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Analog-based fire regime and vegetation shifts in mountainous regions of the western US

Sean A. Parks, Lisa M. Holsinger, Carol Miller and Marc-André Parisien

S. A. Parks (http://orcid.org/0000-0002-2982-5255) (sean_parks@fs.fed.us), L. M. Holsinger and C. Miller, Aldo Leopold Wilderness Research Inst., Rocky Mountain Research Station, US Forest Service, Missoula, MT, USA. – M.-A. Parisien, Northern Forestry Centre, Canadian Forest Service, Natural Resources Canada, Alberta, Canada.

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Climate change is expected to result in substantial ecological impacts across the globe. These impacts are uncertain but there is strong consensus that they will almost certainly affect fire regimes and vegetation. In this study, we evaluated how climate change may influence fire frequency, fire severity, and broad classes of vegetation in mountainous ecoregions of the contiguous western US for early, middle, and late 21st century (2025, 2055, and 2085, respectively). To do so, we employed the concept of a climate analog, whereby specific locations with the best climatic match between one time period and a different time period are identified. For each location (i.e. 1-km^2 pixel), we evaluated potential changes by comparing the reference period fire regime and vegetation to that of the fire regime and vegetation of the nearest pixels representative of its future climate. For the mountainous regions we investigated, we found no universal increase or decrease in fire frequency or severity. Instead, potential changes depend on the bio-climatic domain. Specifically, wet and cold regions (i.e. mesic and cold forest) generally exhibited increased fire frequency but decreased fire severity, whereas drier, moisture-limited regions (i.e. shrubland/grassland) displayed the opposite trend. Results also indicate the potential for substantial changes in the amount and distribution of some vegetation types, highlighting important interactions and feedbacks among climate, fire, and vegetation. Our findings also shed light on a potential threshold or tipping point at intermediate moisture conditions that suggest shifts in vegetation from forest to shrubland/grassland are possible as the climate becomes warmer and drier. However, our study assumes that fire and vegetation are in a state of equilibrium with climate, and, consequently, natural and human-induced disequilibrium dynamics should be considered when interpreting our findings.

Introduction

One important consequence of climate change is the expected change to fire regimes across the globe (Dale et al. 2001, Flannigan et al. 2009). Widespread changes in fire activity (i.e. fire frequency and annual area burned) (Littell et al. 2010, Moritz et al. 2012, Batllori et al. 2013) and fire severity (Parks et al. 2016) are predicted in

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the coming decades. In fact, some changes to fire regimes are already apparent in some regions (Abatzoglou and Williams 2016) and, as fire regimes continue to respond to a changing climate, challenges in anticipating and managing fire will intensify and accelerate (Millar et al. 2007).

Climate directly shapes fire regimes via its influence on fire season length and fuel moisture (Walsh et al. 2008, Pausas and Paula 2012, Jolly et al. 2015). However, climate also indirectly shapes fire regimes via its influence on productivity and dominant vegetation (Miller and Urban 1999a, Krawchuk et al. 2009), and in fact, these indirect effects may be more important than the direct effects (Liu and Wimberly 2016). Feedbacks and interactions between fire and vegetation are also important considerations for understanding and anticipating the consequences of climate change. For example, fire can alter successional trajectories, thereby catalyzing vegetation changes that in turn influence the emerging fire regime (Turner 2010, Donato et al. 2016). Consequently, fire regimes and vegetation are not independent actors (Bond et al. 2005) and their response to climate change is intrinsically coupled (Flannigan et al. 2000, Keane et al. 2015).

To date, most studies of potential changes to fire regimes have used one of two approaches: correlation-based or process-based (Williams and Abatzoglou 2016). The correlation-based approach uses observed contemporary or historical relationships between fire and climate to make predictions under a future climate (Krawchuk et al. 2009, Batllori et al. 2013, Young et al. 2016). This approach borrows heavily from species distribution modelling (Austin 2002) by identifying the climatic niche (or envelope) of fire. In contrast, the process-based approach explicitly models vegetation dynamics to predict future fire regime characteristics (Miller and Urban 1999b, Lenihan et al. 2008). There are tradeoffs associated with each method. Notably, the correlation-based approach cannot account for fire-vegetation feedbacks or potential vegetation responses to increased atmospheric CO_2 concentrations (Harris et al. 2016). Although the process-based approach can overcome some of these limitations, particularly in addressing feedbacks among climate, vegetation, and fire, it incorporates assumptions about processes that are not always well understood and difficult to parameterize and validate (Williams and Abatzoglou 2016). Furthermore, both approaches typically address only one component of the fire regime: fire frequency (Harris et al. 2016, but see Parks et al. 2016).

In this study, we explore an alternative method for evaluating future fire regimes and vegetation. We employ the concept of a 'climate analog', whereby specific locations with the best climatic match between one time period (e.g. historic or contemporary) and a different time period (e.g. future) can be identified (Wuebbles and Hayhoe 2004). Veloz et al. (2012) suggest that climate analogs can be used to evaluate potential ecological consequences of climate change. Consequently, we use climate analogs to make inferences about the response of fire regimes and vegetation to a changing climate, in that geographic localities serving as climate analogs can also function as fire regime and vegetation analogs. That is, for any given locale, the reference period fire regime and vegetation can be compared to the fire regime and vegetation of the location representative of its future climate, thereby allowing an evaluation of potential shifts. Using climate analogs to simultaneously evaluate changes in both the fire regime and vegetation should provide a more complete picture in terms of the biogeographical shifts and ecological changes associated with a warming climate (Harris et al. 2016). In contrast to correlation-based approaches to evaluating changing fire regimes and vegetation, the analog-based approach carries no assumptions about the characterization of climatic niches (or envelopes) (Veloz et al. 2012). However, the analog-based approach assumes that both fire regimes and vegetation are in a state of equilibrium with climate.

