Climate change and the eco-hydrology of fire: Will area burned increase in a warming western USA?

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Abstract. Wildfire area is predicted to increase with global warming. Empirical statistical models and process-based simulations agree almost universally. The key relationship for this unanimity, observed at multiple spatial and temporal scales, is between drought and fire. Predictive models often focus on ecosystems in which this relationship appears to be particularly strong, such as mesic and arid forests and shrublands with substantial biomass such as chaparral. We examine the drought–fire relationship, specifically the correlations between water-balance deficit and annual area burned, across the full gradient of deficit in the western USA, from temperate rainforest to desert. In the middle of this gradient, conditional on vegetation (fuels), correlations are strong, but outside this range the equivalence hotter and drier equals more fire either breaks down or is contingent on other factors such as previous-year climate. This suggests that the regional drought–fire dynamic will not be stationary in future climate, nor will other more complex contingencies associated with the variation in fire extent. Predictions of future wildfire area therefore need to consider not only vegetation changes, as some dynamic vegetation models now do, but also potential changes in the drought–fire dynamic that will ensue in a warming climate.

Key words: climate change; ecosections; lagged response; negative feedback; nonstationarity; water-balance deficit.

INTRODUCTION

Wildfire area is predicted to increase with global warming. The straightforward view of warming climate affecting fire regimes is compelling and is supported by both empirical evidence and process-based models. For example, Flannigan et al. (2009) reviewed the climate–fire literature and found wide agreement on projections of increased area burned in a warmer climate. If statistical models are projected onto future climate space that represents even moderate warming scenarios, estimates of future area burned are so large as to imply broadscale changes in ecosystem composition, structure, and function, with concomitant disruptions to ecosystem services. For example, the fairly crude statistical models of McKenzie et al. (2004) predicted two- to fivefold increases in annual area burned in the western USA under a moderate warming scenario. At finer scales, and using a complex statistical approach focusing on changes in fire-size distributions, Westerling et al. (2011) found analogous outcomes for the Greater Yellowstone ecoregion: Increased area burned shortened fire cycles to the point that conifer forests were expected to change en masse to shrublands.

Such projections, even when statistics are robust or process-based algorithms are fully mechanistic, assume stationarity of fire–climate dynamics within the geographic domain for which they are projecting area burned. By this we mean that the same drivers, whether an index of drought during the fire season as a predictor, its equivalent in the soil–water balance of a process model, or some other predictors representing lagged climate effects or nonclimatic effects, generate the same outcomes. These stationary dynamics in models may vary spatially, so that when multiple models are built within large domains the fire–climate dynamics are different for each (Balshi et al. 2009, Parisien et al. 2014, Knorr et al. 2016). Nevertheless, future projections in these efforts use the same model equations as were initially fit (i.e., same coefficients in statistical models or parameters in process-based models), so future dynamics therefore must necessarily be at best the full set realization of plausible historical stationary dynamics. The only way for nonstationarity to be modeled is if the projections are based on nonstationarity in the coefficients or parameters and if the full plausible set of future drivers is projected onto them.

Interactions and feedbacks associated with vegetation and limiting factors such as available fuels are difficult to capture and often are inferred post hoc. For example, Littell et al. (2009) found that the simple paradigm, hotter and drier equals more fire, was appropriate for most of the northwestern USA, where fuels are always present and fuel moisture is the principal limiting factor. In contrast, fuel availability is often limiting in the arid Southwest and much of the Great Basin, such that abundant precipitation in the previous year sets up current-year fire seasons. Holz et al. (2012) found similar contrasts, forced by oceanic teleconnections, along a latitudinal gradient in
Chile, as did Pausas and Paula (2012), at finer scales, in Mediterranean ecosystems of the Iberian Peninsula.

Attribution of fire–climate dynamics is tempered by the ever-increasing human imprint on fire regimes. Regionally to globally, fire sizes, fire frequency, and fire emissions are driven by both environmental forcings and human activities, and human factors are being incorporated in both empirical and process-based models (Hurteau et al. 2014, Knorr et al. 2014, 2016, Prestemon et al. 2016). Humans both ignite and suppress fires, interacting with climate drivers. For example, almost all of the extreme fires in southern California chaparral, driven by Santa Ana winds, are ignited by humans (National Interagency Fire Center; data available online). In contrast, effective initial attacks on new fires can suppress potential megafires when they are still manageable. Nevertheless, across the western USA, we still expect that the principal control on future area burned will be climate.

