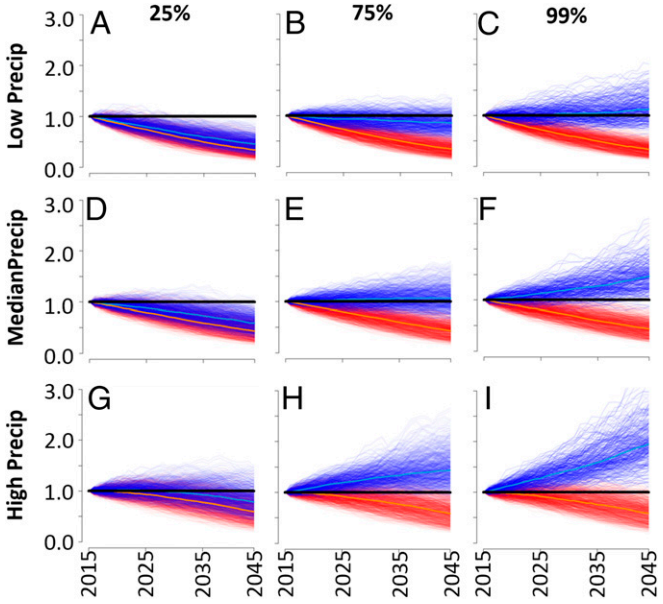


Fig. 5. (*A–I*) Examples illustrating projected sage-grouse λ over the next 30 y (2015–2045) under example management scenarios of 25%, 75%, and 99% reductions in annual average CBA within 5 km of lek sites under low, median, and high amounts of precipitation. The solid black horizontal line indicates a stable population (λ = 1.0). Thin and thick lines represent posterior samples and median effects, respectively, for inside (blue) and outside (red) SGCAs.

those areas targeted for postfire restoration and rehabilitation. For example, reduction in the annual rate of CBA will likely be achieved efficiently through targeted management actions to suppress fire, especially in low R&R areas, and to accelerate sagebrush recovery in moderate to high R&R areas. Although federal wildfire managers may successfully suppress 97% of fires <405 ha in size, and <1% currently exceed 4,046 ha (43), increased suppression in low R&R areas could be critical if the remaining large wildfires (i.e., mega-wildfires) are controlled before they grow to unmanageable sizes. By intensifying these suppression efforts in SGCAs, sage-grouse and other obligates might be more insulated against the cheatgrass–fire cycle. Decision support tools that integrate concepts from ecosystem and population ecology, which include output from our models, help conservationists "pick up Aldo Leopold's lance" (13) against invasive grass and fire in the American West.

Materials and Methods

Complete documentation of data sources and details of statistical analyses and caveats associated with our interpretation of results are provided in *SI Materials and Methods*.

Data Sources and Variable Construction. The study area (extent) encompassed nearly 65 million ha within the Great Basin (Fig. 1), and wildfire and climate variables were sampled within 5 km and 10 km (grain) of sage-grouse leks (26). Sagebrush communities occur on 63% of landscapes within the western range of sage-grouse populations (11) and encompassed over 80% of our sampled areas within 5 km of leks.

Spatially explicit data on annual wildfire extent and severity in the Great Basin from 1984 to 2013 were downloaded from the MTBS (mtbs.gov/index.html). The following wildfire covariates were derived for each year of the study: (*i*) distance to burned area, (*ii*) burned area, and (*iii*) wildfire perimeter-to-area (PA) ratio. Distance to burned area measured the Euclidean distance between lek centers and the nearest burned edge. Burned area and PA ratio within circular buffers of 5 km (78.5 km^2) and 10 km (314 km^2) from lek centers were extracted from raster layers created from corresponding moving windows of 5,160 m and 10,560 m, respectively, that corresponded to a range of distances proposed for limiting surface disturbance near leks (26, 29).

Acute fire effects were modeled to have instantaneous effects on λ, whereas recovery times for chronic effects were based on a published metaanalysis of postwildfire recovery in mountain big sagebrush (*Artemisia tridentata* var. *vaseyana*) communities that ranged from 1.28% of prefire sagebrush per year (slow-track) to 2.28% (fast-track) per year (31) until a threshold of 20% prefire sagebrush cover was reached (Table S2). CBA with high and moderate underlying R&R was considered functional and reclassified to be removed from the CBA once the threshold was reached after 9 y in high R&R and 16 y in moderate R&R (normal recovery time). The recovery clock was reset to zero if a new wildfire burned over a previously burned pixel with high or moderate R&R before the threshold was reached. CBA with low underlying R&R was set to never recover, which reflected a likely conversion to annual grass following fire without extensive and often fruitless management intervention (14, 31). We also constructed additional scenarios representing accelerated and decelerated recovery times for high and moderate R&R pixels to represent variation in recovery times across a broader range of sagebrush ecosystems (30, 44) (Table S2).