We aimed to quantify expected climate-induced changes to fire regimes and vegetation in mountainous regions of the contiguous western US using a novel application of climate analogs. In this study, the fire regime refers to fire frequency and fire severity and vegetation is grouped into broad classes. We use climate analogs and descriptions of fire regimes and vegetation for a reference period (pre-European settlement) to make inferences about potential shifts for early-, mid-, and late-21st century (2011–2040, 2041–2070, and 2071–2100, respectively). We demonstrate how this approach can provide a spatially resolved assessment of environmental change in fire-prone ecosystems, thereby complementing correlation- and process-based approaches.

Material and methods

We conducted our study in mountainous ecoregions of the contiguous western US (hereafter western US) (Fig. 1). We used gridded Landfire data (Rollins 2009) to describe two fire regime characteristics across our study area: mean fire return interval (FRI) and the percent of replacement severity (PRS) fire (resolution = 30-m) (Fig. 2). Mean fire return interval

Figure 1. Ecoregions in the western US for which we evaluated shifts to fire regimes and vegetation in response to climate change.

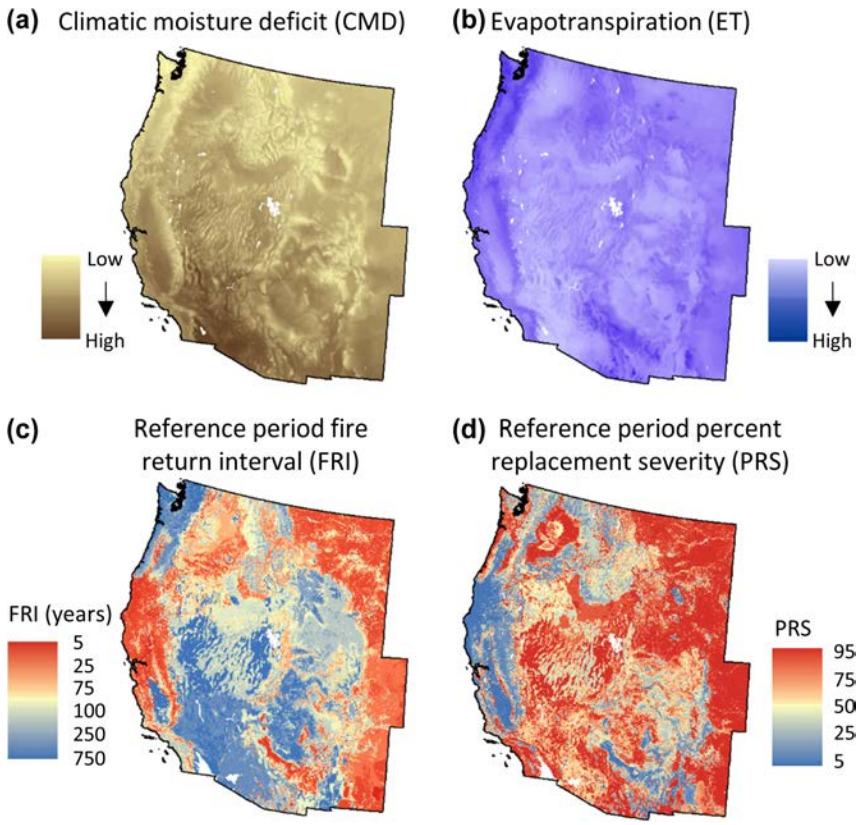

Figure 2. Maps show (a) the climatic moisture deficit (CMD) and (b) evapotranspiration (ET) for the western contiguous US. These climate variables represent the 1961–1990 time period and were used to define and identify climate analogs. Maps show (c) the mean fire return interval (FRI) and (d) percent replacement severity (PRS) (Rollins 2009; <www.landfire.gov>). Because climate analogs (and the associated fire regimes and vegetation) may be located outside of the ecoregions of interest, these maps show the extent of the western contiguous US.

represents the average number of years between successive fires for each pixel. Percent of replacement severity represents the percentage of fire that results in ≥75% canopy consumption and can be interpreted as the probability of stand-replacing fire. Note that non-forested ecosystems (e.g. shrubland/grassland) generally have high PRS (Fig. 2d) because most canopy vegetation is consumed by fire. Each fire regime characteristic was originally classified as categorical ranges (e.g. 26–30 year FRI and 56–60% PRS); we reassigned each pixel to reflect the midpoint of each range. Gridded vegetation data were also obtained from Landfire (Rollins 2009), in which we reclassified the biophysical setting (BpS) vegetation layer into five broad vegetation classes representing mesic forest, cold forest, dry forest, shrubland/grassland, and sparse/barren (see Supplementary material Appendix A). Landfire data are subject to inaccuracies (Swetnam et al. 2010). Given that they represent a historical time period (~1700–1900), errors in these data cannot be fully assessed, although it is worth noting that the Landfire FRI product is qualitatively quite similar to other fire regime assessments (Guyette et al. 2012). We are not aware of any other spatial data products that summarize fire frequency, fire severity, and vegetation across our study domain. All gridded Landfire data were resampled from a resolution of 30-m to 1-km to match the resolution of the gridded climate data (see below).