In an overview of global fire regimes, Krawchuk and Moritz (2011) theorized that the fire–climate coupling shows a unimodal response along a wet–dry gradient of fire-season weather, such that a warming climate will produce both positive and negative feedbacks in fire climatology. This nonlinear response reflects the significant interactions of both climate and fire with vegetation, which can be as strong a driver of fire regimes as climate itself (Higuera et al. 2009). In this paper, we quantify movement along a wet–dry gradient, manifest as changes in water-balance deficit (DEF) between current and projected climate, in ecoregions (Bailey 1995) of the western USA. We highlight ecoregions wherein current correlations between DEF and area burned are strong vs. those where they are nonexistent. We categorize ecoregions by their characteristic associations with fire climatology, following ideas proposed in Littell et al. (2009), as having direct, facilitative, or hybrid responses to climate. From a combination of existing fire–water balance relations between fire and climate.

**Methods**

The domain of this study comprises 56 ecoregions in the western USA, the finest subdivisions of the Bailey (1995) ecoregional classification. We use fire area-burned statistics from the geospatial data aggregated by Littell et al. (2009). In previous work, we built statistical models of fire and climate for the western USA for the next coarser subdivision of ecoprovinces (Littell et al. 2009) and models for the Pacific Northwest at the ecoregion scale (Littell and Gwozdz 2011). In the latter work, water-balance deficit (DEF), the difference between potential evapotranspiration (PET) and actual evapotranspiration (AET) and a key climatological manifestation of drought (Stephenson 1990), was an important correlate of annual area burned. We therefore use DEF as the baseline representative of the hotter and drier equals more fire paradigm, while noting that this is not universally the strongest correlate of area burned, even in regions in which that paradigm clearly holds (Littell and Gwozdz 2011, Higuera et al. 2015). We analyze the ecoregions that describe the direct-to-facilitative gradient and omit coastal and southern California ecoregions differently classified by Littell et al. (2009).

**Climate data**

We use historical simulations (1916–2006) by Elsner et al. (2010) from the Variable Infiltration Capacity (VIC) model (Liang et al. 1994, Hamlet and Lettenmaier 2005) on a 1/16° grid to calculate 112 seasonal climatic and hydrological variables (Littell et al. 2014) and their simple correlations with annual area burned for the 56 ecoregions for the period 1980–2006 (Data S1: Tables S1–S4). These variables were also summarized from monthly 2040s (2030–2059) and 2080s (2070–2099) VIC projections, driven by a composite (ensemble means) of 10 global climate models (GCMs) (BCCR, Cnrm_cm3, csiro 2.5, HadCM, Hadgem1, Echam-g, Miroc 3.2, Miroc 3.2 hires, PCM1, Echam5) under the A1B emissions scenario (Nakicenovic and Swart 2000). We chose downscaling and hydrological scenarios from the Coupled Model Intercomparison Project, version 3 (CMIP3), because no comparable projections from the latest project (CMIP5) were available at the time of analysis, and Knutti and Sedlacek (2013) show that CMIP3 and CMIP5 scenarios can be broadly considered to be from the same distribution.

**Conceptual model**

Based on results from Littell et al. (2009), and keeping in mind the global wet–dry gradient suggested by Krawchuk and Moritz (2011), we propose a gradient from direct influences of climate on fire (direct), exemplified by the effects of drought and high temperatures (hotter and drier equals more fire), to facilitative influences (facilitative), exemplified by previous-year high precipitation enhancing productivity of fine fuels that are cured by the following summer’s fire season. Across the western USA, we identify a forest pattern, where direct influences dominate, a desert pattern, where facilitation dominates, and a hybrid pattern, which is a mixture. To illustrate, Fig. 1b shows how direct influence dominates in the West and how the three patterns are distributed in the two-dimensional space of same-year and lagged correlations between fire and climate.

