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Water balance and topography predict fire and forest structure patterns

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ABSTRACT

Mountainous topography creates fine-scale environmental mosaics that vary in precipitation, temperature, insolation, and slope position. This mosaic in turn influences fuel accumulation and moisture and forest structure. We studied these the effects of varying environmental conditions across a 27,104 ha landscape within Yosemite National Park, California, USA, on the number of fires and burn severity (measured from Landsat data for 1984–2010) and on canopy cover at two heights (>2 m and 2–8 m) and dominant tree height (measured with airborne LiDAR data). We used site water balance (actual evapotranspiration and climatic water deficit) and topography (slope position, slope, and insolation) as environmental predictors. Random forest modeling showed that environmental conditions predicted substantial portions of the variations in fire and forest structure: e.g., 85–93% of the variation in whether a location did not burn, burned once, or burned twice; 64% of the variation in the burn severity; and 72% of the variation in canopy cover >2 m for unburned forests, 64% for once-burned forests, and 59% for twice-burned forests. Environmental conditions also predicted a substantial portion of forest structure following one and two fires, even though the post-fire forest structures were substantially different than pre-fire structures. This suggests a feedback mechanism in which local fire regimes and pre-fire forest structures are related to local environments, and their interaction produces post-fire structures also related to local environments. Among environmental predictors, water balance had the greatest explanatory power, followed by slope position, and then by slope and insolation. Managers could use our methods to help select reference areas that match environmental conditions, identify areas at risk for fires that endanger critical habitat or other resources, and identify climate analog areas to help anticipate and plan for climate change.

1. Introduction

Within mountainous regions, variations in precipitation, temperature, aspect, slope, slope position, and soils (Knapp and Smith, 2001; Dyer, 2009; Dobrowski et al., 2009; Greenberg et al., 2009; Urban et al., 2000; Dobrowski, 2011; Holden and Jolly, 2011) create fine-scale mosaics of environmental conditions. These mosaics in turn create and maintain differences in forest processes, composition, and structure (Stephenson, 1998; Urban et al., 2000; Taylor and Skinner, 2003; Hessburg et al., 2007; Meyer et al., 2007; Underwood et al., 2010; Lydersen and North, 2012). Varying environmental conditions may help explain why mountainous regions are biodiversity hotspots (Körner and Ohsawa, 2005) and why these regions can serve as important areas of conservation and refugia under future climate change (Dobrowski, 2011).

Work in the Sierra Nevada Mountains (California, USA), for example, has shown strong effects of site water balance (actual evapotranspiration and climatic water deficit) on forest species composition and structure (Parker, 1982, 1989; Stephenson, 1998; Lutz et al., 2009, 2010). Other work has addressed the effects of topography and landscape position on both fire behavior and forest structure (Collins et al., 2006; Underwood et al., 2010; Lydersen and North, 2012). In previous work by several of us, we found changes in forest structure following fire along an elevation gradient related to the moisture gradient (Kane et al., 2013, 2014).

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Miller and Urban explored these topics in greater depth for the Sierra Nevada range using a forest gap and climate model to simulate the effects of local climate and topography on fire and forests (Miller and Urban, 1999a, 1999b; Miller and Urban, 2000a, 2000b; Urban et al., 2000). Their work emphasized the role of available moisture for creating mosaics of forest biomass and fuel moisture and accumulation. These moisture patterns were primarily driven by the strong elevation gradient but modified by local topography (Urban et al., 2000).

Variations in the actual weather during fires should weaken the relationship between environmental conditions and forest structure (Peterson, 2002; Lydersen et al., 2014). A triangle of equally important and interactive elements – topography, fuels, and weather – control fire behavior and influence its resulting severity and effects on forest structure (Sugihara et al., 2006). The stochastic nature of weather during the course of fires may result in stochastic patterns of burn severity that mask or replace the relationship between the environmental conditions and fire and forest structure (Collins et al., 2006; Collins, 2014). Large fire growth days are commonly caused by extreme fire weather (hot temperatures, high winds, or atmospheric instability) that overwhelms the effects of topography and fuels on fire behavior (Lydersen et al., 2014).

To our knowledge, no study has examined the integrated effects of the environmental mosaic on fire and forest structure patterns using actual data mapped across a real large landscape. A better understanding of the effects of environmental mosaics would explore important ecological relationships and help managers better predict how re-introduced fire may behave and to determine appropriate restoration goals for forest structure.

One reason for the lack of this type of study may be that within most of the western United States it is difficult to fully test the potential influence of environmental heterogeneity on fire patterns and forest structure. Typically, only fires that burn under extreme fire conditions and with high fire severities escape suppression and become large enough to influence landscape forest patterns (Moritz et al., 2005; van Wagtendonk, 2007; Miller et al., 2012; Mallek et al., 2013). Additionally, over a century of timber harvests, fire suppression, grazing, and low-density residential development have substantially altered the physical structure of forests (Hessburg and Agee, 2003; Romme et al., 2009; Naficy et al., 2010; Knapp et al., 2013).

The majority of Yosemite National Park, California, USA, however, has been managed as a wilderness. Since 1972, park managers have allowed many lightning-ignited fires and prescribed fires to burn (Van Wagtendonk and Lutz, 2007). Park managers recognize the importance of restoring fire as an ecological process, but must balance the risk wildfires present to visitor safety, smoke accumulation, infrastructure, wildlife and endemic plant habitats, as well as other ecosystem services. Managers here as in many areas worldwide would benefit from an understanding of how local environmental factors influence fuel moisture and accumulation and forest structure, and how an intact fire regime may influence them.

In this study, we examine the effects of the mosaic of environmental conditions on fire and forest structure across two landscapes within Yosemite, using as many as 35,000 sample locations from continuous maps of environmental variables, fire, and forest structure. We examine a wider breadth of environmental predictors than previous studies, examine fire patterns from 1984 to 2010, and measure forest structure with airborne LiDAR data. We explore three hypotheses:

- A substantial portion variation in fire and forest structure across a mountainous landscape can be explained by variations in the environmental conditions.
- The relationship of environmental conditions to forest structure will substantially weaken with the occurrence of fire because of the stochastic effects of weather on fire.
- Because of the strong elevation gradient in our study area, changes in water balance (moisture availability) will be the strongest environmental predictor for variations in fire and forest structure.

2. Methods

2.1. Study area

Yosemite National Park (3027 km^2) lies in the central Sierra Nevada, California, USA (Fig. 1). The western portion of Yosemite possesses a Mediterranean climate with July (mid-summer) mean minimum and maximum temperatures of 2–13 °C at higher elevations and 16–35 °C at lower elevations. Most precipitation falls as snow with annual precipitation ranging from 800 mm to 1720 mm (Lutz et al., 2010). The park has multiple wildfires each year, and since 1972 many lightning-ignited fires have been allowed to burn (van Wagtendonk and Lutz, 2007) with many fires burning with low and mixed-severities. This practice has resulted in most fires burning under and moderate weather conditions resulting in a mixture of fire severities that may emulate the historic mixed-severity fire regime (van Wagtendonk, 2007; Sugihara et al., 2006; Mallek et al., 2013). This long period of reintroduced fire has allowed large areas to return towards a self-regulated fire regime (van Wagtendonk, 2007; Mallek et al., 2013) and reduced fuel loads and fuel continuity over a considerable area (Miller et al., 2012). (Low-severity fires generally have overstory tree mortalities <25%; mixed-severity fires create patchworks of overstory mortality that can range from none to complete overstory mortality within a patch, with mortalities of 25–75% being common; and high severity fires have overstory tree mortalities >75% (Sugihara et al., 2006).)