The Landfire data we used represents presumed historical fire regime and vegetation (Fig. 2); 'historical' refers to the time period immediately prior to Euro-American settlement. In limited areas where gridded historical fire regime data are lacking, notably those that are extremely wet or dry, the FRI and PRS were labeled 'indeterminate' in the Landfire dataset. To these locations (representing 1.2% of the area in the mountainous ecoregions we analyzed), we assigned fire regime characteristics based on those values of the nearest geographic neighbor. Similarly, some alpine areas were not assigned fire regime characteristics because they historically did not support fire (i.e. due to a lack of available biomass); in such cases (representing 2.4% of the area in the mountainous ecoregions we analyzed), we assigned a fire return interval of 1000 yr and a percent replacement severity of 100.

We obtained gridded climate data (1-km resolution; 30-year climatic normals) for the contiguous US from Wang et al. (2016) (available at <https://adaptwest.databasin.org/>). We used the earliest time period available (1961–1990) from our climate data source (Wang et al. 2016) to represent the reference period climate. Climate data matching the time period representing our reference fire regime and vegetation (~1700–1900) are not available at an adequate resolution or quality; however, rapid increases in temperature in the contiguous US have largely occurred after

1990 (<www.epa.gov/climate-indicators/climate-change-indicators-us-and-global-temperature>). Therefore, our use of climatic normals from 1961–1990 does not likely have a large influence on the results. Future climate is represented by three time periods: 2011–2040 (hereafter 2025), 2041–2070 (2055), and 2071–2100 (2085). Future climate projections are based on an ensemble of 15 CMIP5 GCMs under the RCP8.5 emissions scenario. We used two variables to represent reference period and future climate: Hargreaves' climatic moisture deficit (CMD; mm yr^{-1}) and Hargreaves' reference evaporation minus climatic moisture deficit (hereafter evapotranspiration [ET; mm yr^{-1}]) (Fig. 2). These are simplifications of the two variables typically used to characterize the water balance (climatic water deficit and actual evapotranspiration, respectively) and are related to temperature and precipitation (amount and timing). These variables are frequently identified as strong predictors of the distribution of fire regimes (Littell et al. 2010, Littell and Gwozdz 2011, Kane et al. 2015a) and vegetation (Stephenson 1990, Lutz et al. 2010).

CMD and ET have different data ranges. To facilitate the objective identification of climate analogs, we rescaled the reference period data for these two variables to range from 1 to 100 for the contiguous US and used the same parameters to rescale the climate data representing future time periods. We rescaled using data for the contiguous US to capture the broadest range of climatic conditions even though our study is focused on the western US. We then defined analogous climates as any pixel that is ± 3.125 scaled units for each climate variable in the bivariate combination (Supplementary material Appendix B). The use of ± 3.125 scaled units indicates a total bin width of 6.25 scaled units. Our bin-width choice of 6.25 scaled units represents 1/16th of the data range from 1961–1990 of each climate variable for the contiguous US. Although the precision of such stratifications of climate have been known to influence climate analog and velocity computations (Carroll et al. 2015, Hamann et al. 2015), a sensitivity analysis revealed that our analysis was insensitive to bin size (Supplementary material Appendix C). When considering only climate combinations that represented $\geq 0.05\%$ of the contiguous US, this bin width yielded 121 unique CMD-ET combinations, a relatively conservative stratification of climate consistent with previous efforts (Batllori et al. 2014, Carroll et al. 2015). In native units, this bin width represents 93 and 75 mm yr^{-1} for CMD and ET, respectively. Approximately 0.3% of pixels (in 2085) do not have a climate analog within our study ecoregions; all of these instances are located in the extremely dry, southern reaches of our study area and were removed from all analyses.

When identifying climate analogs, we followed the same logic as those studies that used climate analogs to evaluate 'backward climate velocities' (Hamann et al. 2015) or 'incoming trajectories' (Dobrowski and Parks 2016). That is, for each pixel, we started with the climate representing the future time periods, and then identified the locations of pixels with a matching climate under reference period climate (Supplementary material Appendix B). Consequently, we often refer to these climate analogs as 'incoming climates' because they represent the climates that may occupy a pixel of interest in future time periods. A comparison of the fire regime and vegetation at any given pixel to that of its incoming climate allowed us to estimate climate-induced changes to fire regimes and vegetation. We evaluated every combination of CMD and ET under future time periods (values were rounded to the nearest integer), yet used a bin width of 6.25 scaled units to identify climate analogs in the reference time period (values were not rounded) (Supplementary material Appendix C). This was intended to reduce boundary effects by ensuring pixels with small differences in climate were always considered as climate analogs as opposed to being treated as separate bins. This approach was adapted from Dobrowski and Parks (2016) and is illustrated in Supplementary material Appendix D. Once we identified all pixels defined as a climate analog, we selected the three nearest (geographic distance) to each pixel of interest (Supplementary material Appendix B). Future fire regime characteristics (FRI and PRS) were averaged among the three nearest neighbors (Supplementary material Appendix B), which allowed us to compare reference fire regimes to those predicted in 2025, 2055, and 2085 for each 1-km pixel. Although we chose to use the three nearest climate analogs, a sensitivity analysis revealed that our analysis was not sensitive to this choice (Supplementary material Appendix C). In order to compare reference period vegetation with that of future time periods, we identified the most frequent (majority) vegetation group associated with the three nearest climate analogs. In cases where there was no majority vegetation type, we selected the vegetation type associated with the nearest climate analog.

To illustrate potential shifts of fire regime characteristics in mountainous regions of the western US, we fitted splines of FRI and PRS for reference and future time periods as a function of climatic moisture deficit (CMD; reference period). This simple illustration depicts potential changes along one climatic gradient, but it is an ecologically relevant gradient that has been shown to be effective in capturing plant growth limitations (Stephenson 1990). Given the complexities of climate's direct and indirect influence on fire regimes, this illustration using a single climate variable is simply intended to show broad-scale biogeographic patterns. We also produced maps of potential changes in FRI, PRS, and vegetation for a sample ecoregion (Sierra Nevada); similar maps for all 17 ecoregions are provided in Supplementary material Appendix E.