**Future locations of ecoregions in climate space**

From the composite output of VIC for each future scenario, we calculated the change in June–July–August
Fig. 1. Spatial variation in the strength of correlations between log(annual area burned; AAB) and climate. (a) Simple correlations between water-balance deficit (DEF; June–July–August, JJA-DEF) and AAB at the scale of ecossections. (b) Positions of ecossections in the two-dimensional space of same-year maximum correlation with a climate variable (x-axis) and maximum lagged correlation (y-axis). Points are absolute values; some correlations are negative. See Data S1: Tables S1–S4 for correlations (from 112 total correlations between log[AAB] and 16 eco-hydrological variables, partitioned into seven sub-annual time periods) and ecossection names. Ovals indicate the overlay of the three patterns (see text above) on ecossection positions in the space.
(JJA) DEF from the current period (1980–2006, used in the fire models) for each ecoregion. We chose the strongest direct influence (JJA-DEF) to illustrate our point simply: that changes of ecossections from their current locations in climate space and their proximity to the hotter and drier paradigm, may vary widely across the West. We quantify the current position of each ecoregion on the direct-facilitative gradient by a simple calculation akin to fuzzy set membership. Membership in the direct set (same-year [SY] influence) is

\[
\text{fuzzySY} = \frac{\text{maxcorrSY}}{\text{maxcorrSY} + \text{maxcorrL1}}
\]

where maxcorrSY is the strongest same-year correlation between annual area burned (AAB) and a climate variable (often DEF), and maxcorrL1 is the strongest correlation at a one-year lag (Data S1: Table S2). We then examine the change in JJA-DEF for each ecoregion for the future scenarios, as a surrogate for its movement along the direct-facilitative gradient, thereby implying a degree of nonstationarity in the fire-climate dynamic. We acknowledge two limitations to this analysis. First, though quantitative in a way, it is heuristic rather than being a rigorous basis for inference, in that the true departure from stationarity (itself an elusive property in statistics in general) can be assessed only qualitatively. Second, to extend the analysis beyond one variable (JJA-DEF), albeit a key one, to all those that had the maximum correlation in one or more ecossections, would involve a combinatorial explosion beyond the scope of this paper and possibly not tractable at all. Nevertheless, we believe that this heuristic analysis, which focuses on clarifying assumptions in fire-climate modeling that are tenuous at best, will inform future fire projections. In particular, we show movement of ecossections both away from and into a climate space in which statistical models are perhaps coincidentally strong.

**Results**

There is substantial variation across the western USA in correlations between AAB and JJA-DEF, from essentially no correlation (just below 0 in 341A) to above 0.9 (Fig. 1a). Most of the strongest correlations are in mountain provinces, in line with the direct influence of same-year climate noted by Littell et al. (2009). The correlation for M331A (0.93), in the Greater Yellowstone ecoregion, was the strongest of any correlation between AAB and JJA-DEF over the historical period (1980–2006, used in the fire models) for each ecoregion. We chose the simplest direct influence (JJA-DEF) to illustrate our point simply: that changes of ecossections from their current locations in climate space and their proximity to the hotter and drier paradigm, may vary widely across the West. We quantify the current position of each ecoregion on the direct-facilitative gradient by a simple calculation akin to fuzzy set membership. Membership in the direct set (same-year [SY] influence) is

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The greatest increases in DEF are projected for the Sierra Nevada and Klamath regions and the eastern Cascade Range, with still substantial increases in the central and northern Rocky Mountains. Most of these ecossections are in the middle of the range (200–350 mm) of historical JJA-DEF (Fig. 4b). JJA-DEF in most of the ecossections with the strongest correlations for the historical period is expected to increase by >60 mm by the 2080s (compare Fig. 4b to Fig. 1a). As DEF is the difference between PET and AET, the same changes in DEF can be the result of multiple trajectories in the two-dimensional space of these latter variables (Stephenson 1990). In our results, most of the largest increases in JJA-DEF are projected for ecossections in which PET increases and AET decreases (Fig. 4a). One exception to this is M332A, in which AET is expected to increase slightly.