We studied two forested areas within the park with a combined area of 27,104 ha that had available airborne LiDAR data. The Northern area runs generally parallel to California State Highway 120, and the Illilouette area encompasses the Illilouette Creek basin. Between 1970 and 2010, the Northern area had 39 fires ⩾40 ha and the Illilouette area 29 fires (Supplement Table 1).

We excluded locations that had burned before 1970 when park managers began allowing fires to burn under low and moderate weather conditions. We assigned forest types within the study areas primarily based on the 1997 park vegetation map (Keeler-Wolf et al., 2012). If the area was not forested in 1997, we used the 1937 vegetation classification (Wieslander, 1935; Walker, 2000) under the assumption that fire had caused a shift in vegetation type. We excluded areas not currently forested, nor forested in 1937.

Three forest types were common between both study areas: sugar pine-white fir (*Pinus lambertiana–Abies concolor*), Jeffrey pine (*Pinus jeffreyi*), and red fir (*Abies magnifica*). Three other forest types occurred primarily in only the Northern area – ponderosa pine (*Pinus ponderosa*) – or the Illilouette area – lodgepole pine (*Pinus contorta* subsp. *murrayana*) and western white pine (*Pinus monticola*). Historically, most of these forest types were dominated by tree species such as ponderosa pine, sugar pine, Jeffrey pine, red fir, and white pine that had high fire tolerance (van Wagtendonk and Fites-Kaufmann, 2006). Since the advent of fire suppression, a less fire tolerant species, white fir, has become common in the ponderosa pine and sugar pine forests.

These forest types are associated with specific elevation ranges with the Illilouette forests types at higher elevations than their Northern study area counterparts (Fig. 2). As elevation increases, mean precipitation increases, mean temperature decreases, fre-

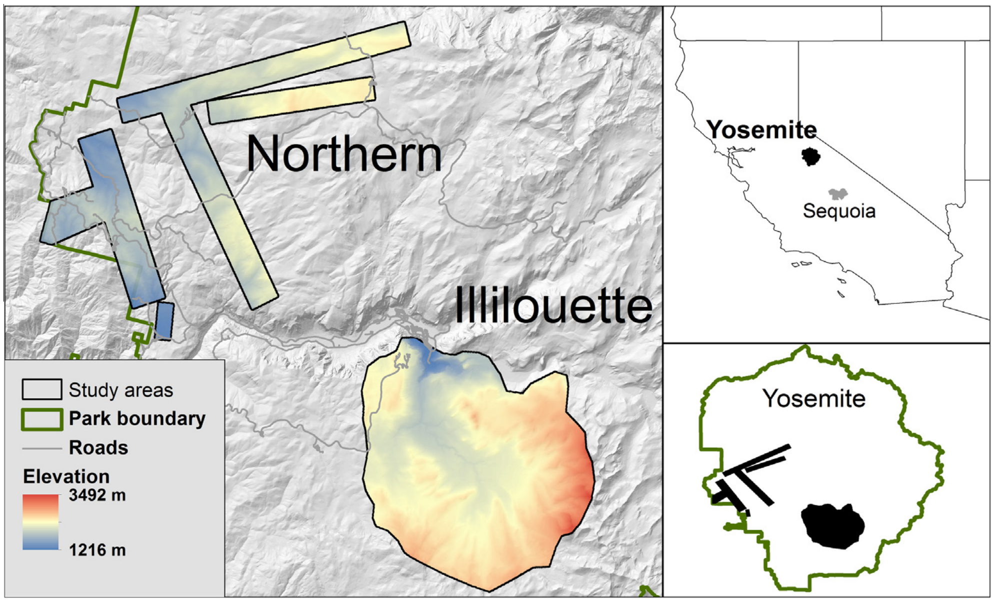

Fig. 1. Location of Yosemite National Park within California, USA, (insert) as well as the two study areas used within the park. Yosemite Valley lies between the two study areas. Location of Sequoia National Park within California also shown where Miller and Urban (1999a) simulated fire patterns and forest biomass using environmental predictors similar to the ones used in our study.

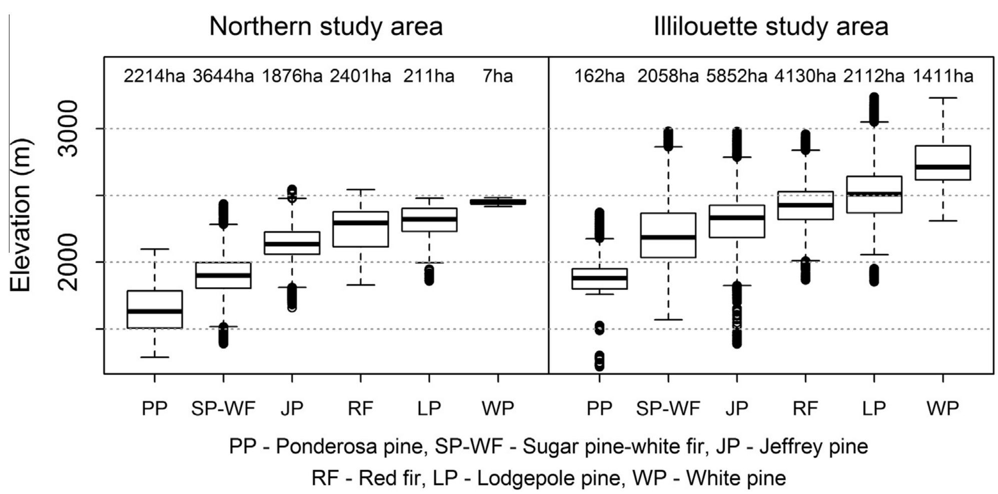

Fig. 2. Elevation ranges and areas (shown at top of panels) for forest types in the two study areas. With increasing elevation, forests tend to have less canopy cover and shorter dominant trees. Each forest type is found at higher mean elevations in the Illiouette study area than in the Northern study area. Bold lines in boxplots show median values; the bottom and top of the boxes show the 25th and 75th percentile values; the upper and lower whiskers show either minimum and maximum values or 1.5 times the interquartile range (approximately two standard deviations), whichever is nearer to the median; and circles show outliers.

quency of fires >40 ha decreases, and mean burn severity decreases (Lutz et al., 2010; Thode et al., 2011). With increasing elevation, forests tend to have less canopy cover and shorter dominant trees (Parker, 1982, 1989; Kane et al., 2013, 2014) with associated reductions in biomass. Illilouette forests tend to be more open and shorter than their Northern study area counterparts (Fig. 3).

Historically, frequent fires created fine-grained mosaics of individual trees, small tree clumps, and openings and with relatively few short trees creating ladder fuels (Larson and Churchill, 2012). Managers suppressed fires from the early 1900s to the early 1970s. This allowed tree species such as white fir that have lower fire tolerance to become established, often creating nearly continuous canopy forests with significant fuel laddering (Beaty and Taylor, 2008; Scholl and Taylor, 2010; Collins et al., 2011). When low- and mixed-severity fires burn through these forests, ladder fuels tend to be removed, overall canopy cover is reduced, and patterns of tree clumps and openings can reemerge (Kane et al., 2013, 2014) (Fig. 3).