We also evaluated how the fire regime characteristics of each vegetation class may change in future time periods. To do so, we plotted the mean FRI and PRS for each vegetation class and time period along the reference period CMD gradient. This illustration is intended to show potential broad-scale biogeographic shifts. Finally, we also show how reference period vegetation may change over time. This was achieved by graphically illustrating, for each reference period

vegetation class, the vegetation that is associated with its incoming climates for each time period.

Results

Fire return interval (FRI) and percent replacement severity (PRS) for the reference period and three future time periods vary along a gradient represented by the climatic moisture deficit (CMD) (Fig. 3). All four time periods show a similar pattern where both FRI and PRS are highest at the extremes in CMD and are lowest at intermediate values (~500–625 mm yr^{-1}). For locations with CMD values less than ~400 mm yr^{-1} during the reference period, FRI decreases in future time periods; at higher CMD values, FRI increases in the future. Percent replacement severity follows a similar pattern, decreasing in future time periods at lower reference period CMD values and increasing at higher values (threshold = ~450 mm yr^{-1}) (Fig. 3).

Maps of the Sierra Nevada ecoregion depicting potential changes to FRI and PRS for future time periods show interesting patterns, where, for example, at the higher elevations (i.e. low CMD), a substantial decrease in FRI is apparent (i.e. an increase in fire frequency) (Fig 4). Maps showing the potential distribution of vegetation through time also show some fairly substantial changes, where the extent of dry forest expands and cold forest and sparse/barren contracts (Fig. 4). Similar maps for all ecoregions are provided in Supplementary material Appendix E.

Results indicate that each of the four broad vegetation types ('sparse/barren' excluded), for the most part, exhibit distinct and coherent directional changes in FRI and PRS in future time periods (Fig. 5a, b). The FRI decreases in future time periods for mesic forest and cold forest, whereas it increases for dry forest and shrubland/grassland. The PRS decreases through time for cold forest but increases for dry forest; no discernible change in PRS is evident for mesic forest and shrubland/grassland.

Substantial changes to vegetation are evident when evaluating the broad vegetation types associated with incoming climates (Fig. 5c). For the cold forest vegetation class, only 16% of incoming climates are associated with cold forest (in 2085), and the remaining climates are associated with mesic forest (19%), dry forest (51%), and shrubland/grassland (14%). Mesic forest appears more stable (compared to cold forest): 59% of mesic forest has an incoming climate associated with mesic forest (in 2085) and therefore is not expected to change vegetation classes. In 2085, however, 36% of the incoming climates for mesic forest are associated with reference period dry forest. In the case of reference period dry forest, 52% of the incoming climates in 2085 are associated with reference period dry forest. However, a large proportion (41%) of incoming climates for dry forest are associated with shrubland/grassland. Finally, for shrubland/grassland, a large majority (68%) of the incoming climates are associated with shrubland/grassland, whereas 28% are associated with dry forest (Fig. 5c).

Discussion

Fire regimes and vegetation will undoubtedly change in response to a warming climate (Millar et al. 2007, Abatzoglou and Williams 2016). For the mountainous regions we investigated, we did not find a universal increase or decrease in fire return interval (FRI) or percent replacement severity (PRS); instead it appears that potential changes to fire regimes depend on the bioclimatic domain (cf. McKenzie and Littell 2016). In wet regions (low CMD), for example, FRI and PRS are expected to decrease in the future, while dry regions should see an increase in FRI and PRS (Fig. 6). Our results also suggest that substantial changes in vegetation could accompany these climate-induced shifts in the fire regime, highlighting important interactions and feedbacks associated with climate, fire, and vegetation (Schoennagel et al. 2009, Terrier et al. 2013, Bowman et al. 2014).

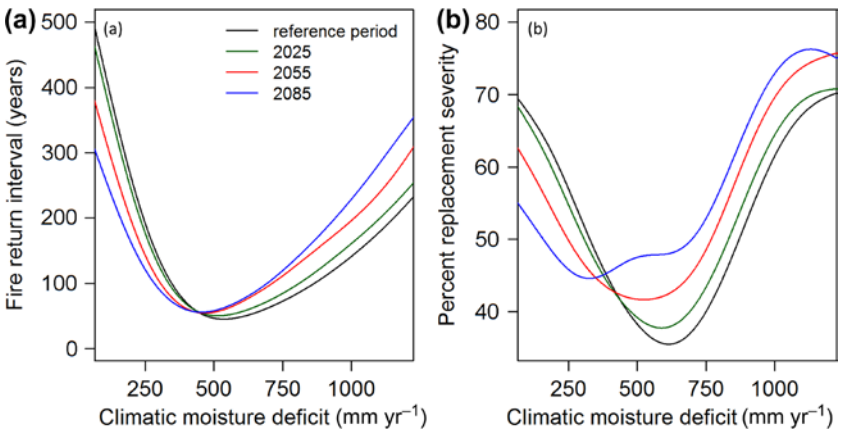

Figure 3. Fitted splines describe (a) the fire return interval (FRI) and (b) percent replacement severity (PRS) for reference and future time periods as a function of the climatic moisture deficit (CMD) for mountainous ecoregions in the western US. The climatic moisture deficit (x-axis) is static and is representative of the reference period climate (1961–1990).