Fuzzy membership in the direct set (fuzzySY) expands our consideration from JJA-DEF as a predictor of AAB to all same-year andlagged variables. The overall pattern in plots of this variable is very similar to that when plotting the simple correlation of JJA-DEF with AAB against JJA-DEF (compare Fig. 4b to Fig. 2). The statistical relationship is slightly weaker but still highly significant ($r = -0.38, P = 0.004$). Superimposing the change in JJA-DEF from historical values to the 2080s on the scatterplot once again shows that ecossections nearer the direct end of the direct-facilitate gradient (i.e., fuzzySY >0.5) are projected to experience larger increases in JJA-DEF, moving them out of the range (<300 mm) in which hotter and drier equals more fire.
**Discussion**

We challenge the projection of statistical fire–climate models onto future climate space, looking ahead two and four decades, and focusing on the assumptions implicit in those models rather than specific outcomes. This is not to impugn the work of authors who have applied a wide range of techniques, from simple to elaborate, to build and evaluate their models. Indeed most of these authors are candid about model limitations and circumspect about projections of changes in fire regimes and ecosystems that they predict (e.g., Westerling et al. 2011). We take the opportunity to make some (often tacit) assumptions of these models explicit and to infer the nature and magnitude of the uncertainties and feedbacks associated with assumptions, both of which are critical for anticipating future fire regimes and their effects (McKenzie et al. 2014).

The first and most obvious assumption, which we refer to only briefly here, is that of unlimited area available to burn. Consider a simple linear model that predicts \( \log(AAB) \) reasonably well as a function of summer temperature, sensu McKenzie et al. (2004). Projecting this model onto a warming future, even one from conservative GCMs, will rapidly increase cumulative area burned beyond the total acreage of wildlands in many regions, as McKenzie et al. (2004) showed. Clearly a host of negative feedbacks will come into play before that point (Héon et al. 2014, Parks et al. 2015).

The second assumption is the simple paradigm, widely represented in statistical models (but see Littell et al. 2009, Batllori et al. 2013, Krawchuk and Moritz 2014), that hotter and drier equals more fire. We have shown here that this paradigm holds only in a subset of ecossections: those near the direct end of the direct–facilitate gradient. As these ecossections move out of the sweet spot in the range of JJA-DEF, we would expect changes in vegetation from increasing water limitation, reducing the abundance and connectivity of fuels, even as what fuels there are become more flammable, and moving them toward a state where facilitation would become primary or at least equally important. Concurrently, some ecossections with negligible JJA-DEF would move away from that complacent state (not water-limited) into one in which the hotter and drier paradigm takes over. It is also conceivable that some ecossections eventually (i.e., by the 2080s) would move back toward a state in which direct influences are primary, e.g., if the fine-scale dynamics in the Southwest in the areas projected by VIC to have decreased water-balance deficit dominate ecossection-scale effects. Given characteristic lags in vegetation response to climate, however, this process could take

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**Fig. 2.** Moderate inverse relationship \( r = -0.39 \) between historical June–July–August water-balance deficiency (JJA-DEF; mm) and its correlation with AAB. Brown and green dots correspond to endpoints of forest and desert systems in Fig. 1b.
decades for fuels to build up to a point at which they are not limiting. Altogether, we expect changing fire climatology to invalidate annual area burned (AAB) projections at ecosection or regional scales, although these changes could cancel each other across the western USA, coincidentally, making continental-scale projections less uncertain than regional ones.

We note that this assumption has been recognized implicitly in both empirical and process-based models (see Williams and Abatzoglou 2016, and references therein, for an exhaustive review), and that modelers have not limited themselves to equations that predict more fire in warmer drier climates. For example, Batllori et al. (2013) projected fire climatology in the Southwest
into the future statistically, predicting essentially that hotter and drier equals less fire, in a clear example of the facilitative end of our gradient, and supporting the initial association of the Southwest with that domain by Swetnam and Betancourt (1998) and Littell et al. (2009). Pausas and Paula (2012) provide a convincing case that fuel shapes and constrains fire climatology, even at the direct end of our gradient. Very few forcings are exclusively climatic (but see Abatzoglou and Kolden 2013, Swetnam and Betancourt 1998 and Littell et al. 2009).