2.2. LiDAR data and forest structure metrics

Watershed Sciences, Inc. (Corvallis, OR) used dual mounted Leica ALS50 Phase II instruments for both LiDAR acquisitions and collected up to four returns per pulse. Northern area data (10,895 ha) was collected on 21 and 22 July 2010 with an average pulse density of 10.9 pulses m^{-2}. Illilouette area data (16,209 ha) was collected on 19–21 July 2010 with an average pulse density of 12.20 pulses m^{-2}. Watershed Sciences created 1 m resolution

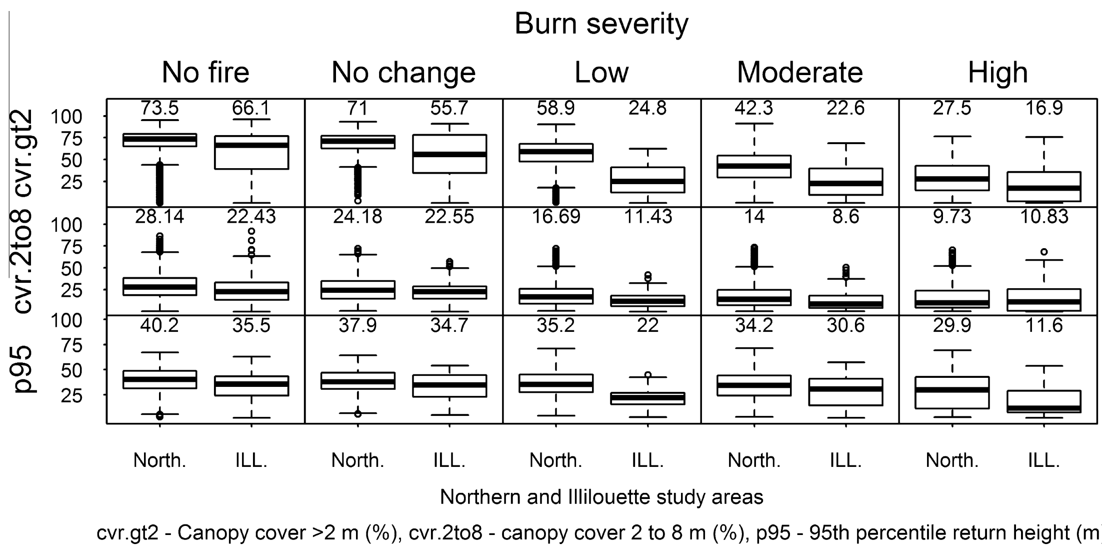

Fig. 3. Differences in forest structure between the two study areas and changes in structure following a single fire using sugar pine-white fir forests as an example. The Northern study area generally had greater canopy cover >2 m (correlated with higher stand density and less area in gaps and openings), greater canopy cover in the 2–8 m stratum (correlated with more shrub or regeneration cover and more ladder fuels), and a higher 95th percentile LiDAR return height (correlated with taller dominant trees) than the Illilouette study area. Fire tended to reduce canopy cover in both strata and to a lesser degree dominant tree height. Bold lines in boxplots show median values; the bottom and top of the boxes show the 25th and 75th percentile values; the upper and lower whiskers show either minimum and maximum values or 1.5 times the interquartile range (approximately two standard deviations), whichever is nearer to the median; and circles show outliers.

Table 1
Response and predictor metrics used in this study. Spatial scales at which metrics were calculated are shown in parentheses. Predictors and scales included in the parsimonious set of environmental predictors are underlined.

Forest structure responses	Source	Units/interpretation
Cover > 2 m (30 m)	LiDAR	Percent
Cover 2–8 m (30 m)	LiDAR	Percent
95th percentile LiDAR return height (30 m)	LiDAR	Meters
Fire response and predictors		
RdNBR burn severity estimate (30 m)	MTBS[a]	Relative severity
Years since previous fire (predictor only)	Park records	Years
Water balance predictors		
Actual evapotranspiration (800 m)	Lutz et al. (2010)	mm water
Climatic water deficit (800 m)	Lutz et al. (2010)	mm water
Precipitation[b]	PRISM	mm water
January min. temperature (800 m)[b]	PRISM	°C
July max. temperature (800 m)[b]	PRISM	°C
Local topography predictors		
Slope (30, 90, 270 m)	LiDAR	Degrees
Solar radiation index (30, 90, 270 m)	LiDAR	Relative index
Heat load (30 m) (McCune and Keon, 2002)	USGS[c] 10 m DEM	Unitless relative index
Aspect (30, 90, 270 m)	LiDAR	Cosine (south = 0)
Slope position predictors		
Topographic position index (100, 250, 500, 1000, 2000 m)	10 m USGS DEM (Jenness, 2006)	Relative index
Cool air pooling (800 m)	Lundquist et al. (2008)	Relative index

[a] Monitoring trends in burn severity.
[b] Key variable for water balance model used.
[c] United States Geological Survey.

LiDAR-derived digital terrain models (DTM) using the TerraScan (v.10.009 & v.11.009) and TerraModeler (v.10.004 & v.11.006) software packages (Terrasolid, Helsinki, Finland).

We processed the LiDAR data using the USDA Forest Service's Fusion software package (version 3.2, http://forsys.cfr.washington.edu/fusion.html). We selected a set of three forest structure metrics (Table 1) identified in previous research that represent forest biomass and change with fire (Kane et al., 2013, 2014). First, the 95th percentile LiDAR return height above the ground was a surrogate for dominant tree height. Second, total canopy cover >2 m was calculated as the proportion of LiDAR returns >2 m in height divided by the total count of returns. Third, canopy cover from 2–8 m was calculated as the proportion of LiDAR returns in this height strata divided by the total count of returns 0–8 m in height. This metric represented tall shrubs, short trees, and lower foliage of taller trees that can serve as ladder fuels.

2.3. Fire number and estimated burn severity

We mapped fire locations from 1930 to 1983 based on park records of fire perimeters and from 1984 to 2010 based on Park records tuned with Landsat-observed fire boundaries (Lutz et al., 2009, 2011). We used the Yosemite burn severity atlas (0.09 ha resolution) assembled by Lutz et al. (2011) and processed by and available from the Monitoring Trends in Burn Severity (MTBS) project (Eidenshink et al., 2007). This atlas includes all fires ⩾40 ha from 1984, the earliest date for data from the Landsat Enhanced Thermal Mapper (ETM and ETM+), through June 2010, which comprised 97% of the area within fire perimeters (Lutz et al., 2009).

The Yosemite fire atlas uses the Relativized differenced Normalized Burn Ratio, RdNBR (Miller and Thode, 2007). This burn severity metric summaries the effects of fire on the abiotic environment and vegetation, including the immediate impacts of the fire and ecosystem responses up to a year post-fire (Sugihara et al., 2006; Miller and Thode, 2007). Higher RdNBR values signify a decrease in photosynthetic materials and surface materials holding water and an increase in ash, carbon, and exposed soil. RdNBR has been validated as a robust estimator of burn severity in the field in the Sierra Nevada (Thode, 2005; Thode et al., 2011) and other in forested areas (Soverel et al., 2010; Cansler and McKenzie, 2012).