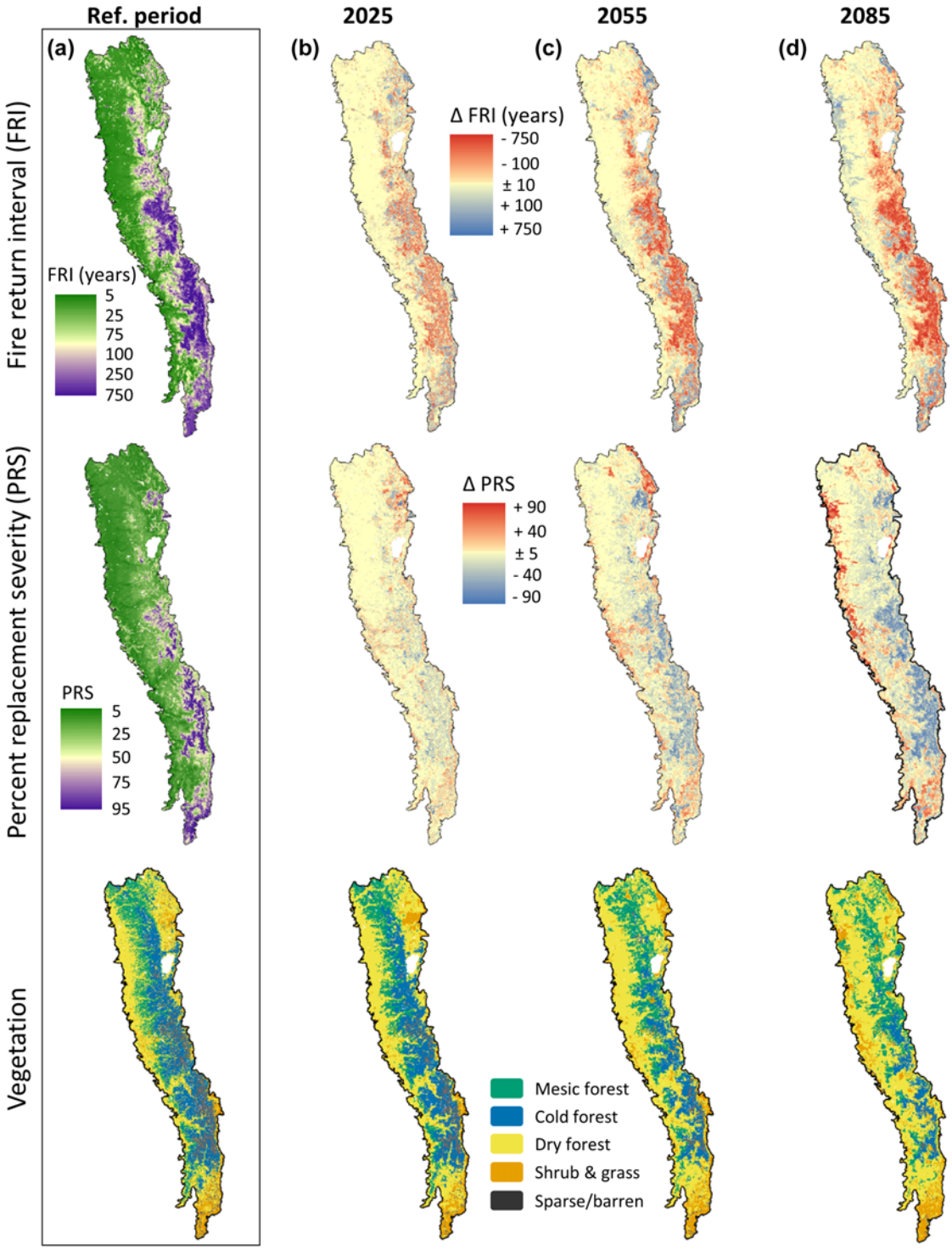

Figure 4. Maps show reference period fire return interval (FRI), percent replacement severity (PRS), and vegetation for the Sierra Nevada ecoregion (a). Also shown are changes in FRI, changes in PRS, and vegetation for three future time periods, 2025 (b), 2055 (c), and 2085 (d). See Fig. 1 to reference the location of this ecoregion.

In particular, the expected increase in FRI and PRS at intermediate moisture conditions (climatic moisture deficit [CMD] = ~500–625 mm yr^{-1}) could have important implications for vegetation, as this CMD range generally coincides with the lower limit for many forests (Fig. 5, Stephenson 1990) that may be especially susceptible to drought and a corresponding state transition to shrubland/grassland (cf. Breshears et al. 2005) (Fig. 6).

Some correlation-based studies conducted at much broader spatial scales than our study have predicted that