The third assumption is stationarity in the fire–climate dynamic, whether characterized broadly as direct or facilitative. As we alluded to earlier, this is a more subtle assumption that cannot be overcome by modeling spatial variation in the fire–climate dynamic across different domains (i.e., space for time). This assumption is not just an element of simple statistical models or models from the hotter and drier paradigm. As the climate changes, so will the dynamics within each domain (and thus the regression equations in statistical models and the parameter choices in process-based models) in ways that will have only coincidental analogs in other domains. For example, one broad pyrogeographic (Krawchuk and Moritz 2014) modeling project might include both direct and facilitative models, but these are only snapshots of potential futures. One could argue that we should modify future projections to anticipate facilitative influences as ecosystems become more water-limited and fuels less continuous. We support this idea in theory. Its implementation would be extremely complex, and always approximate, and would depend on a stationarity-like assumption: that movement of ecosections along the direct–facilitate gradient, itself an approximation of a wet–dry gradient (Krawchuk and Moritz 2011), could be predicted by a space-for-time substitution from the current positions of ecosections. A crude example of this, using Fig. 4b, would be to project the future fuzzySY score of an ecosection by locating the endpoint of its associated arrow and dropping a vertical line to the regression line, identifying a new position on the direct–facilitate gradient. By examining predictive equations of nearby ecosections, the general class of predictive model for the ecosection of interest could be selected, and its likely goodness-of-fit estimated from the predictive models for those nearby ecosections. This procedure leaves considerable uncertainty, of course. Given the residuals associated with the regression in Fig. 4b, there is much variation to be explained, and more basically, the best equation (model) is still unknown.

Given these assumptions, we suggest that future AAB is generally overpredicted and that projecting existing relationships onto future climate space is very fragile (once again, we are not the first authors to make this second point). For example, two regions expected to have the largest increases in JJA-DEF are the Sierra Nevada, including Klamath Mountains and northeastern California (M261 ecoprovince, with eight ecosections; >100 mm), and the northern and central Rocky Mountains (M331, M332, M333 ecoprovinces; >60 mm). Predictions abound for increases in fire extent and severity in these areas under a warmer and drier climate. If these areas, particularly M261, are already in the sweet spot, in which correlations between AAB and JJA-DEF are strong, they are likely to move away a good distance along the gradient toward facilitation. We expect two eventual outcomes: negative feedback to AAB from decreased abundance and connectivity of fuels and a new fire climatology in which facilitative influences become more important. Westerling et al. (2011) projected future area burned in the Rocky Mountain ecoprovinces, with a complex statistical model based on extreme value theory, but ended up with the same predictor (DEF) as our simple correlations (Fig. 1a), with roughly the same model fit. Their model projected a drastic decrease in the fire cycle (i.e., increased AAB) to the point of no longer supporting forest vegetation, but the authors astutely observed that negative feedbacks such as fuel limitations (and we would add the failure of the first assumption about unlimited available area) were likely to set in before that could happen. Our inferences in this paper support that expectation.

In the Southwest, with projected ecosection-scale JJA-DEF very similar to that of the historical period, and given the uncertainties suggested by comparisons with other projections of drought, we expect that the drought–fire dynamic will remain in the facilitative domain. Area-burned projections are complex and may depend sensitively on the timing of wet and dry episodes, with a wetter future possibly associated with more fire (Battlori et al. 2013). The fine-scale projections for the Southwest (lower row in Fig. 3) vary on much finer scales than most area-burned models. The striking variation here may reflect imprecision in humidity estimates (Pierce et al. 2013) or a generic implementation of stomatal resistance in VIC that has different, though small, consequences for forest vs. nonforest, with implications for fire regimes at fine scales (Pierce et al. 2013, Williams et al. 2015).

A geographic outlier ecosection with a projected increase of JJA-DEF >100 mm is M242C: forests east of the crest in the Cascade Range of Washington and Oregon. This ecosection is an area subject to much recent research and controversy regarding expected increases in fire risk in a warmer climate, the need for fuel treatments to reduce fire intensity, and changes in fire severity since the onset of effective fire suppression (Miller and Safford 2012, Abatzoglou et al. 2014, Cansler and McKenzie 2014, Hessburg et al. 2015, Kolden et al. 2015). Our expectation would be that in the long-term, the fire regimes in this ecosection would equilibrate toward those driven by facilitation, because the equilibrium vegetation associated with projected future climate would be sparser and less subject to large fires (Littell and Gwozdz 2011). It is often argued that so-called process-based models are more robust than statistical models for future projections, because they are dynamic and do not depend on assumptions of equilibrium in interactions between
climate, vegetation, and disturbance. Indeed there are many advantages to dynamic models, notably a more causal (vs. correlative) representation of forcings and responses (Keane et al. 2015). Notwithstanding these advantages, process-based models of which we are aware that include fire, whether dynamic global vegetation models (Arora and Boer 2005, Quillet et al. 2010, Prentice et al. 2011) or landscape fire and vegetation models (Scheller and Mladenoff 2007, Keane et al. 2011, 2015), are still limited by the same assumptions that we listed previously. In particular, the assumption about stationarity is implicit in parameter choices, excepting those rare ones, if any, that can be said to be purely mechanistic and not tuned to observations (Keane et al. 2015).