2.4. Environmental metrics

We tested a number of environmental metrics (Table 1, Fig. 4) to determine how well they predict fire and structure, and to determine if a parsimonious set could explain these variations.

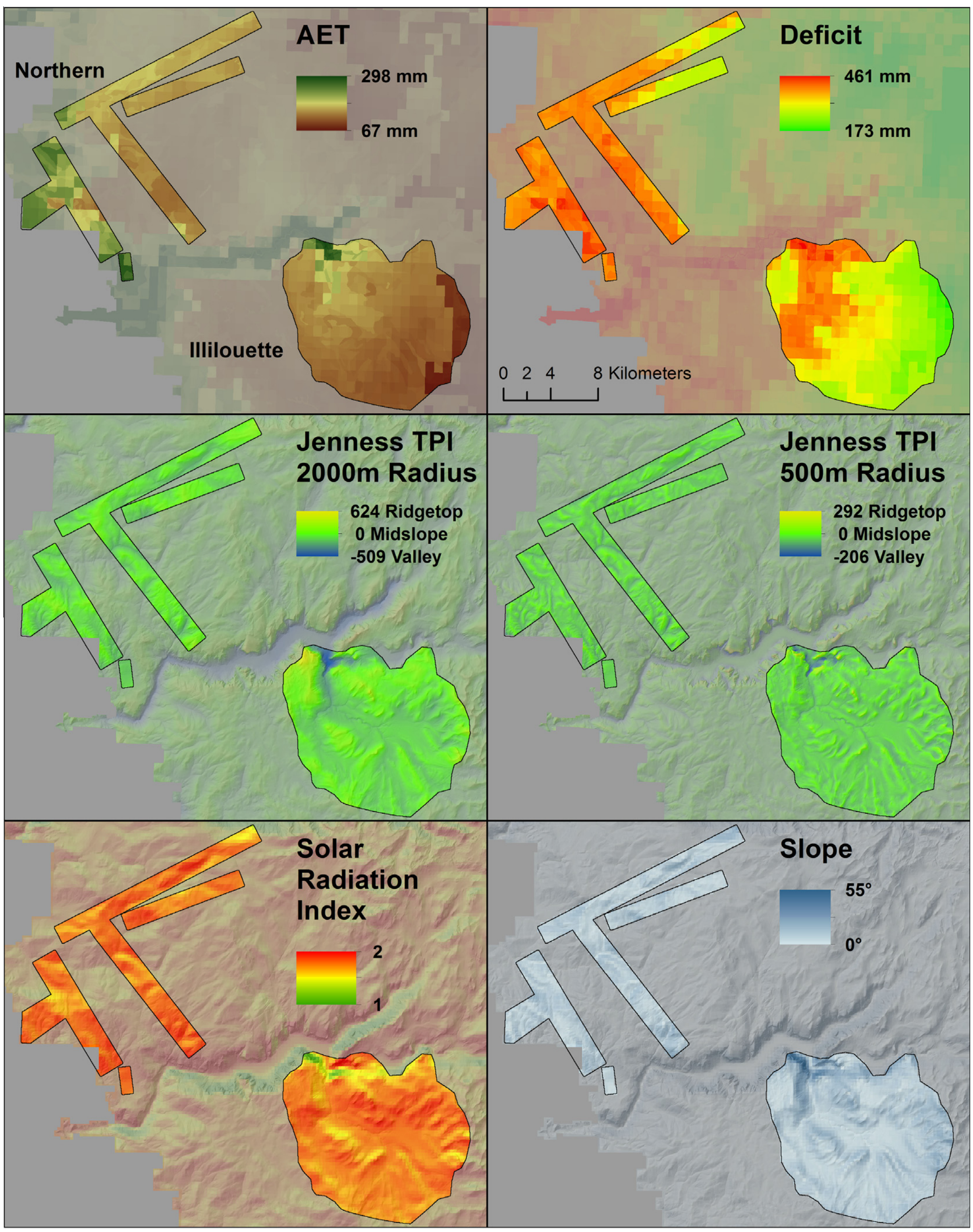

Fig. 4. Variations in key environmental conditions across the study areas. The solar radiation index is a relative index with higher values indicating greater solar radiation.

2.4.1. Water balance metrics

The water balance describes the simultaneous availability of energy and water to support plant growth. The theoretical limit to plant photosynthesis is correlated with potential evapotranspiration (PET), which is a function that combines available energy and water. However, photosynthesis is limited by water availability, so the actual evapotranspiration (AET) is less than the PET when not enough water is available to meet evaporative and transpiration demands. The difference between PET and AET is the climatic water deficit (Deficit, *sensu* Stephenson (1998)), which estimates vegetation stress due seasonal lack of water. Deficit is also correlated with fuel moisture and hence fire behavior (Miller and Urban, 2000b). In the Sierra Nevada range, AET and Deficit are strongly correlated to the elevation gradient that strongly influences patterns of precipitation (higher elevations receive more) and temperature (higher elevations are colder) leading to water-limited forests at lower elevations and energy-limited forests at higher elevations (Greenberg et al., 2009).

We calculated the water balance of the study areas in monthly increments. We modeled annual AET and Deficit using monthly climate normal data (1971–2000) for precipitation and temperature from PRISM (Daly et al., 2008) mapped at 30 arc-second (~800 m) resolution. Our models used a Thornthwaite-type (Thornthwaite and Mather, 1955) calculation where PET is based on temperature. We used the Dingman (2002) water balance algorithm that calculates AET and Deficit based on an exponential model of soil water depletion as implemented by Lutz et al. (2010) without their heat load modifier. To determine soil water holding capacity within the top 200 cm, we used maps from the Natural Resources Conservation Service (SSURGO) database (http://soils.usda.gov/survey/geography/ssurgo/) that had a resolution of 0.4 ha surrounding developed areas to 16 ha in remote areas.

To ensure that our results were not an artifact of a particular water balance model, we also calculated all results using AET and Deficit calculated with a second model. The Flint and Flint model (Flint and Flint, 2007; Flint et al., 2013, http://climate.calcommons.org/dataset/10) calculates PET based on the Priestley–Taylor method (Priestley and Taylor, 1972), itself a simplification of the Penman–Monteith model (Monteith, 1965) based on solar radiance. Because results using the Flint and Flint model were nearly identical to, but usually slightly poorer, than those using the Thornthwaite-Dingman model, we report results only from the latter.

2.4.2. Slope position metrics

We calculated larger-scale topographic patterns from a 10 m resolution US Geological Survey digital elevation model (DEM) based on the topographic slope position index (TPI) algorithm developed by Weiss (2001) and implemented by Jenness (2006) using ArcMap 10.1 (ESRI, Redlands, CA, USA) for neighborhoods of 100 m, 250 m, 500 m, 1000 m, and 2000 m. More negative TPI values indicate a position towards a valley or canyon bottom, values near zero indicate flat areas or mid-slope, and more positive values indicate a hill or ridge top. We also tested an index that relates topography and slope position to cold air pooling (Lundquist et al., 2008).