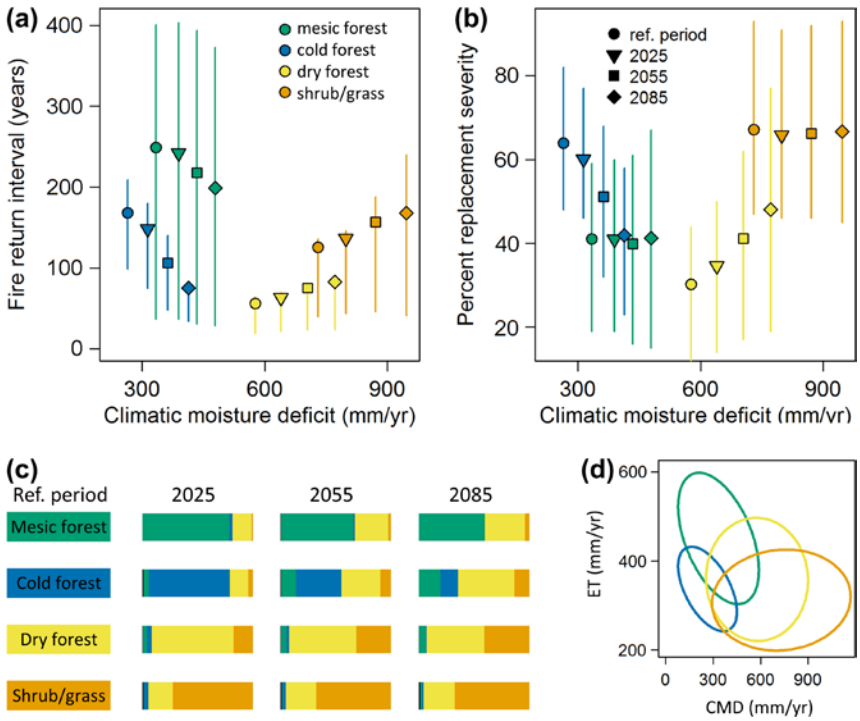

Figure 5. Plots describe (a) the fire return interval (FRI) and (b) percent replacement severity (PRS) for four vegetation groups for four time periods (see Methods) along the climatic moisture deficit gradient. The symbols (e.g. open circles) represent the mean values and the vertical lines show the inter-quartile range for FRI and PRS for reference and future time periods. The CMD values are representative of each time period (this is in contrast to the static CMD axis in Fig. 3). (c) Bar plots show the four reference period vegetation groups and the vegetation associated with incoming climates of each group; widths represent the relative proportion of each group. (d) Ellipses encapsulate 67% of data depicting the reference period climate space (in terms of climatic moisture deficit [CMD] and evapotranspiration [ET] of each vegetation group; note the large amount of overlap between dry forest and shrubland/grassland. The sparse/barren vegetation class is excluded in this figure because it comprises only ~1% of the study area.

fire activity will almost universally increase in mountainous regions (or portions thereof) of the western US in response to climate change (Spracklen et al. 2009, Moritz et al. 2012, Stavros et al. 2014, Barbero et al. 2015). In contrast, our study, which incorporates fairly fine-scale variability, suggests a more nuanced response where some bioclimatic settings will experience an increase in frequency and others will experience a decrease. Our results are thus coherent with studies that indicate hotter and drier climates in the future will not necessarily result in more frequent fire (Batllori et al. 2013, McKenzie and Littell 2016). However, our results suggesting that changes in severity depend on the bioclimatic domain build upon a correlation-based study that predicted a widespread decrease in severity (Parks et al. 2016). We suggest that dissimilarities in results between the two studies are due to methodological differences. Whereas the study here defined high severity fire as stand-replacing regardless of vegetation type, Parks et al. (2016) measured fire severity using spectral differences between pre- and post-fire satellite imagery, which may underestimate severity in some non-forest settings where stand replacement is more common (e.g. shrubland/grassland). Although most correlation-based studies have not evaluated both fire and vegetation, there are two noteworthy exceptions that are consistent with our results. Liu and Wimberly (2016) predicted both increases and decreases in fire frequency (depending on the location and scenario) in the western US that were accompanied by substantial shifts in the distribution of vegetation (e.g. expansion of desert scrub). Littell et al. (2010) evaluated both fire frequency and vegetation in the state of Washington; fire frequency, for the most part, was predicted to increase and large swaths of the state that are currently climatically suitable for Douglas fir are expected to become climatically unsuitable (too dry) by mid-century.

Direct comparison to studies that used process-based models to evaluate climate-induced fire regime and vegetation change is challenging due to large differences in study extents and how fire and vegetation are measured and quantified. However, there is general coherence with our findings. Lenihan et al. (2008) showed that, in agreement with our general findings, fire frequency will not universally increase across the state of California; decreases in fire frequency are also predicted, which are generally restricted to the drier regions of the state. In Yellowstone National Park, USA, cold forests are predicted to experience an increase in fire frequency and shift to drier forest types under moderate warming (>2° C) (Clark et al. 2017); this pattern is consistent with our overall findings for cold forests and with those of a

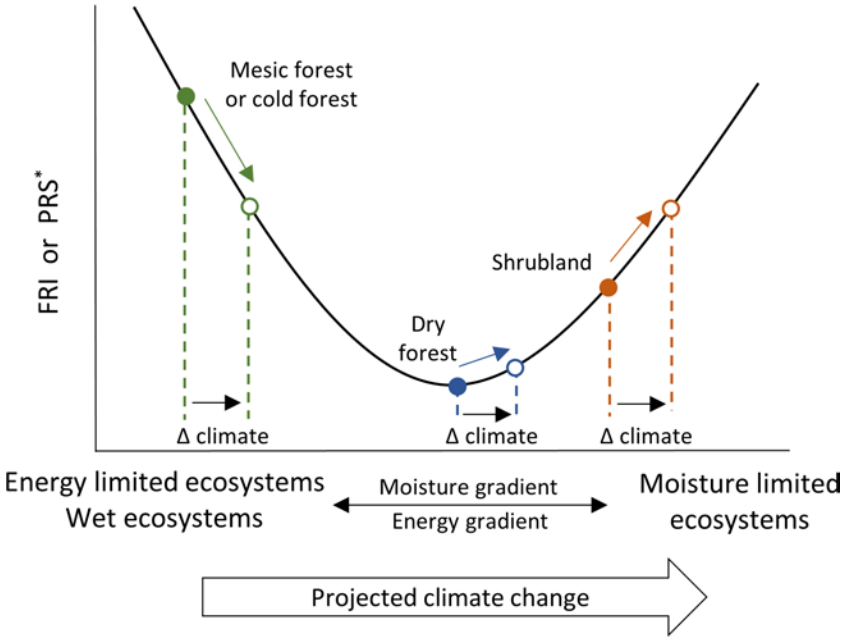

Figure 6. Conceptual model describing predicted climate-induced shifts in fire return interval (FRI) and percent replacement severity (PRS) along a resource gradient representing moisture and energy. As the climate warms, mesic forests and cold forests are expected to experience decreased FRI and PRS*. Dry ecosystems, such as shrubland/grassland, are expected to experience increased FRI, which is likely in response to decreased productivity and available biomass. Dry forests, especially those on the ecotone between forest and non-forest, are predicted to experience increased FRI and PRS, which may be an indication of transition from forest to non-forest. Note that climatic moisture deficit is projected to increase across the entire western US in coming decades (data not shown) (Wang et al. 2016). *Note that mesic forest and shrubland/grassland did not exhibit predicted decreases and increases in PRS, respectively (Fig. 5).