The presence of these assumptions can be subtle and associated with the scale mismatch between the process-based understanding of fire behavior at fine spatial scales and the regional scales associated with projections of AAB (McKenzie et al. 2014). The case is clearest with the second assumption that hotter and drier equals more fire. At the meter to submeter scales of heat transfer and fire spread, the assumption certainly holds, but for the top-down forcing of fire area by regional climate (Littell et al. 2009), we see that it does not. Furthermore, as we implied previously, when the second assumption does not hold, neither does the stationarity of fire climatology (and of course, as we mentioned, there are cases in which the second assumption is relaxed but models are still stationary).

Analogous scale mismatches occur in the temporal domain. For example, it could be argued that finer-resolution (daily or monthly instead of annual) or coarser-resolution (e.g., 30-year normals) models will accentuate different drivers, e.g., weather vs. climate for fine scales, and vegetation dynamics vs. annual climatic forcings for coarse scales. Stavros et al. (2014a), in a study of extreme fires, found that choices of predictors were sensitive to varying time windows around fire dates. In contrast, Parisien et al. (2014), in an explicit study of multiple temporal scales, found that little change in the overall dynamics was suggested by varying scale. Clearly scale mismatches in process need to be considered thoughtfully in modeling fire (McKenzie et al. 2014).

Limitations

This paper provides an overview of the limitations of area-burned projections for the West, rather than deconstructing specific modeling efforts. In turn, we acknowledge two limitations to our own inferences. First, we suggest above that future AAB, projected to increase generally across the West, is probably overpredicted. Whether this is true, or even whether area burned will increase at all (and over what period), depends on many things other than changes in the drought–fire dynamic in response to changes in JJA-DEF. For example, lagged responses of forest vegetation to climate could slow the changes of ecosections along the direct–facilitate gradient by conserving fuels (mature trees surviving in a warmer and drier climate than one in which they can regenerate). On the other hand, these conserved fuels could drive large high-intensity fires that would accelerate changes on the gradient (Johnstone et al. 2010). The variation around the regression line in Fig. 4b suggests much complexity.

The second limitation is that the most extreme fires push back on our (and other authors’) claims that there is more to wildfire than hot dry climate. It may be that extreme events dominate area burned in the West more and more going into the future, and there is compelling evidence that they are primarily climate-driven (direct), even in regions in which the facilitative dynamic normally dominates (Abatzoglou and Kolden 2013, Stavros et al. 2014a, b). This limitation dovetails with the first in that it undermines our suggestion that area-burned projections are too high.

Future directions

What are the next steps, then, in projecting future wildfire? We offer no exact prescription here, but we believe that a multi-scale approach will be necessary, because feedbacks operate at different scales. Ecosystem change in a rapidly warming climate may also be locally to regionally discontinuous; at such points the stationarity assumption will be most violated. We hypothesize that in high-productivity environments, as soil and fuel moisture are depleted at large scales, contagion of fuel availability increases linearly in time until a threshold is crossed and previously distinct burnable patches merge to create a percolating fire potential and potential area burned increases rapidly. This is a top-down forcing. In low-productivity environments, facilitation via fuel production is mediated by patch- and species-level responses at finer scales. Fuels increase with moisture availability until they are connected, patches merge, fuel continuity percolates, and fire potential increases quickly. This is a bottom-up forcing. Given these contrasting effects at different scales, a top-down statistical model is most robust in the case of direct climate forcing, but a bottom-up model, perhaps process-based, works in the facilitative domain. Most of the ecosections for which we present fire–climate relationships fall somewhere along a gradient between these two limiting processes, and both
climate and vegetation are transient. The skill of fire projections will be determined by the underlying models’ ability to incorporate both processes, at multiple scales. There is clearly opportunity for theoretical, empirical, and simulation studies that incorporate the nonstationarity of fire climatology to characterize future uncertainties better and to quantify the many feedbacks associated with fire regimes in a rapidly changing climate.

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Literature Cited


**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1420/full

**Data Availability**

Data associated with this paper is available in the US Forest Service Research Data Archive: http://dx.doi.org/10.2737/RDS-2016-0018.4