2.4.3. Local topography metrics

We calculated three aspects of local topography, slope, aspect, and a solar radiation index (SRI), from the LiDAR-derived 1 m digital terrain model using the Fusion software (McGaughey, 2014) at scales of 30 m, 90 m, and 270 m. The SRI models solar radiation during the hour surrounding noon on the equinox (Keating et al., 2007):

$$\mathrm{SRI} = 1 + \cos(\mathrm{latitude}) * \cos(\mathrm{slope}) + \sin(\mathrm{latitude}) * \sin(\mathrm{slope}) * \cos(\mathrm{aspect}) \quad (1)$$

where latitude and slope are in degrees and aspect is relative to south. We also calculated the Heat Load Index of McCune and Keon (2002) at a scale of 30 m as an alternative measure of solar radiation.

2.5. Random forest modeling for fire behavior and forest structure

We used the random forest supervised learning algorithm (Breiman, 2001) to (1) determine how well water balance and topography predict variation in fire and forest structure, (2) to analyze which environmental characteristics were most influential in those predictions, and (3) to develop maps of predicted number of fires, burn severity, and canopy cover >2 m across our study landscape.

Random forest modeling (Breiman, 2001; Cutler et al., 2007) is an extension of non-parametric classification and regression trees (CART) (Breiman et al., 1984). A CART model recursively partitions observations into statistically more homogeneous groups based on binary rule splits on the predictor variables, which can be categorical or continuous. CART models deal effectively with non-linear relationships between predictor and response variables and impose no assumptions on the distribution of the response or predictor variables.

Random forest models develop "forests" of CART trees. For each CART model, a random portion of the data is selected to train the model (bagging) and the remaining data are used for model validation (i.e., out-of-bag or generalization error), and a random subset of predictors are selected at each node split to ensure that the effects of all predictors are tested.

We report the variance explained for each model. This metric is similar to the coefficient of determination (R^2) for linear regressions and reports how well a statistical model fits a given dataset. Random forest variance explained can be calculated using either the internal out-of-bag error rate, or by predicting to a separate independent validation sample. We report the variance explained based on the latter method using a second random sample of equal size to the training sample.

We also report the normalized importance of each predictor to the variance explained by models. To measure predictor importance, the random forest algorithm randomly permutates out-of-bag values for a single predictor, and these data are then used for prediction across all trees within the random forest model. The resulting change in mean square error (regression of continuous values) or decrease in GINI index (classification of categorical data) from the original out-of-bag data is recorded and used as the variable importance measure. This process is repeated for each predictor.

We ran two sets of random forest models. In the first set, we used different subsets of predictors to explore the relative importance of water balance, slope position, and local topography to variation in fire and forest structure over the entire study area. In the second set, we used the importance of predictors reported by random forest models from the first set of modeling to identify a parsimonious set of predictors that would enable simpler interpretation of the relationship between predictors and responses.

For areas that had burned once since 1984, we used burn severity (RdNBR) values both as a response variable and as a predictor. When used as a response, we used the water balance and topographic predictors to model RdNBR for locations that burned just once between 1984 and 2010. We did not analyze the predictability of burn severity for second and third fires because the severity of the earlier fires and time since fire would influence the severity of a subsequent fire (Collins et al., 2008; van Wagtendonk et al., 2012) and exploring these relationships was beyond the scope of this study. When used as a predictor, we used RdNBR, years since

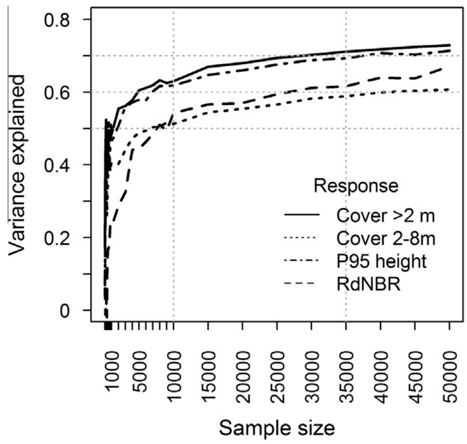

Fig. 5. Variance explained for burn severity and forest structure as a function of the size of the random sample used for the training data. The flattening of the curves beyond approximately 35,000 samples indicates an upper bound to information in the predictors and indicates that the models were not over fitting the data with increasing sample sizes. Results shown are for areas with no fires for the forest structure metrics and for a single fire for RdNBR with samples randomly selected from across the study area. Results calculated using the parsimonious set of predictors: AET, Deficit, topographic slope position index for 2000 m and 500 m scales, slope at 270 m scale, and solar radiation index at 270 m scale. Table 2 provides more detail on results for sample sizes of 10,000 and 35,000.

fire, and the environmental predictors to model post-fire forest structure for locations that burned just once between 1984 and 2010. We repeated the modeling using the parsimonious predictor set for the entire study area and then by forest type, which are associated with specific ranges of water balance regimes and therefore elevation (Fig. 2) (Stephenson, 1998; Lutz et al., 2010).

We used the randomForest function in the randomForest package (http://cran.r-project.org/web/packages/randomForest/index.html) for the R statistical program (release 2.6.1) (R Development Core Team, 2007) to develop and analyze our models. We used the AsciiGridPredict function in the R yaImpute package (Crookston and Finley, 2008, http://cran.r-project.org/web/packages/yaImpute) to apply random forest models to map modeled response values.

3. Results

Preliminary modeling showed that sample size affected the variation in fire patterns and forest structure explained by models (Fig. 5). We report detailed results for models using 35,000 samples (34–50% of area) and for 10,000 samples (10–15% of area) drawn from across all forest types. We report results for models using a substantial portion of the study area because we are seeking to explain variation rather than build predictions, but samples larger than 35,000 explained little addition variation. Modeling with smaller samples such as 10,000 revealed similar relationships between environmental conditions and fire and forest structure as larger samples but explained somewhat less variance.

We found that random forests models that used a parsimonious set of predictors performed better than models that used all environmental variables (Table 4). The parsimonious set had six predictors: AET, Deficit, slope position at 2000 m and 500 m scales, slope at 270 m scale, and solar radiation at 270 m scale. We selected this set by examining which predictors within the three types of environmental predictors (water balance, slope position, and local topography) were most commonly ranked as highly influential across random forest models.

3.1. Variance explained by environmental conditions for fire and forest structure responses

Models using 35,000 random samples explained 0.44–0.72 (mean 0.59) of the variance for canopy cover >2 m, 95th percentile of LiDAR return height, and estimated burn severity (RdNBR) using the parsimonious predictor set (Table 2, Fig. 6). We found that results were similar for models run using samples from each forest type separately compared the global model once the effects of the smaller sample sizes available for some forest types were taken into account (Supplement Table 2).

The model explaining the number of fires at each location had an error rate of 7% for areas that did not burn, 11% for areas that burned once, 15% for areas that burned twice, and 29% for areas that burned three times (Table 3). Less than 1% of the study area burned more than three times, and the sample size was too small for accurate classification (error rates >55%).

3.2. Predictability of forest structure following fire

Models predicting forest structure explained less variance in areas that had burned than in areas that had not burned. In areas that had burned once, the variance explained was 7.8–21.9% lower than in areas that had no fire with 95th percentile of return height and canopy cover >2 m being more predictable and canopy cover 2–8 m being less predictable. For areas that burned two or more times, the variance explained declined again by similar percentages. However, when estimated burn severity (RdNBR) and time since fire were added to the parsimonious set of environmental predictors, variance explained following fire was similar to unburned areas for canopy cover >2 m and 2–8 m. Including these two fire-related predictors improved variance explained for 95th percentile height of returns by a smaller amount.