correlation-based study in the same region (Westerling et al. 2011). Furthermore, our reports of fairly substantial changes to vegetation type and distribution are in agreement with other studies that evaluated the influence of climate change on vegetation distributions in the US (Bachelet et al. 2001, Iverson and Prasad 2001, Lenihan et al. 2008).

Fire regimes and vegetation are not independent (Bond et al. 2005); a warming climate will alter fire regimes and vegetation concomitantly (Whitlock et al. 2003, Terrier et al. 2013). We found distinct and directional changes in FRI and PRS for each vegetation type (Fig. 5a, b), but substantial changes to vegetation are also possible in the coming century. Indeed, only 16% of reference period cold forest has an incoming climate associated with cold forest in 2085 (Fig. 5c); this corresponds to a decrease in the fire return interval and fire severity. Feedbacks and interactions between fire regimes and vegetation confound efforts to identify whether a warming climate alters fire regimes (and subsequently results in change to vegetation) (Flannigan et al. 2000) or a warming climate alters vegetation (and subsequently results in changes to the fire regime) (Breshears et al. 2005). The climate analog approach used in this study is unable to clarify these interactions, and continued investigations on this topic is a worthwhile avenue of research (Carcaillet et al. 2001, Turner 2010, Liu and Wimberly 2016).

Our results have strong implications for forest loss in the western US. Specifically, we interpret the inflection point depicted in many of our figures (i.e. the lowest reference period values for FRI and PRS) as a potential tipping point at which small shifts in climate may result in conversion from forest to non-forest (cf. Johnstone et al. 2016). This domain of the climate gradient represents intermediate CMD values (~500–625 mm yr^{-1}), coincides with the distribution of most dry forests (Fig. 5d), and generally agrees with previous work that evaluated the distinct climate space of forest and non-forest in temperate regions (Stephenson 1990). However, climate's influence on vegetation is complex, and various biophysical mechanisms, as well as interactions among climate, fire, and vegetation, will ultimately control whether or not forest converts to non-forest. Nevertheless, conversions from forest to non-forest have been recently documented in response to high-severity fire (Coop et al. 2016, Donato et al. 2016) and drought (Breshears et al. 2005). Such conversions are likely to become more common as the climate warms (Allen et al. 2010) and are supported by our findings. We estimate that, within the mountainous ecoregions of the western US, climate change could potentially result in the loss of ~94 000 km^2 of forest before 2100 and a corresponding increase in shrubland/grassland (Supplementary material Appendix F); this represents 12% of reference period forest. However, because the climate space of dry forest and shrubland/grassland substantially overlap (at least for the CMD and ET variables we examined) (Fig. 5d), more research is necessary to elucidate the drivers, mechanisms, and consequences of

climate change on fire regimes and vegetation of dry forest types (cf. McWethy et al. 2013).

The analog-based approach used in this study represents a substantially different paradigm compared to correlation- and process-based approaches and offers some advantages for projecting future fire regimes and vegetation patterns in heterogeneous regions. The use of climate analogs enabled us to simultaneously make predictions on two fire regime characteristics (fire return interval and severity); this is not a trivial distinction given that most studies to date involving climate change and fire regimes have focused solely on fire activity (Harris et al. 2016). The analog-based approach also allowed us to evaluate potential vegetation changes associated with fire regime shifts. Furthermore, whereas the correlation-based approach fits a function through observed data (i.e. a cloud of points), thereby smoothing the response of fire to its environment and ignoring potentially meaningful departures (i.e. the residuals), the analog-based approach does not have this constraint and more fully incorporates spatial variability in climate, fire, and vegetation.

Our approach implicitly assumes that there is equilibrium among climate, fire, and vegetation; this assumption implies that fire regimes and vegetation will keep pace with changing climate. Although this is a common assumption in many climate change studies involving fire (Moritz et al. 2012) and species distributions (Engler et al. 2011), lags in the response of vegetation often result in 'disequilibrium'. Disequilibrium, also called 'climatic debt' (cf. Bertrand et al. 2016), occurs when changes in climate do not immediately result in changes to fire regimes and vegetation (Sprugel 1991, Svenning and Sandel 2013). For example, disequilibrium naturally arises when long-lived organisms, such as trees, can survive and persist under a warming climate even though seedlings and juveniles of the same species cannot (Grubb 1977). This lagged response to climate change has been documented in paleo-ecological studies of vegetation change (Delcourt et al. 1982, Overpeck et al. 1992).