We obtained spatially explicit precipitation data from the PRISM Climate Group (www.prism.oregonstate.edu/) at a resolution of 800 m^2 from 1985 to 2013, and extracted mean values within 5-km and 10-km radius buffers from lek centers using raster layers created from moving windows of 5,160 m and 10,560 m, respectively. For modeling, we aggregated precipitation into seasonal (spring, summer, fall, and winter) combinations and annual intervals based on a priori hypotheses that synchronized with the timing of sage-grouse life-history stages.

Counts of male sage-grouse attending breeding leks provide reliable and widely used spatially explicit data for analyses of population trends (45). We used data from annual lek counts collected by state wildlife agencies within the Great Basin from 1985 to 2014 (Table S3). We calculated the instantaneous annual rate of change *r* for sage-grouse populations, which took the form: $r_{ij} = ln(N_{ij}/N_{i,j-1})$, where *N* represents maximum male lek count, *i* represents lek, *j* represents year, and *j*−1 represents a previous year. We used *r* as the response variable in all predictive models for population rate of change, and convert to finite rates of change ($\lambda = e^r$) for interpretation. By R&R index class, 28% of leks used in the analysis were in areas dominated by high R&R within 5 km of lek centers, 37% were in moderate R&R, and 35% were in low R&R.

Model Structure and Selection. We used a Bayesian mixed-effects model framework to investigate density dependence, precipitation, and wildfire as linear predictors for λ, while accounting for intraclass correlations associated with leks and years from 1985 to 2013. Posterior distribution parameter estimates were derived using Program JAGS within the rjags package in R version 3.1.1, and were generated using Markov-chain Monte Carlo chains and uninformative prior probabilities (Table S4).

We carried out a two-step model procedure. Step 1 was designed to select and carry forward the covariates with the most support from model groups representing: (*i*) density dependence, (*ii*) wildfire, and (*iii*) precipitation. Input data were aligned so that wildfire and precipitation covariates at year *j*−1 influenced numbers of grouse counted at leks in year *j*. Within a model group, covariates carried forward to step 2 had to meet all three of the following: (*i*): lowest DIC value within a group, (*ii*) DIC value is at least two units less than the DIC value of the random effects-only (null) model, and (*iii*) DIC value is at least two units less than the DIC value of the density dependence-only model. For step 2, we fit two additive models that combined selected covariates from each group carried forward from step 1 (i.e., density-dependent effect; acute distance to burn edge; CBA normal recovery within 5 km of a lek; spring, summer, and fall precipitation within 10 km of a lek). We also fit a model that included an interaction between the effects of precipitation and wildfire to test if wildfire effects on population rate of change varied by precipitation. Multicollinearity among covariates ($r > |0.65|$) was not detected among any step 2 models. The interactive model with the lowest DIC was chosen for predictive modeling (Table S5). Stochastic search variable selection values (>0.5) indicated support of all covariates, and the fit of the final model was excellent (Bayesian *P* value = 0.496).

A Bayesian linear regression model was used to estimate the average annual rate of increase in CBA from 1984 to 2014. Specifically, each lek was assigned an R&R class (low, medium, high) based on the dominant class within a 5-km buffer. For each R&R class, we then estimated specific annual rates of CBA and projected 30-y increases in CBA in relation to leks (5-km buffer area). Parameter estimates were derived from distributions of uninformative prior probabilities (Table S6).

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Management Scenario Projections. We used a range-wide population index model for sage-grouse (46) that incorporated indices of sage-grouse habitat suitability generated from random forest models (47) and spatially explicit abundance indices based on fixed kernel density functions over lek locations to demarcate areas most meaningful to sage-grouse populations. Specifically, we clipped the range-wide continuous population index layer to the Great Basin study extent (buffered by 10 km), and extracted isopleths for the percentage of cumulative volume under the layer at 5% increments starting at 65%. We overlaid locations of leks on the clipped layer and extracted the maximum lek count from 2009 to 2014 as an index of population size within each isopleth class. For each successive isopleth class, we calculated the ratio of the cumulative increase in population size to cumulative area added to the population index model, and rescaled the ratio between zero and 100. To determine a cut-point for the population index model that represented where sage-grouse density was most concentrated, we fit an exponential regression between population index model isopleth values and the cumulative ratio of increasing population size to area added, and determined where the slope of the line equaled 1.0. The slope equaled 1.0 at the 76.4% isopleth, and was rounded to 75% to demarcate example SGCAs (Fig. S4).

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