Table 2
Variance explained by random forest models predicting estimated burn severity (RdNBR) and forest structure for the entire study area using the parsimonious set of six environmental predictors (Table 1). For areas that burned once we also modeled forest structure using the environmental predictors and estimated burn severity (RdNBR) and years since fire. Results shown for models using both 35,000 and 10,000 random samples used as training data selected from across the study areas. Variance explained calculated using a second random sample of equal size to the training sample. Supplement Table 2 shows comparable results for each major forest type within the study area.

Fire *N*	Sample *N* 30 × 30 grid cells (% area)	Variance explained			
		RdNBR as response	Cover > 2 m	Cover 2–8 m	95th percentile height
			RdNBR[a] not used/RdNBR used as predictor		
0	35,000 (34%)	–	0.72	0.59	0.70
1	35,000 (35%)	0.64	0.64/0.70	0.54/0.56	0.54/0.57
2+	33,758 (50%)	–	0.59	0.43	0.53
0	10,000 (9.7%)	–	0.65	0.52	0.62
1	10,000 (10%)	0.55	0.56/0.67	0.47/0.50	0.45/0.51
2+	10,000 (14.8%)	–	0.49	0.35	0.45

[a] When RdNBR used as a predictor, years since fire also used as a predictor.

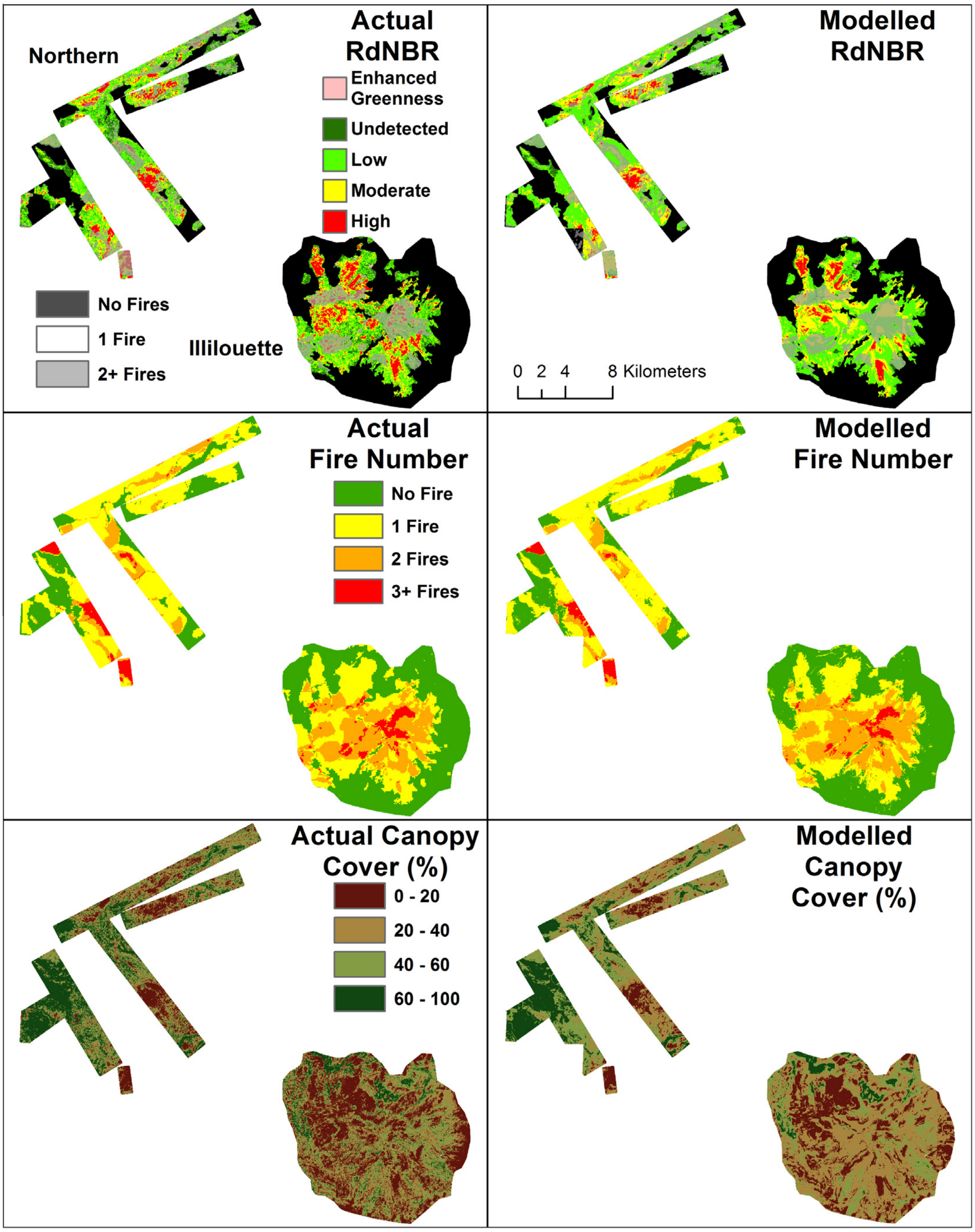

Fig. 6. Actual versus modeled fire number and burn severity (RdNBR) for study area based on random forest models using 35,000 random samples from all forest types and the parsimonious environmental predictor set. For burn severity, areas that experienced a single fire from 1984 to 2010 are shown in bright colors, areas that experienced two or more fires are shown in muted colors, and areas that experienced no fires are masked out. We modeled continuous values for burn severity and canopy cover >2 m, but show classified values here for interpretability. RdNBR burn severity class breakpoints used were from Miller and Thode (2007): Enhanced greenness, ≤150; no change detected, −150 to 68; low severity, 69–315; moderate severity, 316–640; high severity, ≥641. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.3. Importance of predictors

Models that included predictors from all types of environmental factors – water balance, slope position, and topography (Table 4, the Parsimonious and All models) – explained the greatest variance. When only predictors from a single environmental type were used, models that used only the water balance predictors explained 78–89% of the variance explained by the parsimonious predictor set, slope position 6–20%, and local topography 3–9%. When fire and time since fire were used as the only predictors for areas that burned once, they explained 61–90% of the variance of the parsimonious environmental predictor set.

When the parsimonious set of environmental predictors were used, the water balance predictors explained 46–54% of the variance, slope position 26–32%, and local topography (16–24%). When fire predictors were added to the parsimonious set of environmental predictors to model forest structure for single fires, estimated burn severity (RdNBR) and years since fire explained 28–41% of

Table 3
Results of random forest classification for the number of fires at each location based on random training sample of 35,000 grid cells of all forest types. Results shown are from testing the models with a second validation set of 35,000 randomly selected grid cells. Correct predictions are underlined. The lower prediction accuracies for three to five fires may result either from the small sample size or because they are inherently less predictable.

	Actual fire number						Error rate
	0	1	2	3	4	5	
Predicted							
0	11,636	783	63	1	1	0	0.07
1	787	12,385	688	13	0	0	0.11
2	85	855	5989	112	2	0	0.15
3	6	75	321	1050	20	0	0.29
4	2	6	22	36	54	0	0.55
5	0	0	0	3	4	1	0.88
						Overall	0.11
% of area	35.8%	40.3%	20.2%	3.4%	0.1%	0.0%	

the variance; the remaining proportion of variance was divided across the environmental predictors in similar proportions as they were without the fire predictors.