Although disequilibrium dynamics and a lagged response to climate change will most likely influence the timing and magnitude of potential changes to fire regimes and vegetation in the coming decades, some evidence suggests that ecosystems are indeed changing. For example, a general upslope and poleward shift in many species ranges has been well documented (Walther et al. 2002, Parmesan and Yohe 2003, Chen et al. 2011). More specifically, shifts in the trailing edges of species distributions have been observed, particularly in the presence of disturbance such as fire and insect outbreaks (Renwick et al. 2016, Donato et al. 2016); leading edge range shifts are also evident (Harsch et al. 2009). Widespread tree mortality resulting from drought and insect outbreaks has also been observed (Bentz et al. 2010, Allen et al. 2010). Many of these changes are catalyzed by disturbance, and as the climate changes, the post-disturbance vegetation may resemble communities from warmer regions (Stevens et al. 2015). As these changes occur, the newly established vegetation will likely be more aligned with the emerging climate and disturbance regime (Overpeck et al. 1990, Millar et al. 2007).

An important caveat of our study is that anthropogenic factors that exclude fire, such as livestock grazing, fire suppression, and landscape fragmentation, have more or less weakened the relationships among fire, vegetation, and climate (Marlon et al. 2012, Higuera et al. 2015, Parks et al. 2015). This human-induced disequilibrium must be considered when interpreting our results. For example, many studies have demonstrated that fire is currently much less prevalent in western US landscapes compared to earlier time periods (~1700–1900) (Kilgore and Taylor 1979, Heyerdahl et al. 2001, Taylor and Skinner 2003, Wright and Agee 2004). This reduction in fire activity has resulted in substantial changes to vegetation composition and structure. Forests that historically experienced periodic fire are now generally denser (with smaller trees) and have more shade-tolerant (and fire-sensitive) species (Keane et al. 2002, Hessburg et al. 2005, Dolanc et al. 2014a, b). As such, the strong influence of anthropogenic factors suggests that historical time periods (i.e. ~1700–1900) may not be the most appropriate reference period for fire regimes and vegetation when making inferences about the future (Flatley and Fulé 2016). However, as suggested by Pechony and Shindell (2010), it is possible that climate change may overwhelm the ability of humans to suppress fire and that human-induced disequilibrium may diminish in the coming decades; this point is supported by Abatzoglou and Williams (2016), who found that ~50% of the area burned since 1984 is due to climate change.

Although the human influence on fire regimes confounds nearly every study involving fire, vegetation, and climate, even those using contemporary fire data (Parisien et al. 2016), our results are highly relevant to land managers who aim to restore fire as a natural process (Hessburg et al. 2015, Stephens et al. 2016). This is particularly relevant to protected areas where natural processes such as fire are not suppressed (van Wagtendonk 2007, Miller and Aplet 2016) and where the fire-climate relationships are typically stronger (Archibald et al. 2009, Parks et al. 2014). Our findings may also be useful in quantifying future disequilibrium, potential departures in expected fire activity and severity under a changing climate (cf. Mallek et al. 2013, Safford and de Water 2014, Parks et al. 2015), and provides important insights in terms of restoring natural fire regimes in future decades (Flatley and Fulé 2016).

The reference period fire regime and vegetation data obtained from Landfire are subject to inaccuracies (Swetnam et al. 2010); errors in these data are not quantified and probably unknowable, particularly in regions and vegetation types where reliable fire history data are lacking (e.g. shrubland/grassland). Furthermore, our analog-based method does not incorporate mechanisms that process-based approaches can, such as improved water use efficiency resulting from CO_2 fertilization (cf. Williams and Abatzoglou 2016), and dynamic interactions and feedbacks that result in altered fire regimes, vegetation composition, and fuel bed structure (Miller 2003). Instead, the analog-based method assumes that reference

period fire regimes and vegetation are an emergent property of relevant processes. Another potential drawback is that we characterized climate analogs using only two climate variables (climatic moisture deficit and evapotranspiration averaged over 1961–1990). In doing so, our approach simplified the complexities of climatic influences on fire regimes and vegetation. Seasonality, inter-annual variability, and climatic extremes are known to influence fire regimes and vegetation but were not explicitly included in our study. Nevertheless, the two climate variables we used are often strongly correlated with the distribution of both fire regimes and vegetation (Stephenson 1998, Lutz et al. 2010, Parks et al. 2014, Kane et al. 2015b, Whitman et al. 2015, McKenzie and Littell 2016). Furthermore, a parallel analysis in which 26 climatic variables (some of which are measures of seasonality and extremes) were collapsed into two orthogonal variables using principal components analysis yielded results similar to those presented here (Supplementary material Appendix C).

Conclusions

The analog-based approach presented here provides an alternative to correlation- and process-based approaches for quantifying potential climate-induced changes to fire regimes and vegetation. This approach allowed us to simultaneously evaluate fire frequency, fire severity, and vegetation. Virtually every study of climate change impacts on fire and vegetation predicts substantial changes in future decades (Moritz et al. 2012, Bowman et al. 2014, Liu and Wimberly 2016). We found that the magnitude and direction of predicted changes in the fire return interval and fire severity depend on the bioclimatic domain (cf. Krawchuk et al. 2009, Batllori et al. 2013, McKenzie and Littell 2016). Regions with cooler and wetter climates are generally expected to experience shorter fire return intervals (increased fire frequency) and decreased fire severity, whereas warmer and drier regions are predicted to experience longer fire return intervals (decreased fire frequency) and increased fire severity. Our analyses suggest these changes in fire frequency and severity will be accompanied by substantial shifts in vegetation, the most notable of which is a potential tipping point in climate space at which conversion from dry forest to non-forest is possible (Fig. 6). Although our results show that climate is pushing fire regimes and vegetation away from reference period conditions, there may be a lagged and nuanced response due to natural and human-induced disequilibrium. Consequently, our results should not be strictly interpreted in terms of the exact magnitude or timing of change. Instead, we emphasize the general direction of change as shown in the conceptual model (Fig. 6).

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Supplementary material (Appendix ECOG-03378 at <www.ecography.org/appendix/ecog-03378>). Appendix A–F.