4. Discussion

We found a strong relationship between environmental conditions and fire and forest structure across our study areas. As we had hypothesized, the environmental mosaic predicted substantial portions of the variations in fire and forest structure. Contrary to our second hypothesis, environmental conditions continued to predict a substantial portion of forest structure following one *and* two fires. However, the results supported our third hypothesis: Differences in the water balance (as reflected in AET and Deficit) were the most influential predictors of variations in fire and forest structure.

While ecologists have recognized relationships between site productivity and factors such as forest structure and fire regime (e.g., Parker, 1982, 1989; Thode et al., 2011), our results quantify the strength of those relationships. They also are consistent with conceptual models (Greenberg et al., 2009; Miller and Urban, 1999a, 2000b; Lydersen and North, 2012) that have proposed that site productivity, associated with AET, influences potential forest biomass (i.e., 95th percentile return heights and canopy cover >2 m). Productivity also influences understory conditions such as surface fuel loads (van Wagtendonk and Moore, 2010) and the presence of ladder fuels (canopy cover 2–8 m). The degree to which a site has seasonal drought (climatic water deficit) affects burn potential (Miller and Urban, 1999b) and the local fire regime (fire number and severity), influencing post fire forest structures that in turn influences future fires (van Wagtendonk, 2006; Collins et al., 2010; Larson and Churchill, 2012; Kane et al., 2013, 2014). Our modeling with the random forest algorithm allowed us to build on previous work to explore the effects of a wider range of predictors than previous studies and quantify their relative importance across an actual landscape.

4.1. Fire and environmental conditions

Our study area had a primarily low- and mixed-severity fire regime with 68 fires between 1984 and 2010 (Fig. 6) with a range of fire regimes related to the elevation gradient (Thode et al., 2011). We found a strong relationship between fire and the envi-

Table 4
Predictive power of different sets of predictors (upper panels) and individual predictors in the parsimonious set (lower panels) to explaining variations in fire and forest structure. For sets of predictors, total variance explained by all predictors within the set for a model is shown; for individual predictors within the parsimonious set, normalized importance of each predictor to achieving the variance explained for a model is shown.

	Responses										
	No fire			One fire – environmental predictors only				One fire – environmental and fire predictors			Fire number
	95th percentile height	Canopy cover > 2 m	Canopy cover 2–8 m	95th percentile height	Canopy cover > 2 m	Canopy cover 2–8 m	Burn severity (RdNBR)	95th percentile height	Canopy cover > 2 m	Canopy cover 2–8 m	
Sets of predictors											
Variance explained											
Parsimonious	0.63	0.64	0.51	0.46	0.56	0.47	0.50				
All	0.60	0.63	0.50	0.43	0.51	0.44	0.44				
Water balance	0.54	0.57	0.44	0.38	0.51	0.41	0.39				
Fire				0.28	0.51	0.32	–				
Slope position	0.20	0.19	0.13	0.10	0.07	0.06	0.08				
Local topography	0.07	0.09	0.07	0.06	0.03	0.03	0.04				
Parsimonious predictors											
Predictor importance											
AET	0.31	0.28	0.28	0.25	0.24	0.21	0.24	0.18	0.15	0.16	0.24
Deficit	0.23	0.25	0.24	0.21	0.31	0.29	0.26	0.15	0.20	0.23	0.27
Slope position 2000 m	0.12	0.12	0.14	0.17	0.15	0.14	0.16	0.11	0.07	0.10	0.15
Slope position 500 m	0.17	0.17	0.14	0.15	0.11	0.11	0.10	0.12	0.07	0.08	0.11
Slope 270 m	0.09	0.10	0.12	0.12	0.11	0.12	0.14	0.06	0.05	0.07	0.11
Solar radiation index 270 m	0.07	0.07	0.09	0.11	0.09	0.12	0.10	0.07	0.05	0.07	0.11
Burn severity (RdNBR)								0.11	0.26	0.11	
Years since fire								0.20	0.15	0.17	

Predictor sets: Parsimonious: AET and Deficit; slope position (2000 m and 500 m); slope and solar radiation index (270 m).
All: AET and Deficit; Slope position (2000 m, 1000 m, 500 m, 250 m, 100 m); slope, aspect, and solar radiation index (30 m, 90 m, 270 m); January and July temperature; precipitation; heal load index (30 m); cool air pooling.
Water balance: AET and Deficit.
Fire: RdNBR and years since fire.
Slope position: slope position (2000 m, 1000 m, 500 m, 250 m, 100 m).
Local topography: Slope, aspect, and solar radiation index (30 m, 90 m, 270 m).

ronmental conditions with environmental conditions explaining half to two-thirds of the variation in burn severity (Table 2, Fig. 6) and most of the variation in where fire did not burn or burned once or twice (Table 3).

Miller and Urban (1999a) related environmental conditions to fire in the Sierra Nevada range through several mechanisms. AET influenced forest biomass and hence the rate of live and dead fuel accumulation (Miller and Urban, 1999a; van Wagtendonk and Moore, 2010). Once sufficient fuels accumulated, the likelihood of a location burning was related to whether or not Deficit was high enough to reduce fuel moisture below thresholds where fire spread can occur. The patterns of fuels and fuel moisture determined the pattern of spread (Miller and Urban, 1999a, 2000b). Similarly, Holden and Jolly (2011) found that the fire danger rating within mountain forests varied with the fine-scale patterns in fuel moisture related to surface air temperature, humidity and snow ablation dates driven by topographic variation. Miller and Urban (1999a) also found that patterns of moisture affected patterns of fire intensity through its influence on tree species distribution (Lutz et al., 2010). Species such as ponderosa pine produce needle litter that burns with greater intensity than species such as red fir (van Wagtendonk and Moore, 2010).

Using environmental data and random forest model methods and similar to ours, Holden et al. (2009) examined a 20 year fire record across a New Mexico, USA, wilderness. They found that fire patterns were correlated with topographically induced moisture patterns influencing both fuel accumulation and fuel moisture. Their results and ours may reflect relationships between the environmental mosaic and fire that resemble those of the historic fire regime before decades of fire suppression. However, the link between these environmental conditions and fire severity, and thus forest structure, may not be as strong in landscapes where fire suppression is still the norm. Fires that escape containment typically do so under extreme climate and weather conditions and those conditions have been linked to weakening of the influence of local elevation gradients and topography (Turner and Romme, 1994; Dillon et al., 2011; Cansler and McKenzie, 2014).

4.2. Forest structure and environmental conditions

The strongest relationships between the environmental conditions and forest structure were correlated with biomass: the area covered by trees (canopy cover >2 m) and the height of dominant trees (95th percentile height) (Lutz et al., 2012) (Table 2). This is consistent with studies that found that stand biomass increases with greater moisture availability (Miller and Urban, 1999a, 2000b; Lydersen and North, 2012). For unburned areas, the models likely reflected variations in productivity because fire had not removed biomass for decades.

Environmental conditions were less directly associated with understory conditions. The 2–8 m stratum represents tall shrubs, saplings, and lower foliage of taller trees. Foliage in this stratum is common in unburned forests following decades of fire suppression (e.g., Lutz et al. 2014), but fire removes most cover in this stratum followed by regrowth (Kane et al., 2013, 2014). In the absence of fire, we found that the environmental conditions typically explained about half of the cover in the 2–8 m stratum for unburned areas. However, following fire, predictability fell more than it did for canopy cover >2 m or 95th percentile return height. This lower predictability could reflect the effects of fire intensity (which is less predictable from environmental measures alone than burn severity (Lydersen and North, 2012)), variations in time since fire, and the effects of year-to-year climate variations on the success of re-establishment.

4.3. Multiple fires and environment conditions

We found that the environmental conditions still explained most of the variation in forest structure following one or more fires. Conversely, we found that adding the estimated burn severity (RdNBR) and years since fire to the environmental predictors only modestly improved our ability to model post-fire forest structure compared to using environmental predictors alone. This suggests a feedback loop where the environmentally-influenced patterns of forest structure and fuel moisture and accumulation influences fire patterns that in turn influence the post-fire forest structure. We cannot uniquely ascribe forest structure following fire to the environment or to the actual burn severity because they are related through a feedback mechanism.

Historically, forests in much of the western United States had frequent low- and mixed-severity fires. Frequent fire substantially alters the relationship between environmentally driven patterns of productivity and forest structure (Peterson, 2002; Lydersen and North, 2012; Hagmann et al., 2013, 2014). These fires created forest structures distinct from current structures that developed under decades of fire suppression (Hessburg and Agee, 2003; Romme et al., 2009; Naficy et al., 2010).

However, our results show a continued relationship between environmental conditions and post-fire forest structure following one and two fires even though the post-fire structures were considerably different than pre-fire structures (Kane et al., 2013, 2014). This observation is consistent with the findings of Kane et al. (2013, 2014) who studied our Northern study area. Their results showed two mechanisms for tying moisture gradients to post-fire structure. First, low- and moderate-severity fires in Yosemite burn in a fine-scale mosaic (van Wagtendonk and Lutz, 2007; Lutz et al., 2009; Kane et al., 2013), removing all trees in some tree clumps but leaving all or most trees in adjacent clumps (Kolden et al., 2012; Kane et al., 2014). The surviving tree clumps retained much of their pre-fire overstory structure (Kane et al., 2014), which developed in the context of their local environments. The second mechanism was that the percentages of canopy cover >2 m, and hence the area in tree clumps, that remained following fire was related to forest type, which was related to elevation (Fig. 2) and hence the dominant moisture gradient (Stephenson, 1998; Lutz et al., 2010).

4.4. Relative importance of environmental predictors

We found that the measures of water balance, AET and Deficit, were the most influential environmental predictors followed by topographic slope position and then by measures of local topography (Table 4). We generally found that AET was a stronger predictor than Deficit for forest structure before fire, while Deficit was a stronger predictor for structure following a fire as well as for burn severity and fire number. In other work, Stephenson (1998) and Lutz et al. (2010) found that Deficit best explained the distribution of tree species in the Sierra Nevada, and different species produce fuels with different burn characteristics and have different resiliencies to fire (van Wagtendonk and Fites-Kaufmann, 2006). (We found only modest reductions in model performance when we experimentally replaced AET and Deficit with combinations of elevation, temperature, and precipitation as predictors; where good climate data are not available, using these substitutes for AET and Deficit may produce good results (e.g. Holden et al., 2009).)

Topographic slope position also was an important predictor for variations in fire and forest structure. Location on a ridge, mid-slope, or in a valley bottom has been related to fire intensity and frequency (Beaty and Taylor, 2001; Taylor and Skinner, 2003), soil depth (Urban et al., 2000; Meyer et al., 2007), and sub-surface water flow (Scholl and Taylor, 2010; Underwood et al., 2010). Lydersen and North (2012) found that slope position explained a large portion of the variation in burn severity and forest structure for locations that had at least two fires in Yosemite and the nearby Sequoia National Park.

In our study areas, local topography modified the broader-scale environment set by the water balance and slope position but did not explain large portions of variance in fire and forest structure on their own. We were surprised by the relatively small proportion of variance explained by the local-scale topographic predictors given the importance of solar radiation and its correlate, heat load, in the explanation of tree density and slope to fire frequency and behavior (North et al., 2009). Steeper slopes have higher rates of fire spread and more rapid drainage of soil moisture. Indexes of solar radiation and heat load that integrate solar azimuth, slope, and aspect to estimate solar heating and therefore drying across a landscape are used to explain local variations in forest structure (McCune and Keon, 2002; Keating et al., 2007) but had only a minor influence in our study areas.

4.5. Management implications

Our study was guided by a substantial body of work (e.g., Miller and Urban, 1999b; Collins et al., 2006; Dillon et al., 2011; Cansler and McKenzie, 2014) that has explored aspects of the relationships between the mosaic of environmental conditions and fire and forest structure. In the Sierra Nevada, this knowledge has been assembled into a set of guidelines and tools that use slope position and local topography to classify environmental conditions and guide restoration activities (North et al., 2009; Underwood et al., 2010; North and Sherlock, 2012).

Our results suggest that incorporating AET and Deficit into the way that environmental conditions are classified in management guidelines would improve their ability to guide restoration toward desired fire behavior and forest structure. Landscapes could be evaluated to see where existing forest structures are significantly different than those expected for their environmental conditions to identify priority areas for treatments. Landscapes could also be evaluated in terms of likely burn severities and post-fire forest structures based on environment conditions to evaluate the potential effects for prescribed burns and natural ignitions to better align potential post-burn forest structures with desired conditions (Collins et al., 2011; Kane et al., 2014). We note, however, that our methods cannot be used to predict the behavior of any individual fire because they do not include actual fuel and weather conditions. Rather they may aid in predicting likely patterns of fire severity under moderate fire weather conditions.

Another management application of water balance metrics would be the selection of reference areas. The contrast between our two study areas illustrates this. Because the Illilouette study area was never harvested and has had a near-natural fire regime since the 1970s (Collins et al., 2006; van Wagtendonk et al., 2012), it has been used as a reference condition for forest restoration in the Sierra Nevada range. However, the LiDAR data shows that the higher elevation Illilouette forests are substantially more open and shorter than their Northern study area counterparts for the same forest type (Figs. 2 and 3). Biomass in the Illilouette forests likely is limited compared to the Northern study area because lower temperatures reduce the growing season through lower PET and therefore lower AET. When possible, managers should seek reference areas that match the AET and Deficit patterns in the forests they manage. Once an area with similar AET and Deficit are found, managers can then match combinations of slope position and local topography to specific project areas. Climate analog reference areas can also be selected using downscaled future projections of AET and Deficit as part of climate adaptation strategies (Churchill et al., 2013; Dobrowski et al., 2013).

At the start of our study, we were uncertain whether the imprint of the environmental mosaic would be clear in a real landscape using data sources available to us. Fire behavior is strongly influenced by weather conditions throughout the burn season and during the fire event, data that we did not include in our modeling. Also, our climate data were at a relatively coarse scale (800 m) while actual climate within mountainous terrains is strongly influenced by finer scale patterns of slope position and solar radiation (Dobrowski et al., 2009; Greenberg et al., 2009; Holden and Jolly, 2011). Our results in the face of less than perfect predictors suggest that the environmental influence can be strong in mountainous regions and that our approach may be useful to ecologists and managers in other mountainous regions around the world.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.10.038.

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